

# 1 The Fish Fauna of Tubbataha Reefs is highly Biodiverse 2 and distinctively Oceanic

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## 13 **Abstract**

14 We surveyed the fish fauna of Tubbataha Reefs, a remote and well-protected coral reef  
15 system in the Philippines. Tubbataha is located in the Coral Triangle, the region with the  
16 highest marine biodiversity in the world, and is a no-take marine protected area. We found  
17 a total of 534 species, with the Labridae (65 species), Pomacentridae (60 species), Gobiidae  
18 (60 species), Chaetodonidae (33 species), Serranidae (33) and Acanthuridae (32 species)  
19 being the most species-rich families present. Species accumulation curves predicted that  
20 fish richness across all surveyed stations will asymptotically reach 603 species. Shannon  
21 and Simpson diversity indices were calculated to be 329 and 260, respectively, and are  
22 predicted to asymptotically reach 343 and 266. Within Tubbataha, the North and South  
23 Atolls show similar ichthyofauna, with the Jessie Beazley Reef (a shoal) slightly differing. The  
24 ichthyofauna of the lagoons of both the North and the South Atoll are distinct from the outer  
25 reefs and cluster together, with distinct, and fewer species. Our study provides a baseline

26 for the fish fauna of a coral reef ecosystem in the Coral Triangle affected by a few local  
27 anthropogenic stressors.

## 28 **Introduction**

29 Coral reefs are the most biodiverse marine habitats on the planet, with exceptionally high  
30 numbers of species of corals, other invertebrates, and fishes (Carpenter et al., 2011).  
31 Among coral reefs, those in the Coral Triangle between eastern Indonesia, Papua New  
32 Guinea, and the Philippines (precise geographic delineations vary; see Veron et al., 2009)  
33 are the most biodiverse (Carpenter & Springer, 2005).

34 Besides their importance for marine biodiversity, coral reefs also provide ecosystem  
35 services to several hundred million humans, such as fishing grounds and coastal protection.  
36 Anthropogenic stressors have, however, led to a decline in ecosystem health in many coral  
37 reefs worldwide. Problems include warming seawater and the resultant coral bleaching  
38 (Hughes et al., 2017), ocean acidification (Guinotte & Fabry, 2008), eutrophication as a  
39 result of coastal agriculture, as well as pollution with the discarded plastic products of  
40 industrial societies (Gomez et al., 2023).

41 Tubbataha Reefs Natural Park is an isolated and well-protected coral reef system in the Sulu  
42 Sea of the Philippines. Tubbataha is a well-enforced, no-take marine protected area (MPA),  
43 and besides a small number of marine park rangers living in a single structure on one of the  
44 atolls, it is devoid of human habitation. There is no coastal pollution or agriculture on  
45 Tubbataha, and any marine plastic found is likely to be of non-local origin. The Tubbataha  
46 coral reef system hence provides the opportunity to investigate a comparably pristine coral  
47 reef in the Coral Triangle, only affected by global (ocean warming, ocean acidification) but  
48 not by local anthropogenic stressors.

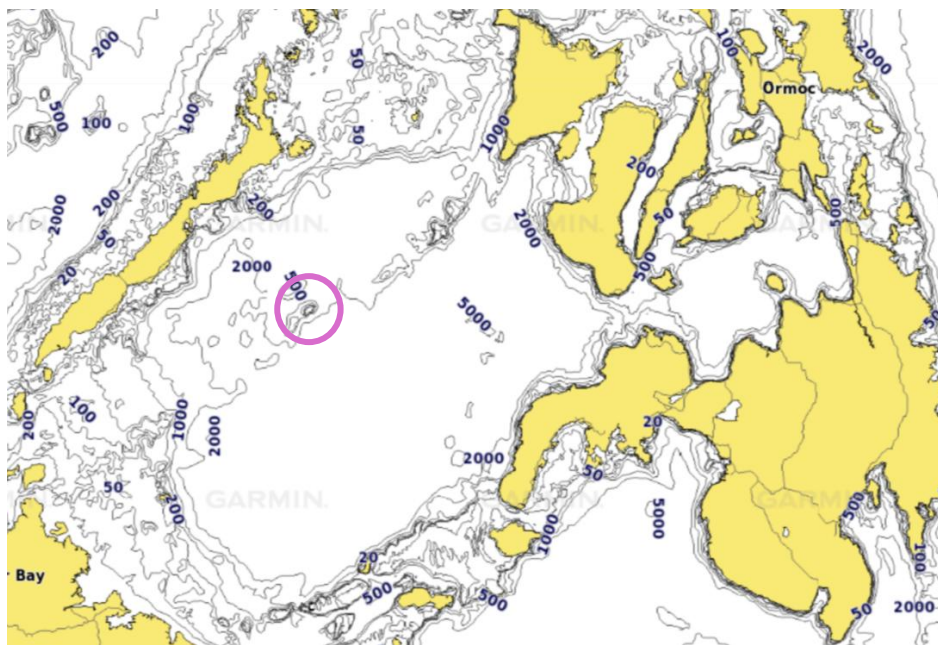
49 We surveyed the coral reef fish fauna of Tubbataha for five years between 2018 and 2025,  
50 with no surveys from 2020 to 2022 due to the COVID-19 pandemic). We aimed to 1.) Provide  
51 a characterization of the ichthyofauna of Tubbataha as part of ongoing monitoring efforts 2.)  
52 Provide a baseline with the Tubbataha ichthyofauna, for future comparisons with less-well  
53 protected reefs, subjected to local stressors.

54 **Methods**

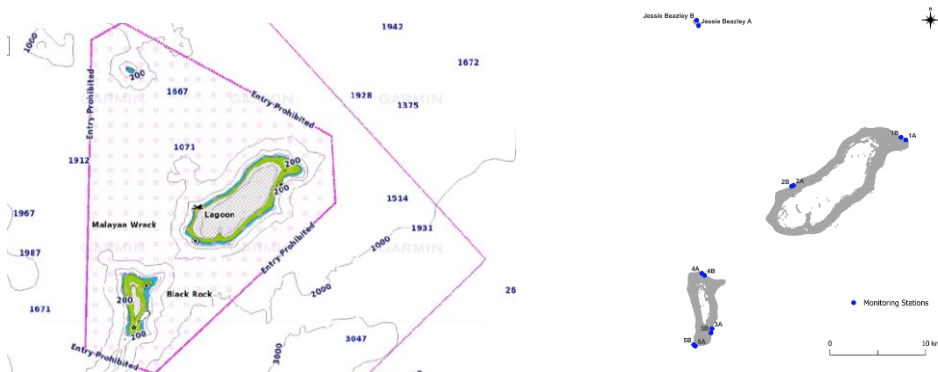
55 *Location*

56 The Tubbataha Reefs Natural Park is located at 8°51'23.74"N, 119°57'26.50"E, in the Sulu  
57 Sea of the Philippines. The larger islands surrounding the Sulu Sea are Palawan to the west,  
58 Mindoro to the north, Panay and Negros to the east, Mindanao to the southeast, and Borneo  
59 (Malaysia) to the south (Fig. 1). The closest larger island is Palawan, 155 km distant. The  
60 Tubbataha reefs are administratively a part of the island municipality of Cagayancillo, 160  
61 km to the northeast.

62



63



64 Figure 1: Bathymetric map of the Tubbataha reef system in relation to its surrounding  
65 Philippine islands (top) and bathymetry of the Tubbataha Reef system (bottom, left). Source:  
66 Navionics.com. Benthic cover monitoring stations (bottom, right).

67

68 The Tubbataha Reef System consists of a smaller South Atoll, a larger North Atoll, and the  
69 Jessie Beazley Reef to the northwest. A small area on the North Atoll is permanently above  
70 sea level and populated by eight breeding species of seabirds (Jensen and Songco, 2016).  
71 The atolls are the result of the Sulu Sea plate and the Palawan microcontinent colliding  
72 (Munar et al., 2024).

73 Tubbataha Reefs was declared a national park in 1988 and is a no-take marine protected  
74 area (MPA). The park is regularly monitored by marine park rangers, composed of personnel  
75 from the Philippine Coast Guard, Philippine Navy, Cagayancillo Local Government Unit, and  
76 Tubbataha Management Office. They live on a stilted station on the North Atoll and patrol  
77 the area with the aid of speedboats and a primary radar. Attempts at illegal fishing are rare,  
78 with only eight attempted or actual cases of illegal fishing from 2017 to 2025 (source:  
79 records of the Tubbataha Management Office).

80 Scuba tourism based on liveaboard diving brought an average of 2039 visitors per year to  
81 Tubbataha since 2010, which included 2020 and 2021, when tourism was non-existent due  
82 to pandemic measures. Excluding these years, the average number of visitors to Tubbataha  
83 is 2220 per year, during the April to June fair-weather season. Each tourist diver typically  
84 spends a week of diving at Tubbataha, with 10-20 dives per person. Before their trip  
85 commences, tourist divers are briefed in detail regarding environmentally safe diving  
86 practices by natural park staff. The relatively small number of visitors, plus their education  
87 and supervision during their dives, limits the mechanical damage done by divers.

88 The lagoons of the North and South Atolls are off-limits to tourist divers.

89 *Roving Diver Census*

90 We used the Roving Diver Census (RDC) method (Schmitt et al., 2002; Cartier & Carpenter  
91 2014), modified for use on walls.

92 This method is more comprehensive for measuring the diversity of fishes but is less accurate  
93 for estimating the abundance of species than belt transect methods (Schmitt et al., 2002).  
94 Controlling for depth effects on fish communities using a transect belt or point-count  
95 methods (Bohnsack and Bannerot, 1986) is difficult on uneven topographies, especially  
96 those with variable depth.

97 When surveying the outer reefs of the atolls, we started our fish survey at a depth of 22 to 28  
98 m on the face of the wall and proceeded upwards, towards the reef top at a depth of about  
99 5 m, within 60 minutes. When surveying the lagoons we adjusted our survey method based  
100 on local topography. Where the reef transitioned into a sandy area on a slope, we began the  
101 survey descending to the deepest part of the slope down to a maximum of around 28 m and  
102 we ascended along the inner slope to the shallowest part of the slope surveying for 60  
103 minutes. Alternatively, when we encountered patch reefs, we covered as much coral reef  
104 area in arbitrary directions for 60 minutes.

105 We recorded all species observed, as well as their relative abundance (N; single = 1  
106 individual, few = 2–10, many = 11–100, abundant = over 100) encountered throughout the  
107 60-minute duration of the census. Each survey was conducted by two observers in parallel:  
108 One observer focused on the cryptobenthic reef fishes, the other observer on all remaining  
109 fishes. We noted our data on a list of species pre-recorded on waterproof paper secured to  
110 a plastic slate.

111 We surveyed 16 stations on North Atoll, 14 on the South Atoll and 8 on Jessie Beazley. We  
112 also surveyed 8 stations in the lagoons of the North and South Atolls.

### 113 *Species Diversity Measures*

114 All data analysis was conducted in R.

115 Fish diversity was estimated with the R package iNEXT, with survey stations treated as  
116 sampling units (datatype = "incidence\_raw"; Hsieh, Ma, & Chao, 2016). Since the field

117 abundance categories indicate ordinal encounter classes rather than actual counts,  
118 inferential analyses were conducted using presence–absence data. We calculated the total  
119 number of species, Shannon entropy, and Simpson diversity (corresponding to Hill numbers  
120 0, 1 and 2; Hsieh et al., 2016). Sample-size-based interpolation and extrapolation (into the  
121 future, past the end of sampling) curves were used to assess sampling sufficiency for the  
122 outer reefs overall. We paid particular attention to the species accumulation curve (total  
123 number of species, Hill number = 0), as it is most sensitive to additional sampling effort.  
124 Comparisons among North Atoll, South Atoll, and Jessie Beazley Reef were interpreted  
125 primarily using coverage-based inter- and extrapolation curves, so that groups were  
126 compared at more similar levels of sampling completeness rather than at equal sample  
127 sizes (Hsieh et al., 2016). For multi-assemblage species richness comparisons,  
128 extrapolation was limited to a common endpoint based on the smallest observed group,  
129 following the recommendation to keep richness extrapolation modest relative to the  
130 minimum reference sample size (Hsieh et al., 2016). Standardized point estimates at a  
131 common sample coverage were also extracted (using estimateD() in iNEXT) to support  
132 among-group comparison.

### 133 *Non-Metric Multidimensional Scaling*

134 To assess the similarity between the fauna of the three atolls/reefs (excluding lagoons), we  
135 used non-metric multidimensional scaling (Kruskal, 1964, veganpackage version 2.7-1)  
136 based on a station x species presence-absence matrix and Jaccard dissimilarity.. In this  
137 method, survey stations are represented in a multidimensional space according to their  
138 similarity in species composition, and the first two dimensions are plotted for visualization.  
139 Stations that cluster more closely in the ordination have similar fish assemblages.

### 140 *Trophic Levels and Maximum Lengths*

141 To estimate the trophic structure of the fish fauna, we correlated the known trophic levels  
142 of the species we observed with their estimated biomass. Trophic levels and maximum  
143 lengths were retrieved from FishBase (Froese & Pauly, 2010). We used both the trophic level  
144 values derived from individual food items as well as from diet/stomach contents. These

145 values have been shown to correlate very well with trophic levels derived from stable isotope  
146 measurements in cases where this was investigated (Mancinelli et al., 2013). We calculated  
147 the fish weights from the values for maximum length, and  $a$  and  $b$  retrieved from Fishbase,  
148 according to  $w = aL^b$ .

149 Since the trophic level values were not available for all species we observed, for each  
150 species we used the averaged value from all members of a genus, assuming that the weights  
151 and trophic levels are *comparable* for all snappers of *Lutjanus*, for instance.

152 We estimated the number of individuals from their relative abundance (single = 1 individual,  
153 few = 2–10, many = 11–100, abundant = over 100). This estimate will likely under-estimate  
154 the abundance of highly numerous species; However, it is unlikely that this estimate will  
155 introduce a systematic error in our analysis (that species at certain trophic levels are more  
156 or less subject to under-estimation).

157 We calculated the fish biomass per species by multiplying this estimated number of  
158 individuals with the fish weights derived from Fishbase.

## 159 **Results**

### 160 *Family Richness*

161 In a total of five weeks of survey (2018/19; 2023-25) by two observer pairs (K.E.C. & J.W;  
162 K.E.C. & K.M.S.), we observed 534 species of coral reef fishes in the Tubbataha reef system  
163 (see Fig. 2 for example species images). The most species-rich fish families were the  
164 Labridae (65 species; Fig. 3), Pomacentridae (60), Gobiidae (60), Serranidae (33) and  
165 Chaetodontidae (33). Tubbataha's fish fauna contained charismatic megafauna such as  
166 whale sharks (*Rhincodon typus*) and tiger sharks (*Galeocerdo cuvier*), which are increasingly  
167 rare in many locations in the Coral Triangle.

168



***Plagiotremus rhinorhynchos***



***Gobiodon okinawae***



***Taeniura lymna***

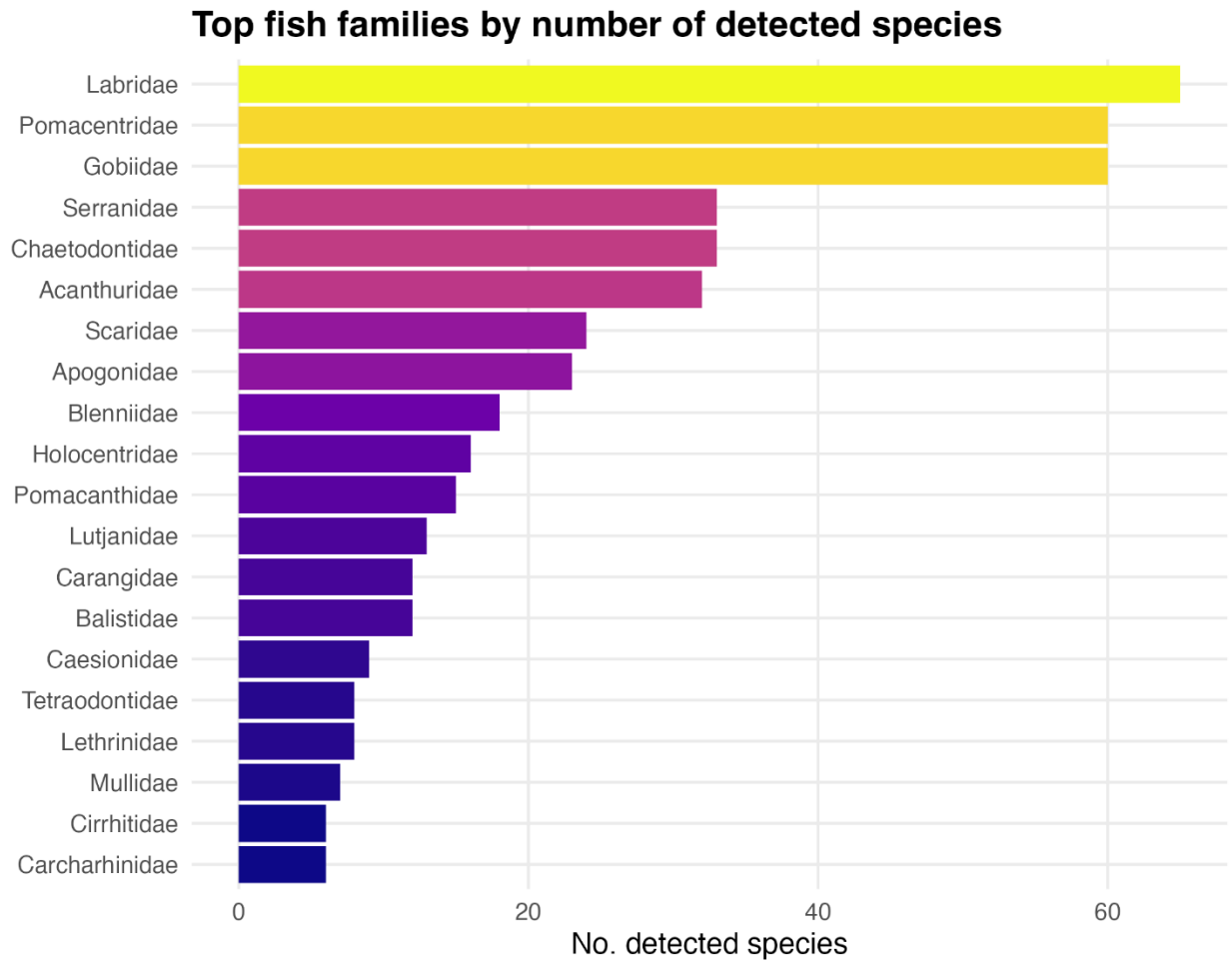


***Cephalopholis polleni***

170

171 Figure 2: The Tubbataha coral reef fish fauna. Photographs taken during the 2023 and 2024  
172 fish census. *Plagiotremus thinorhynchos*, Blennidae, retreated in a cavity formed by  
173 coralline algae. *Gobiodon okinawae*, Gobiidae, an obligatory hard coral commensal,  
174 common in the North Atoll lagoon. *Taeniura lymna*, Dasyatidae, rarely seen, in the lagoons.

175 *Cephalopolis polleni*, Serranidae, seen in the deeper sections on the walls explored during  
 176 our survey (>25 m).



177

178 Figure 3: Species numbers per family observed by two observers over five weeks in  
 179 Tubbataha.

180

181 A notable feature of the Tubbataha fish fauna is the relative sparsity of Syngnathidae (1  
 182 observation of 2 species in 4 years) and Scorpaenidae (13 observations of 3 species in 4  
 183 years). We observed a single individual of a single species of the Callionymidae (Dragonets;  
 184 *Synchiropus bartelsi*), and a single individual of a single species of Solenostomidae (Ghost  
 185 pipefishes; *Solenostomus paradoxus*). These families are generally abundant (especially  
 186 Syngnathidae & Scorpaenidae) at coastal coral reefs in the Coral Triangle, and the oceanic

187 location (with strong currents) of Tubbataha might be responsible for the sparsity of these  
188 typically weakly swimming fishes.

189 Shrimp-associated gobies were also rare, with 10 species and 195 observations during 46  
190 survey dives, a reduced number compared to the typical fauna of many coastal areas in the  
191 Coral Triangle. This is in accord with earlier observations that oceanic sites with strong  
192 currents, steep walls, and few protected sandy areas harbor fewer of these symbiotic pairs  
193 (Stiefel et al., 2014).

#### 194 *Fish Diversity Measures*

195 We calculated the total number of species, and Shannon and Simpson diversity indices for  
196 the outer reefs overall, for North and South Atolls, Jessie Beazley Reef and for the lagoons of  
197 both atolls combined. We calculated both the values corresponding to the present level of  
198 surveying, as well as extrapolations to near-asymptotic values (Tab.1; Fig 4).

199 Table 1: Total number of species, Shannon diversity, and Simpson diversity at the current  
200 level of sampling and their asymptotic estimates for the assemblage.

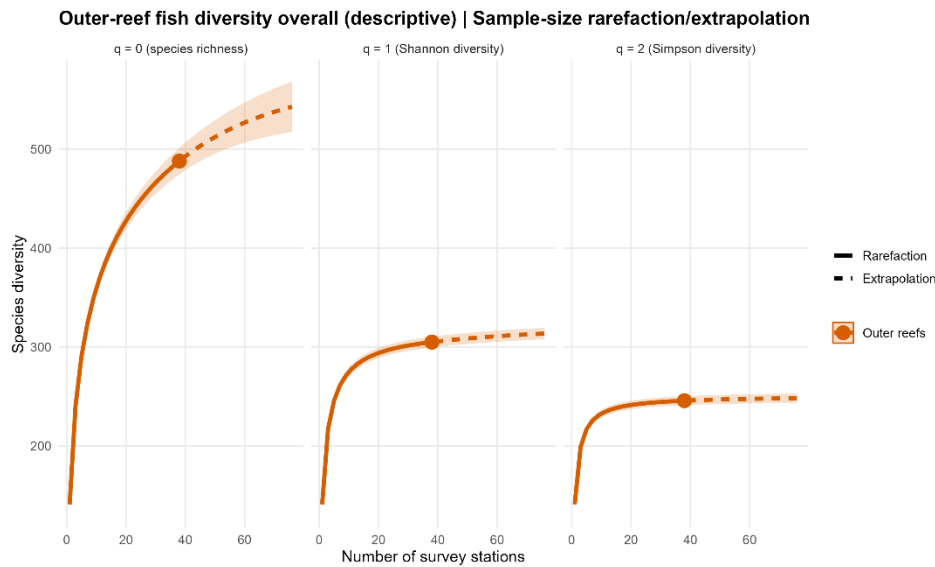
<b>Assemblage</b>	<b>Species richness observed (q=0)</b>	<b>Species richness asymptotic</b>	<b>Shannon observed (q=1)</b>	<b>Shannon asymptotic</b>	<b>Simpson observed (q=2)</b>	<b>Simpson asymptotic</b>
Outer reefs overall	488	568.97	304.95	318.73	245.73	250.77
North Atoll	409	460.57	293.64	318.39	242.6	254.82
South Atoll	380	448.38	280.56	306	237.18	249.68
Jessie Beazley Reef	291	378.45	231.18	263.14	201.35	216.37
Lagoon (combined)	215	317.67	168.55	212.58	141.12	161.62

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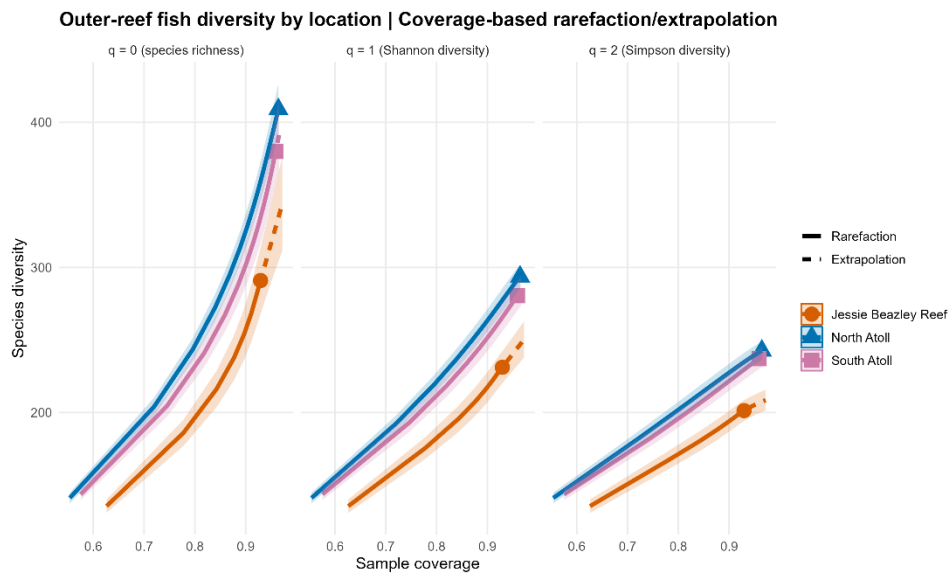
203 Sample-size-based inter- and extrapolation curves for the outer reefs overall showed that  
 204 species richness (Hill number = 0) continued to increase across the observed and  
 205 extrapolated range and did not reach a clear asymptote (Fig. 4A). This indicates that  
 206 additional sampling would likely detect additional taxa. In contrast, the Shannon and  
 207 Simpson diversity (Hill numbers = 1, 2) curves leveled off more readily, indicating that the  
 208 common and dominant components of the assemblage were sampled more completely.

209 **A**



210

211 **B**



212

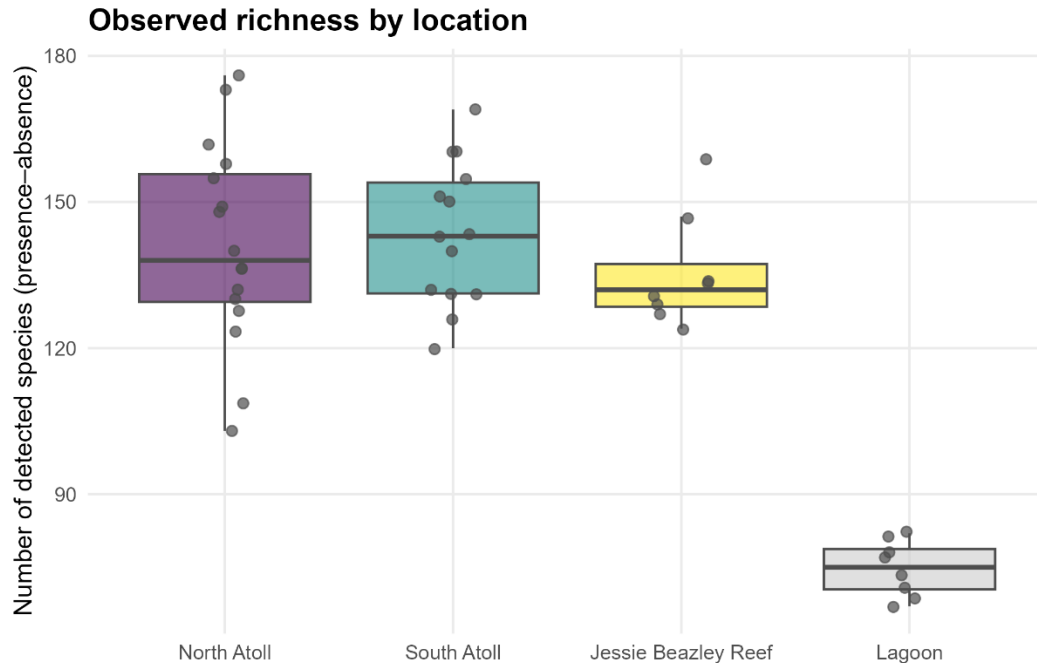
213 *Figure 4. **A:** Sample-size-based interpolation/extrapolation curves for outer-reef fish*  
214 *diversity overall. The continued upward trajectory for the total number of species indicates*  
215 *that additional surveys would likely still detect new taxa, whereas Shannon and Simpson*  
216 *diversity level off more readily.*

217 ***B:** Coverage-based interpolation/extrapolation curves for outer-reef fish diversity by*  
218 *location. After standardizing by sample completeness, North Atoll is highest, South Atoll is*  
219 *slightly lower but similar, and Jessie Beazley Reef remains lower across the shared coverage*  
220 *range.*

221

222 Coverage-based comparisons among outer-reef locations showed the same pattern across  
223 the species richness as well as for Shannon and Simpson diversity: North Atoll had the  
224 highest estimated diversity, South Atoll was slightly lower but similar, and Jessie Beazley  
225 Reef remained lower across the shared coverage range (Fig. 4B). This pattern was  
226 still evident after standardizing by sample completeness. These location contrasts are  
227 descriptive and are not presented as formal tests of significance.

228 The lagoons exhibit lower observed species richness compared to the other three locations,  
229 as seen by their lower median value (75 species). The lower whisker suggests that some  
230 areas within the lagoons have much lower observed richness, potentially due to habitat  
231 differences than those in the outer reefs. The lagoon's lower observed richness possibly  
232 results from its unique habitat structures, water quality, or ecological pressures such as  
233 sedimentation, as water movement is naturally restricted within the lagoon compared to the  
234 outer reefs.



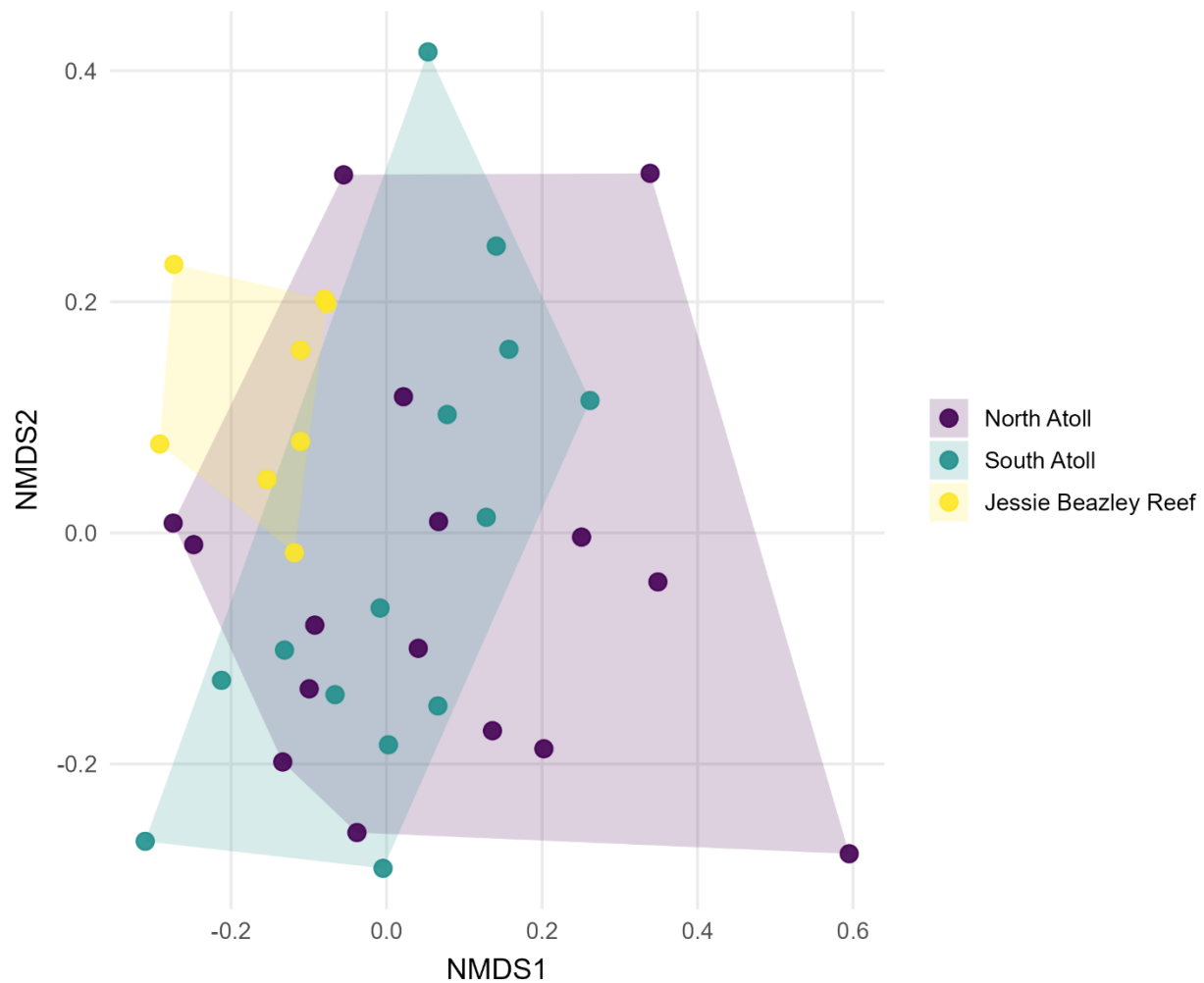
235

236 Figure 5: **Observed species richness by location.** Each dot represents one survey station.  
 237 Boxplots show the distribution of detected species richness (presence-absence) across  
 238 locations.

239 *Faunal Overlap between Atolls/Reefs*

240 Non-metric multidimensional scaling suggested broad overlap in fish species composition  
 241 between the North and South Atoll, while Jessie Beazley Reef showed modest separation in  
 242 ordination space, (Fig. 6). This indicates that the fish assemblage at Jessie Beazley Reef is  
 243 somewhat different from those of the two atolls. This clustering suggests that stations at  
 244 Jessie Beazley Reef may somewhat share similar species compositions, likely due to  
 245 ecological factors or habitat types differences relative to the two atolls. Most importantly,  
 246 Jessie Beazley lacks a lagoon and resultant outflow nutrient rich low-visibility water during  
 247 tidal cycles.

### NMDS (Jaccard, presence–absence) | Stress = 0.257



248

249 Figure 6: Non-metric multi-dimensional scaling ordination of outer-reef fish species  
250 presence-absence data distinguishing fish fauna of each station. Each datapoint represents  
251 one survey site. NMDS was performed using Jaccard dissimilarity and two dimensions ( $k =$   
252 2), with a final stress value of 0.256, indicating a broad visualization of assemblage pattern.

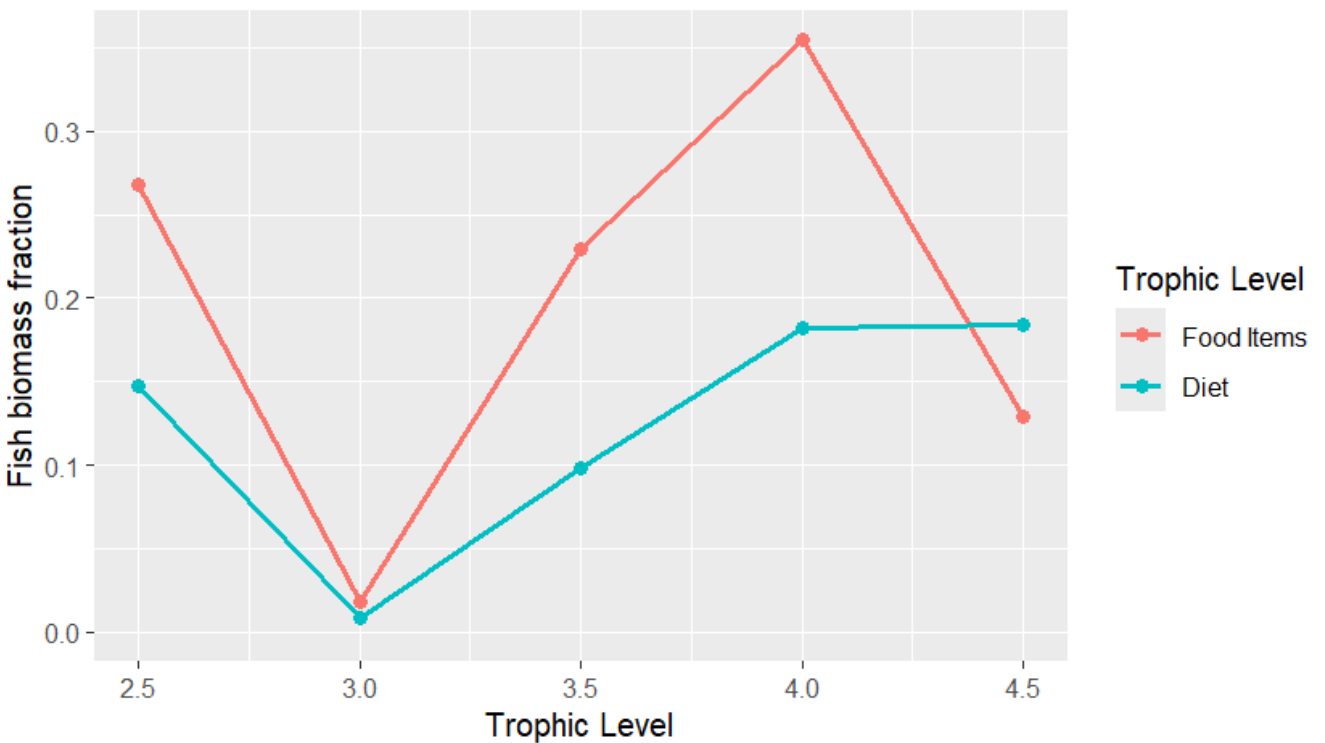
#### 253 *Fish Trophic Levels and Maximum Lengths*

254 We plotted the estimated fraction of the total fish biomass as a function of the trophic levels,  
255 both derived from individual food items as well as from diet/stomach contents. We found  
256 that the fish biomass centers at the bin around a trophic level of 4 (3.75 to 4.25; Fig. 7A), at  
257 a high, but not the highest level. The most abundant fish, the midnight snapper *Macolor*  
258 *macularis* (a very long-lived species living up to 81 years: Taylor et al., 2021) is the species

259 in Tubbataha with the highest estimated biomass, and is in this category, with a trophic level,  
260 (food items) of 3.99. The fish is known to be a predator of benthic invertebrates and larger  
261 zooplankton.

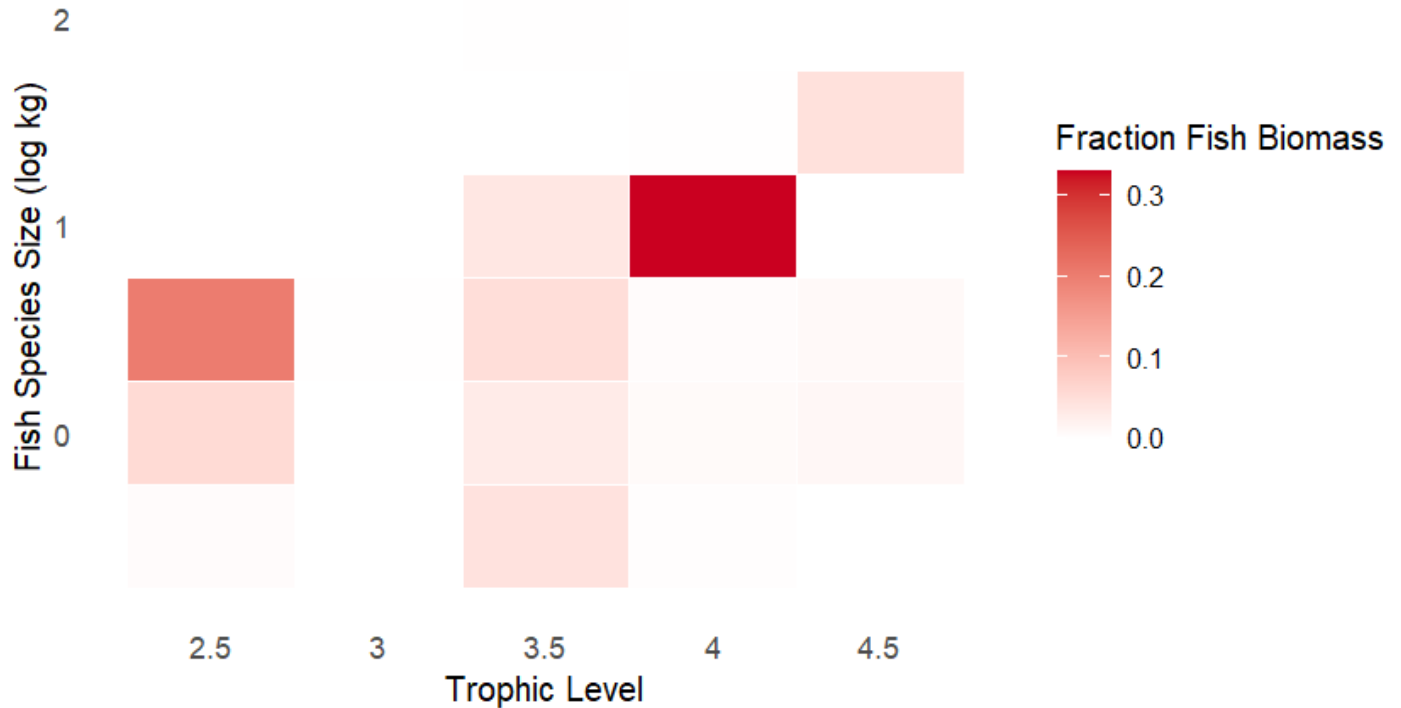
262 The fraction of fish biomass at the highest trophic levels is either somewhat less or near-  
263 identical to the next-to-highest trophic level. This is in contract to the inverted food pyramids  
264 seen in some other pristine coral reef ecosystems (see discussion). This result is supported  
265 by the common but not extremely abundant occurrence of reef sharks. For example  
266 *Carcharhinus amblyrhynchos*, the grey reef shark, was sighted on 19 out of 45 survey dives,  
267 with 18 of these sightings in the single (1) or few (2-10 individuals) categories.

268 To further characterize the trophic web of the fish fauna of Tubbataha, we plotted a 2-  
269 dimensional histogram of the fish biomass as a function of the weight of an individual of the  
270 species, and of the trophic level (Fig. 7B). This histogram peaks at a size of 10 kgs and a  
271 trophic level of 4.



272

273



275

276 Figure 7: A: Fraction of the estimated fish biomass as a function of trophic levels, both  
 277 derived from individual food items as well as from diet/stomach contents, as a function of  
 278 trophic levels. B: 2-dimensional histogram of the trophic level (derived from food items), as  
 279 a function of the weights of fish species, and their trophic levels.

280 **Discussion**

281 *A Biodiverse Oceanic Ichthyofauna*

282 The fish fauna of Tubbataha Reefs appear to show a community structure typical of an intact  
 283 coral reef ecosystem, with all major fish families and trophic groups well-represented. The  
 284 relative absence of groups typical for protected bays (Syngnathidae, Scorpaenidae), is may  
 285 be related to the physical oceanographic conditions in Tubbataha, including frequently  
 286 strong currents.

287 We hope that our survey and analysis provide a useful baseline for comparison to other coral  
288 reef systems in the Coral Triangle, either equally (almost) free of local stressors, or subject  
289 to varying sources and degrees of environmental degradation.

#### 290 *Not an Inverted Trophic Pyramid*

291 Ecological studies of near-pristine coral reefs have found inverted trophic pyramids, with  
292 the biomass of fishes at the higher trophic levels larger than the biomass of fishes closer to  
293 the primary producers. Sandin et al. (2008) found that on Kingman atoll in the nation of  
294 Kiribati, top predators accounted for 85% of total fish biomass. Presumably the mismatch  
295 between the fast turnover of fishes low in the trophic chain, and the longevity of piscivorous  
296 sharks is the reason for this trophic structure.

297 An alternative mechanism for the emergence of an inverted trophic pyramid in a coral reef  
298 fish fauna is the influx of prey fish biomass from neighboring reefs. Such a scenario was  
299 observed by de Omena et al. (2019) at Fakarava Pass in French Polynesia, where groupers  
300 from neighboring reefs aggregate to spawn and fall prey to resident reef sharks.

301 We do not find such an inverted trophic pyramid in the fish fauna of Tubbataha. Our roving  
302 diver fish visual census method provides us with abundance estimates, not with precise fish  
303 biomass values, but we can nevertheless exclude such a trophic structure. While an intact  
304 shark fauna exists at all three reefs (6 species of piscivorous sharks in addition to the  
305 planktivorous whale shark, *Rhincodon typus*), we only observed any sharks during 25/47  
306 survey dives in Tubbataha (the whitetip reef shark, *Triaenodon obesus*, was most common  
307 and seen in 22 survey dives). This is in contrast to frequent shark observations at Kingman  
308 atoll.

309 Possible reasons for the lack of an inverted trophic pyramid of the fish fauna of Tubbataha  
310 could be commercial fishing outside of the Tubbataha Reefs Natural Park, which,  
311 nevertheless, could remove prey fish from the reef's top predators. Shark population  
312 declines are significant with only 1000 humans within 200km, leading to an approximately  
313 60% reduction in shark density (Nadon et al., 2012). The human populations in French

314 Polynesia are much smaller than in the Philippines, and the resultant fishing pressures are  
315 much higher in the Philippines.

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325 our survey team on their boat.

### 326 **AI Use Statement**

327 We didn't use any AI software in any part of this study.

### 328 **Conflict of Interest**

329 There is no conflict of interest with any of the authors of this study.

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