

1 *Patterns of fish utilisation in a tropical Indo-Pacific mangrove-coral seascape, New*

2 *Caledonia*

3 *Fish utilisation of a mangrove forest in New Caledonia*

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14 **Abstract (300 words max)**

15 Mangrove forests are important habitats for fish. However, their utilisation by fish, and
16 the specific values they confer, are still not fully understood. This study details how
17 fish use mangrove forests in an Indo-Pacific mangrove-coral reef seascape. Sampling
18 was conducted using underwater video cameras (UVCs) to describe spatial and
19 temporal variations in fish assemblages across a small-scale (~ 2.5 km²) system, and
20 over the tidal and lunar cycle. UVCs were deployed in the two main component
21 habitats of mangrove forests: at the mangrove forest edge, and inside the forest (5 m
22 from the forest edge). The patterns of utilisation of fish were established across the
23 tidal and lunar cycle. Proximity to coral reefs had a strong influence on the mangrove
24 fish community, as most fish recorded were reef-associated. Juveniles of 12 reef

25 species were observed, including two species classified as vulnerable on the IUCN list
26 and one endemic species. Fish assemblages on the mangrove edge differed
27 substantially from those inside the forest. Most fish utilised the forest edge with few
28 species making regular use of in- forest habitats, supporting the contention that most
29 fish species remain on the edge and potentially retreat into the forest for opportunistic
30 feeding, or when threatened by larger predators. Species-specific patterns of
31 utilisation varied across the tidal and lunar cycle. Small differences in depth profiles
32 and substrate across the small-scale system had a substantial effect on fish
33 assemblages, highlighting the importance of accounting for spatial heterogeneity in
34 these factors. These data provide important information for managers to implement
35 adequate conservation strategies that includes broader interconnected habitat
36 mosaics.

37 **Introduction**

38 Mangrove forests are a fundamental component habitat of mangrove systems
39 [1], and confer many of the attributes that attract juvenile fish [2, 3]. However, recent
40 work in mesotidal Australia suggests that few fish there penetrate beyond the forest
41 boundary [4]. This brings into question the specific ways in which mangrove forests
42 are utilised and indicates the need for studies to characterise fish assemblages at
43 locations with different tidal ranges and contexts, and to investigate how widespread
44 such patterns of utilisation of mangrove forests are.

45 At a broader scale, studies have found that some mangrove forests, especially
46 in the Indo-Pacific, seem to be used less intensively as nursery or feeding grounds by
47 reef fish [4-6] than in the Caribbean [7-9]. These observations suggest that not all
48 mangrove forests provide equivalent functions and services. This dissimilarity has

49 been attributed to differences in the settings in which mangrove forests occur (coastal,
50 estuarine, island, embayment), different tidal ranges (micro-, meso- or macrotidal),
51 proximity of other high value habitats such as seagrass beds and coral reefs, or
52 climatic zones [10-13]. Comparing fish assemblages between the Indo-Pacific and the
53 Caribbean in mangrove habitats with similar micro-tidal settings would provide crucial
54 information on how those factors influence the value and functioning of mangrove
55 habitats.

56 Intertidal mangrove forests are challenging environments, most notably
57 because they are only available to most aquatic organisms while they are flooded at
58 high tide [13-15]. In many parts of the Indo-Pacific, the tidal range is greater than in
59 the Caribbean, where mangrove forests are usually continually available to fish [2].
60 The intermittent availability of mangrove forests may explain the low use by fish in the
61 Indo-Pacific [11]. Tidal variation (extent, duration and frequency of flooding) generates
62 a range of constraints for fish utilising mangrove forests. Most obvious is the decrease
63 in water depth and eventual drainage of the forest as the tide ebbs. Several studies
64 have demonstrated that fish undertake regular migrations in tidally driven mangrove
65 systems, with different patterns of mangrove use according to fish species, lunar cycle
66 (neap vs spring tide) and tidal phase (flooding vs ebbing) [4, 16-19]. Migration of fish
67 in response to tidal movements results in substantial connectivity between the three
68 major tropical coastal habitats: coral reefs, seagrass beds and mangrove forests [14,
69 20], giving rise to the idea that mangrove forests are part of a wider interconnected
70 habitat mosaic [15]. Therefore, investigating tidal and spatial variations in fish
71 assemblages in mangrove forests is a crucial step towards fully appreciating the value
72 and functioning of the whole tropical coastal ecosystem.

73 The difficulty of sampling these habitats goes a long way to explaining the
74 paucity of information available on fish assemblages inside mangrove forests [21, 22].
75 The use of conventional techniques such as underwater visual censuses or netting
76 techniques is restricted across much of the Australasian region where saltwater
77 crocodiles (*Crocodylus porosus*) are common, and where dense mangrove forests
78 reduce the efficiency of most net-based approaches [4]. Recently, underwater video
79 has been successfully applied to study in-forest fish assemblages [4, 23], most notably
80 because it overcomes a lot of sampling issues, substantially reduces field labour
81 intensity, and allows for high -temporal and -spatial resolution data collection
82 simultaneously in different habitats, such as the edge and the inside of a mangrove
83 forest [24].

84 We used underwater cameras on the edge and inside a mangrove forest [4,
85 16], coupled with high frequency depth loggers, to examine how fish use mangrove
86 forests in a micro-tidal Indo-Pacific mangrove-coral reef seascape. In particular we
87 assessed the fish species that used the mangrove forest, how their utilisation changed
88 between the forest edge and in-forest habitats, and how fish assemblages changed
89 across the tidal cycle.

90 **Materials and methods**

91 **Study site**

92 Our study focused on a relatively pristine mangrove forest in Bouraké, South
93 Province of New Caledonia (Fig 1). New Caledonia experiences a semi-arid to tropical
94 climate with annual total rainfall of 1,000 mm, and a mixed semi-diurnal microtidal

95 regime (maximum 1.8 m tidal range). Bouraké receives little freshwater inflow with no
96 defined drainage.

97 The area comprises approximately 2.5 km² of mangrove forest dominated by
98 *Rhizophora stylosa* on the seaward edge and *Avicennia officinalis* on the landward
99 margin, with a large semi-enclosed central lagoon (1.2 km long, 60 m wide, 1-2 m
100 depth). A channel (20-70 m wide, 2-6 m depth, 700 m long) connects the main lagoon
101 to the coastal waters of Pritzbuer Bay (~ 20 km²). The channel comprises two
102 sheltered inlets (approximately 0.01 km² each), and a shallow (1-2 m depth) coral reef
103 platform that extends from the middle of the channel to the edge of the mangrove
104 forest. Coral reefs occur up to a first few meters into the forest in some places (Fig 1).
105 We chose a mangrove-coral reef seascape, a setting comparable to the one in which
106 mangrove forests occur in the Caribbean, so we could relate our findings to this other
107 ecoregion [25] where many studies have been conducted.

108

109 **Fig 1. Map and picture of the study system in Bouraké, South Province, New**
110 **Caledonia.** The nine study sites in the mangrove channel sampled from the 21
111 February to 1 March 2017 are represented by their respective number. Light grey
112 areas represent mangrove forest, dark grey areas represent mainland, and white
113 areas represent water.

114

115 **Data collection**

116 The fish community using the mangrove forest was examined at nine sites on
117 an inland/offshore gradient along the channel (Fig 1). To assess differences in fish
118 assemblage composition between edge and inside the forest, sites 1 to 8 comprised
119 4 paired sites where each odd site number was located on the mangrove forest edge,
120 and even site numbers were located approximately 5 m inside the mangrove forest.

121 Site 9 (considered an edge site in the analyses) was located on the reef platform of
122 the innermost bay, at the edge of scattered mangrove trees slightly away from the
123 main forest. The substrate at sites 1 and 9 consisted of dead corals, small live coral
124 boulders and sand, while on other edge sites it comprised mainly dead corals and
125 small and larger live coral boulders. The substrate was homogeneous and consisted
126 of silt material at in-forest sites.

127 Fish assemblages were sampled using underwater video cameras (UVCs;
128 Model ATC9K Oregon Scientific) to investigate tidal variations in fish assemblages
129 simultaneously on the edge and inside the forest. Unbaited UVCs mounted on stable
130 bases were deployed at each site during neap (21 to 23 February 2017) and spring
131 tides (28 February to 1 March 2017). A sampling day consisted of cameras first
132 deployed at sites early in the morning (first light), continuing until the battery was fully
133 discharged, and again deployed mid-afternoon at all sites until the battery was again
134 fully discharged (recording lasted between 2h and 2.5h). A total of four sampling days
135 were completed (two during neap tides and two during spring tides). Cameras were
136 positioned around 7 cm above the substrate, facing towards the channel. A marker
137 mounted on a flexible rod (3 mm diameter, 0.5 m long) was placed 0.5 m in front of
138 the camera lens as a visibility indicator to ensure a minimum visibility of 0.5 m was
139 achieved in all videos. Visibility was very good during the sampling period, and fish
140 could be identified confidently up to approximately 2 m from the UVCs in all videos.
141 As depth is one of the main limiting factors to mangrove accessibility, tidal variations
142 in water depth (cm) were measured every 15 minutes at each site with depth loggers
143 (In-Situ Inc. Rugged Troll 100 model).

144 **Data analyses**

145 While UVCs allow large amounts of data to be gathered quickly in the field,
146 considerable time is required to process these videos. Therefore, we subsampled the
147 acquired video footage. From the two neap tide sampling days, one day was randomly
148 selected and videos at all sites were processed for that day. For the remaining
149 sampling day, all videos were processed from five sites; being the reef platform (site
150 9) and two pairs of in-forest and forest edge sites (sites 5-8). The same selection was
151 applied to the two sampling days conducted during spring tides.

152 Once sediments had settled after camera deployment (typically 2-3 min), videos
153 were viewed using VLC media player (VideoLAN, 2001) and subdivided in 5-min
154 intervals to follow tidal variations in fish assemblages. The occurrence of each fish
155 taxon in each 5-min interval was recorded. Only presence/absence data were
156 recorded to avoid biases induced by count data when using UVCs [4]. Fish were
157 identified to the lowest possible taxonomic level. Features useful in discriminating
158 species within some genera or families such as *Plectorhinchus* spp., Mugilidae spp.,
159 or Gobiidae spp. were difficult to distinguish in videos, therefore these taxa were
160 identified to genus or family level only. Where possible, juvenile fish were identified
161 based on colour patterns and body shape. Any activity such as feeding, hiding,
162 cruising or escaping was also noted. All fish identifications were validated by two
163 additional experts.

164 The frequency of occurrence of each taxon was calculated per site (the total
165 number of 5-min intervals in which a taxon was observed at a site was divided by the
166 total number of 5-min intervals recorded at this site). Only taxa with a frequency of
167 occurrence ≥ 0.05 at one or more sites were retained for analyses (referred to as
168 “common taxa”). Taxa with a frequency of occurrence < 0.05 (referred to as “rare taxa”)
169 were excluded from analyses.

170 Frequency of occurrence of each common taxon in-forest and on the edge was
171 calculated and plotted using horizontal bar plots to investigate differences graphically.
172 The same methodology was followed to investigate differences in frequency of
173 occurrence of fish between neap and spring tides. As fewer fish were observed during
174 spring tides, a logistic regression was performed in R using the presence of any
175 common taxa for each 5-min interval as the dependent variable (1 if any common taxa
176 were observed in the 5-min interval, or 0 if no common taxa were observed), and
177 “Lunar phase” (neap vs spring) as the independent variable, to determine whether
178 “Lunar phase” had a significant effect on the presence/absence of taxa.

179 Depth cumulative time curves were plotted for each site to highlight differences
180 in temporal dynamics. Patterns of mangrove habitat use over flooding and ebbing tide
181 on the edge and in-forest were investigated graphically for each common taxon. Each
182 5-min interval was allocated to a class of water depth of 10 cm (from 10-20 cm to 120-
183 130 cm) according to the water depth value recorded. The mean frequency of
184 occurrence of each common taxon was then calculated per class of water depth during
185 flooding and ebbing tide. Boxplots were used to represent the average square root
186 transformed frequency of occurrence for each common taxon at each depth interval,
187 and a LOESS curve was used to analyse the general pattern of habitat use. To avoid
188 false absence recordings, only taxa recorded in the habitat of interest were
189 considered. Frequencies of occurrence were square root transformed to reduce the
190 impact of extreme values.

191 Non-metric multidimensional scaling (nMDS) was used to compare fish
192 assemblages among sites during spring and neap tides. The frequency of occurrence
193 of each common taxon was calculated per site per lunar phase. Data were square root
194 transformed to decrease the impact of extreme values, and an nMDS analysis based

195 on Bray-Curtis dissimilarities, the most appropriate distance measure when using
 196 abundance data [26], was performed using the package “vegan” in R [27]. Groupings
 197 within the nMDS were determined using similarity profile tests (SIMPROF) based on
 198 hierarchical clustering at a significance level of 95 %.

199 Results

200 Fifty-six video deployments were processed (totalling more than 118h of video).
 201 Seventy-two taxa from 29 families were recorded, with 36 common taxa (frequency of
 202 occurrence ≥ 0.05) retained for further statistical analyses (Table 1). Most species
 203 recorded were marine and reef-associated [28] including fish of families Scaridae,
 204 Chaetodontidae, Pomacanthidae, Siganidae, Acanthuridae, Lutjanidae, or Labridae.

205 **Table 1. Summary of all the families and taxa identified at Bouraké, New**
 206 **Caledonia.**

Family	Taxon	Table 1 (continued)	
		Family	Taxon
<u>Acanthuridae</u>	<i>Acanthurus auranticavus</i> * ¹		
	<i>Acanthurus grammoptilus</i> ²	Haemulidae	<i>Plectorhinchus lineatus</i>
	<i>Acanthurus sp. cf. blochii</i>		<i>Plectorhinchus spp.</i> ²
	<i>Ctenochaetus sp.</i>		<i>Pomadasys argenteus</i> ²
	<i>Zebrasoma velifer</i>	Hemiramphidae	<i>Hyporhamphus sp.</i>
Apogonidae	<i>Fibramia lateralis</i> * ⁴	Labridae	<i>Choerodon graphicus</i>
	<i>Ostorhinchus septemstriatus</i>		<i>Labridae spp.</i>
Belonidae	<i>Belonidae spp.</i>	<u>Lethrinidae</u>	<i>Lethrinus harak</i> * ¹
Blenniidae	<i>Blenniidae spp.</i>		<i>Lethrinus lentjan</i> ¹
<u>Carangidae</u>	<i>Caranx ignobilis</i>		<i>Lethrinus obsoletus</i>
	<i>Caranx papuensis</i> ¹	Lutjanidae	<i>Lutjanus argentimaculatus</i> * ⁴
	<i>Caranx sp.</i>		<i>Lutjanus fulviflamma</i> ³
Chaetodontidae	<i>Chaetodon auriga</i> * ³		<i>Lutjanus fulvus</i> ³
	<i>Chaetodon bennetti</i> ²		<i>Lutjanus russellii</i> ⁴
	<i>Chaetodon ephippium</i>	Monodactylidae	<i>Monodactylus argenteus</i> * ¹
	<i>Chaetodon flavirostris</i>	Mugilidae	<i>Mugilidae spp.</i> * ⁴
	<i>Chaetodon lineolatus</i> ²	Mullidae	<i>Mulloidichthys flavolineatus</i> ²
	<i>Chaetodon lunula</i> ²		<i>Parupeneus ciliatus</i>
	<i>Chaetodon melannotus</i>		<i>Parupeneus indicus</i> ³
	<i>Chaetodon speculum</i>		<i>Upeneus tragula</i> ¹
	<i>Chaetodon vagabundus</i> ²	Pomacanthidae	<i>Pomacanthus sexstriatus</i> ²
	<i>Heniochus acuminatus</i> ¹	Pomacentridae	<i>Neopomacentrus spp.</i> ²

Clupeidae	<i>Clupeidae spp.</i> ²	Scaridae	<u><i>Bolbometopon muricatum</i></u>
Diodontidae	<i>Diodon hystrix</i>		<u><i>Scarus sp. cf ghobban</i></u> ¹
Ephippidae	<i>Platax pinnatus</i>	Scatophagidae	<i>Scatophagus argus</i>
Fistulariidae	<i>Fistularia spp.</i>	Serranidae	<u><i>Epinephelus caeruleopunctatus</i></u>
Gerreidae	<i>Gerres filamentosus</i>		<u><i>Epinephelus lanceolatus</i></u>
	<i>Gerres oyena</i> ^{*3}		<i>Epinephelus malabaricus</i>
Gobiidae	<i>Amblygobius linki</i>		<i>Epinephelus sp.</i>
	<i>Amblygobius nocturnus</i>	Siganidae	<i>Siganus canaliculatus</i> ¹
	<i>Amoya gracilis</i> ⁴		<u><i>Siganus lineatus</i></u> ^{*3}
	<i>Asterropteryx sp. cf striata</i> ³		<i>Siganus punctatus</i>
	<i>Cryptocentrus leptocephalus</i> ⁴	Sparidae	<u><i>Acanthopagrus sp. cf akazakii</i></u> ²
	<i>Eviota sp.</i>	Sphyraenidae	<i>Sphyraena barracuda</i>
	<i>Exyrias puntang</i>	Tetraodontidae	<i>Arothron hispidus</i>
	Gobiidae spp. ^{*4}		
	<i>Gobiidae spp.</i> ²		
	<i>Redigobius balteatus</i> ⁴		

207 Taxa highlighted in bold represent the taxa with frequency of occurrence ≥ 0.05 on at
 208 least 1 site that were kept for statistical analyses. Taxa highlighted with a * represent
 209 the 10 most common taxa. Taxa or families underlined mean that juveniles were
 210 potentially observed for that taxon or for at least one taxon within the family that could
 211 not be identified. The superscript number corresponds to the pattern of mangrove
 212 habitat utilisation across depth followed by the taxon (Fig 5).

213

214 Taxonomic richness was lower at in-forest sites compared to edge sites (21 and
 215 34 common taxa recorded respectively; Fig 2a). *Fibramia lateralis*, and all the common
 216 taxa belonging to the Gobiidae family, except *Cryptocentrus leptocephalus* and
 217 *Asterropteryx* spp., were frequently observed at in-forest sites compared to edge sites
 218 (Fig 2a). *Lutjanus fulviflamma* was the only common taxon recorded evenly in-forest
 219 and edge sites. All the other common taxa were more frequently observed at edge
 220 sites (Fig 2a).

221 **Fig 2. Proportion of time spent by each of the most common taxa a) on**
 222 **the edge versus inside the forest, and b) at neap tide versus spring tide.** On Fig
 223 2a: edge=green and in-forest=brown, and on Fig 2b: neap=deep pink and spring=blue
 224 navy Proportions range from 0 to 1, 1 corresponding to a taxon exclusively recorded
 225 a) on the edge or in-forest or b) at neap tide or spring tide, and 0.5 corresponding to a
 226 taxon recorded a) on the edge as frequently as in-forest or b) at neap tides as
 227 frequently as at spring tides.

228

229 Lunar phase had a significant impact on presence of common taxa and
230 frequencies of occurrence. Twenty-five of the 36 common taxa had higher frequency
231 of occurrence during neap compared to spring tides (Fig 2b). Moreover, the logistic
232 regression highlighted a significant relationship between lunar phase and fish
233 presence ($p < 0.001$), with fish observed less frequently during spring than neap tides.

234 Average depth was substantially shallower at in-forest than edge sites (neap
235 tides (mean \pm SE): 34 ± 0.57 and 55 ± 0.66 cm respectively; spring tides: 48 ± 1.11
236 and 71 ± 1.23 cm respectively) as was maximum depth (95 cm and 133 cm
237 respectively; Fig 3). Moreover, in-forest sites were exposed (i.e. not flooded) for 4-5 h
238 per day during neap tides, and 2-3 h per day during spring tides, while sites on the
239 edge were always submerged. Sites could be classified into three groups according
240 to depth profiles (Fig 3): deep edge sites (sites 3, 5, 7; maximum depth 133 cm);
241 shallow edge sites (sites 1 and 9; maximum depth: 107 cm); in-forest sites (sites 2, 4,
242 6, 8; maximum depth: 95 cm; Fig 3).

243 **Fig 3. Site-specific cumulative time curves for depth.** Each colour represents a
244 paired edge and in-forest site, and edge sites are represented by dashed lines and
245 in-forest sites by solid lines. The dashed dark line indicates the mean cumulative
246 time for depth across all edge sites. The solid black line indicates the mean
247 cumulative time for depth across all in-forest sites.

248

249 Frequencies of occurrence of fish varied across the tidally driven depth profile
250 (Figs 4a and 4b). Patterns of fish occurrence were quite similar between edge and in-
251 forest sites with overall frequencies of occurrence highest at mid-tide, especially mid-
252 ebb tide (Figs 4a and 4b), and lowest at extreme depth values (low or high tide).

253 **Fig 4. Boxplots of average square root transformed frequency of occurrence**
254 **for each common taxon across depth on a) edge sites; b) in-forest sites.** The
255 blue line is the LOESS curve representing the general pattern of habitat use for all
256 common taxa considered. Shaded area around the LOESS curve represents the
257 95% confidence interval.

258

259 We identified 4 main taxa-specific patterns of utilisation across the depth profile:

260 1) taxa using mangrove habitats at high tide (High tide users); 2) taxa using mangrove

261 habitats at mid-tide (flood or ebb; Mid-tide users); 3) taxa without any apparent

262 preferences for depth (Generalist users); 4) taxa accessing and leaving mangrove

263 habitats at low depth (Shallow water users) (Fig 5).

264 **Fig 5. Taxa-specific patterns of mangrove habitat utilisation across the depth**

265 **profile.** The curves represent the LOESS curves constructed with the square root

266 transformed (SQRT) frequency of occurrence of fish across depth. Common taxa

267 followed four main patterns of mangrove habitat utilisation across depth: 1) taxa

268 using mangrove habitats at high tide (High tide users); 2) taxa using mangrove

269 habitats at mid-tide (flood or ebb; Mid-tide users); 3) taxa without any apparent

270 preferences for depth (Generalist users); 4) taxa accessing and leaving mangrove

271 habitats at low depth (Shallow water users).

272

273 Fish composition varied greatly among sites, with distinct assemblages

274 generating four different clusters on the nMDS plot (Fig 6). The 1st cluster comprised

275 all the samples conducted in-forest, the 2nd cluster comprised 5 of the 6 samples

276 conducted at shallow edge sites (Fig 3), the 3rd cluster comprised all the samples

277 conducted at site 5, and the 4th cluster comprised 3 of the 4 samples conducted at site

278 7 and 1 sample conducted at site 3. The samples conducted on the first day (X) and

279 the ones conducted on the following day (Xrep) during the same lunar phase plotted

280 close to each other on the nMDS plot and were for most of them grouped in the same

281 clusters. Three sites were outliers (1, 3 and 7) during spring tides and did not group

282 into any cluster. This could be explained by the presence of sedentary species

283 (*Cryptocentrus leptocephalus* at site 1, and *Neopomacentrus sp.* at site 7), thus if the

284 camera was placed in front of their home, the same individual was most of the time

285 recorded across the entire video driving the fish assemblage composition

286 (*Neopomacentrus* spp. and). Lunar phase did not influence fish assemblages given

287 that the same sites during spring and neap tides grouped together in the same
288 respective clusters.

289 **Fig 6. nMDS analysis performed on square root transformed frequency of**
290 **occurrence for each taxon per site per tide.** Edge sites are represented by
291 squares and in-forest sites by circles. Sites sampled at neap tide are coloured in
292 deep pink, and sites sampled at spring tide in navy blue. Dotted line ellipses
293 represent clusters determined using similarity profile tests (SIMPROF) based on
294 hierarchical clustering at a significance level of 95 %.

295

296 Discussion

297 Mangrove edge and mangrove forest, the two major component habitats of the
298 Bouraké mangrove system, featured distinct taxonomic diversity and fish assemblage
299 composition. Fish assemblages varied substantially across the tidal cycle, with
300 species-specific patterns of mangrove habitat utilisation. Spatial differences in water
301 depth among sites within a same habitat also seemed to influence fish assemblages
302 across this mangrove/coral system.

303 The setting of this tropical mangrove/coral system influenced the nature of the
304 fish assemblages recorded. At least 72 taxa made use of this relatively small
305 mangrove/coral system, with most species classified as tropical marine and reef-
306 associated [28]. Most taxa recorded have not been identified as mangrove-associated
307 in previous studies in coastal estuarine mangroves in the west Pacific [4, 29, 30],
308 suggesting that their presence is linked to the proximity of coral reefs, further
309 supporting the contention that mangrove-coral habitats are interconnected.
310 Conversely, many families important in other Indo-Pacific mangrove systems remote
311 from coral reefs, such as Leiognatidae, Ambassidae, Sillaginidae, Terapontidae, or
312 Toxotidae [4, 18, 29, 31] were not recorded in Bouraké. Juveniles of at least 12 reef

313 fish species were recorded (*Lutjanus fulviflamma*, *Lutjanus argentimaculatus*,
314 *Lutjanus russellii*, *Lethrinus* spp. (2 species), *Bolbometopon muriculatum*, *Siganus*
315 *lineatus*, *Caranx* sp., *Epinephelus caeruleopunctatus*, *Scarus* sp., *Acanthurus* sp.,
316 *Neopomacentrus* sp.). Additionally, relatively small individuals of *Epinephelus*
317 *lanceolatus* and *Acanthopagrus akazakii* were observed. Therefore, juveniles of two
318 species classified as vulnerable on the IUCN list (*E. lanceolatus* and *B. muricatum*),
319 and one endemic species (*A. akazakii*) [32] used this system. These findings highlight
320 that near-coral mangrove habitats in the Central Indo-Pacific, such as Bouraké,
321 function as important habitats for juvenile reef fish in parallel to the situation in the
322 Tropical Atlantic [8, 33, 34].

323 While early studies concluded that high connectivity between coral reefs and
324 mangroves had little influence on mangrove fish assemblage [5, 18, 35], recent
325 evidence suggest that in many instances there are high occurrence of reef-associated
326 fish in mangroves adjacent to reefs [6, 7, 22, 36]. While supporting this idea, the
327 current study emphasises that the utilisation and value of mangrove systems vary
328 locally and cannot be generalised without understanding of location-specific factors [4,
329 7, 12].

330 Fish assemblages varied temporally across the tidal cycle. Tide-induced depth
331 variation has been linked to changes in fish assemblages [16, 18, 37]. This result was
332 corroborated here as fish assemblages varied across depths, with more fish observed
333 during mid-tides, and most species generally avoiding extreme shallow or deep water.
334 In fact, fish seem to display species-specific responses to depth with four main
335 patterns identified: taxa using mangrove habitats at high tide (High tide users); 2) taxa
336 using mangrove habitats at mid-tide (flood or ebb; mid-tide users); 3) taxa without any
337 apparent preferences for depth (Generalist users); 4) taxa accessing and leaving

338 mangrove habitats at low depth (Shallow water users). The first two patterns mainly
339 comprised taxa known to use mangrove habitats extensively such as *Fibramia*
340 *lateralis*, *Lutjanus argentimaculatus*, *Siganus lineatus*, *Gerres oyena*, or species
341 belonging to the Gobiidae family [4], while the other two profiles comprised mainly
342 marine and reef-associated species. In essence, rather than accessing mangrove
343 habitats as soon as they become available, many species seem to use mangrove
344 habitats only for a restricted period of time later in the tide. Other studies that looked
345 at variations in fish assemblages across the tidal cycle also reported species-specific
346 responses to the depth profile and highlighted that species using mangrove habitats
347 extensively were accessing them at shallower depth than other less frequently
348 observed species [16, 37-41]. These patterns could be the result of behavioural
349 adaptations to avoid adverse DO conditions that can occur early or late in the tide [42].
350 Species using extensively mangrove habitats must be adapted to tolerate lower depth
351 and DO conditions compare to species occasionally using mangrove habitats when
352 they are more suitable. More studies are needed to link tidal fish migrations with DO
353 conditions in mangrove habitats because DO is likely be a critical environmental factor
354 determining the value of these habitats.

355 Lunar phase was another influential factor, largely responsible for temporal
356 variations in mangrove utilisation by fish. More fish were detected during neap tide
357 than spring tide, however, taxonomic richness and fish assemblage composition were
358 similar. These data contradict previous studies that observed more fish at spring tide
359 than neap tide [43-45]. These authors suggest that spring tides result in more habitats
360 available and for longer duration, attracting more fish. We firstly thought that this result
361 was an artefact of the methodology, with fish disappearing from the field of view as
362 water became too deep. However, we compared fish abundance within the same

363 depth intervals between neap and spring tides, and fish abundance was still
364 significantly lower during spring tides, which suggests that there may be another
365 explanation. One explanation could be that at spring tides fish can access more
366 intertidal habitats, reducing the probability of encounter with the UVCs. We also
367 observed very strong currents in the channel and along the mangrove edge that could
368 prevent fish from benefiting from using mangrove habitats as the energy needed to
369 remain on the mangrove edge may be too high.

370 This study highlighted clear spatial variations in fish assemblages across the
371 different mangrove habitats. Indeed, fish assemblages were distinctly different
372 between the mangrove edge and just a few meters inside the mangrove forest. Most
373 fish were recorded cruising on the edge of the mangrove forest, while sightings inside
374 the mangrove forest were sparser. The two hypotheses that are usually made to
375 explain why fish use mangrove forests relate to foraging and finding shelter, however,
376 neither were confirmed by the current study as few foraging activities were observed
377 and few individuals were observed actively sheltering among mangrove prop-roots. In
378 fact, few species made regular use of the mangrove forest, supporting the idea that
379 most fish species simply remain on the edge and potentially retreat into the forest for
380 opportunistic feeding, or when threatened by larger predators [46]. This result aligns
381 with the observations in estuarine mangrove forests of northern Australia where few
382 species make regular use of the in-forest habitat [4]. These two habitats (edge and in-
383 forest) probably confer different values to fish, however, fish could benefit from most
384 attributes that physically attract them in mangrove systems [47] by using the mangrove
385 fringe, without venturing into the forest. Accessing the forest could be
386 disadvantageous because of adverse dissolved oxygen [42] or because of increased
387 risk of stranding.

388 Fish assemblages exhibited small-scale spatial (ten or so meters)
389 heterogeneity, particularly along the forest edge compared to in-forest sites. There
390 was a clear distinction in terms of fish assemblages in the nMDS plot between sites 1
391 and 9, and sites 3, 5 and 7. This pattern could be explained by water depth profile
392 differences, or because of differences in substrate, with sites 1 and 9 featuring dead
393 corals, small live coral boulders and sand, and shallow depth, while other edge sites
394 also had dead corals, along with small and larger live coral boulders but lacked sand,
395 and deeper depth. Conversely, all the in-forest sites were quite similar in terms of fish
396 assemblages, suggesting that they provide a homogeneous habitat with similar
397 substrate and depth profile throughout the system. [Johnston and Sheaves \(2007\) \[48\]](#)
398 also identified species-specific responses to different small-scale habitats according
399 to their depth and substrate composition. The importance of accounting for spatial
400 heterogeneity of fish assemblages was highlighted by [Becker et al. \(2012\) \[37\]](#) who
401 observed the influence of small spatial scale changes in water depth and substrate
402 composition on fish assemblages at seagrass beds in South Africa. It is important to
403 consider small-scale spatial heterogeneity when characterising the habitat value of a
404 system to fish, or when using fish assemblages as a bio-indicator of ecological change
405 or ecosystem health [\[49\]](#).

406 **Conclusion**

407 The settings in which mangrove systems occur is important in determining the
408 values they provide to fish. Within a mangrove system, mangrove forest and mangrove
409 edge proved to be two distinct habitats from the point of view of fish. The values
410 reflected in their patterns of utilisation were species-specific, suggesting that utilisation
411 and value need to be considered species-by-species if we are to fully understand the

412 role mangrove systems play in maintaining fish communities. The high spatial and
413 temporal heterogeneity of fish assemblages complicates the characterisation of
414 mangrove systems value and utilisation, suggesting that simplistic models are unlikely
415 to be suitable and that care needs to be exercised when transferring understanding to
416 a new location. These data provide important information for managers to implement
417 adequate conservation strategies that includes location-specific knowledge and
418 integration to broader interconnected habitat mosaics.

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560

561 **Supporting information**

562 **S1 Appendix. Presence/absence of all common taxa for each 5-minute interval**
563 **recorded during the study.**

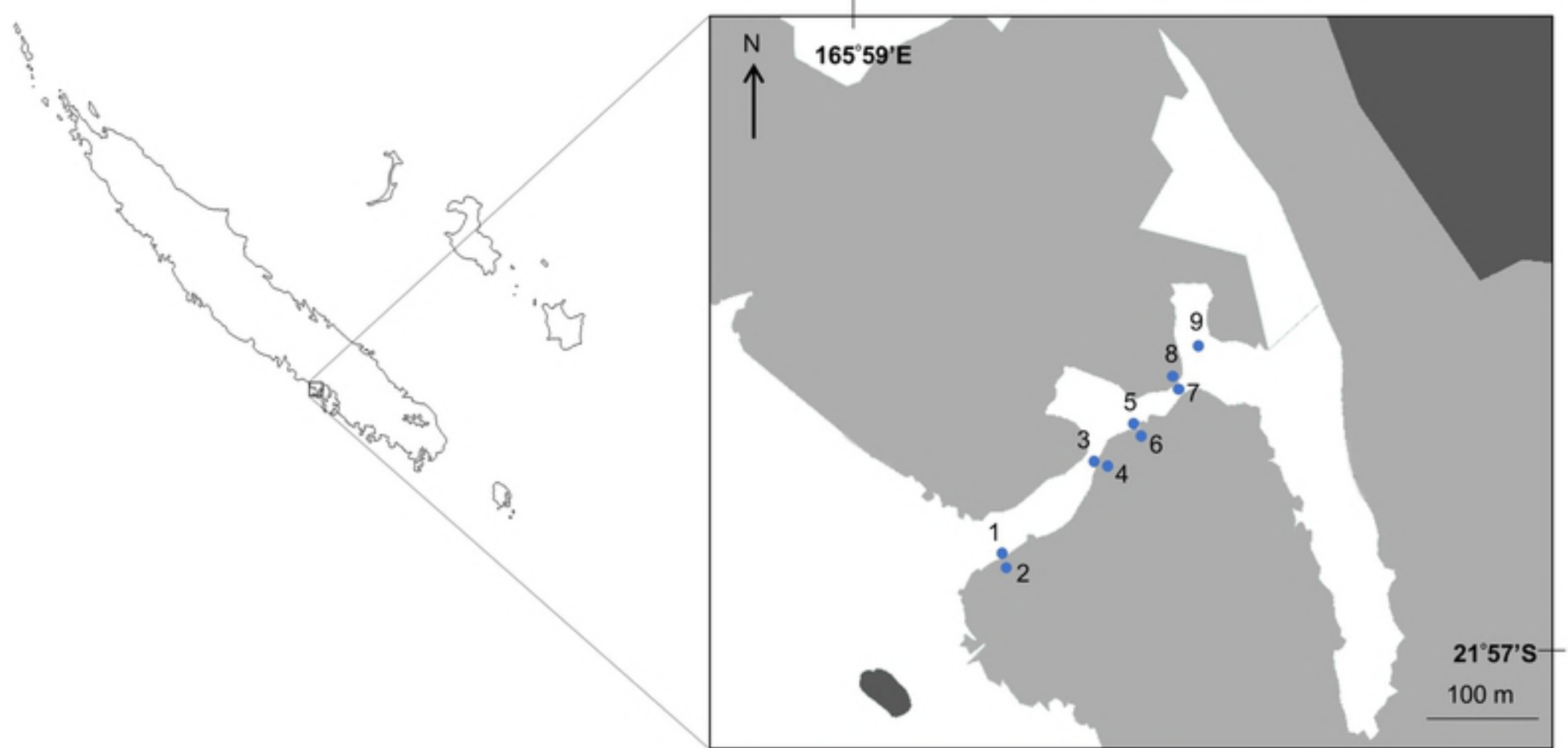


Fig 1

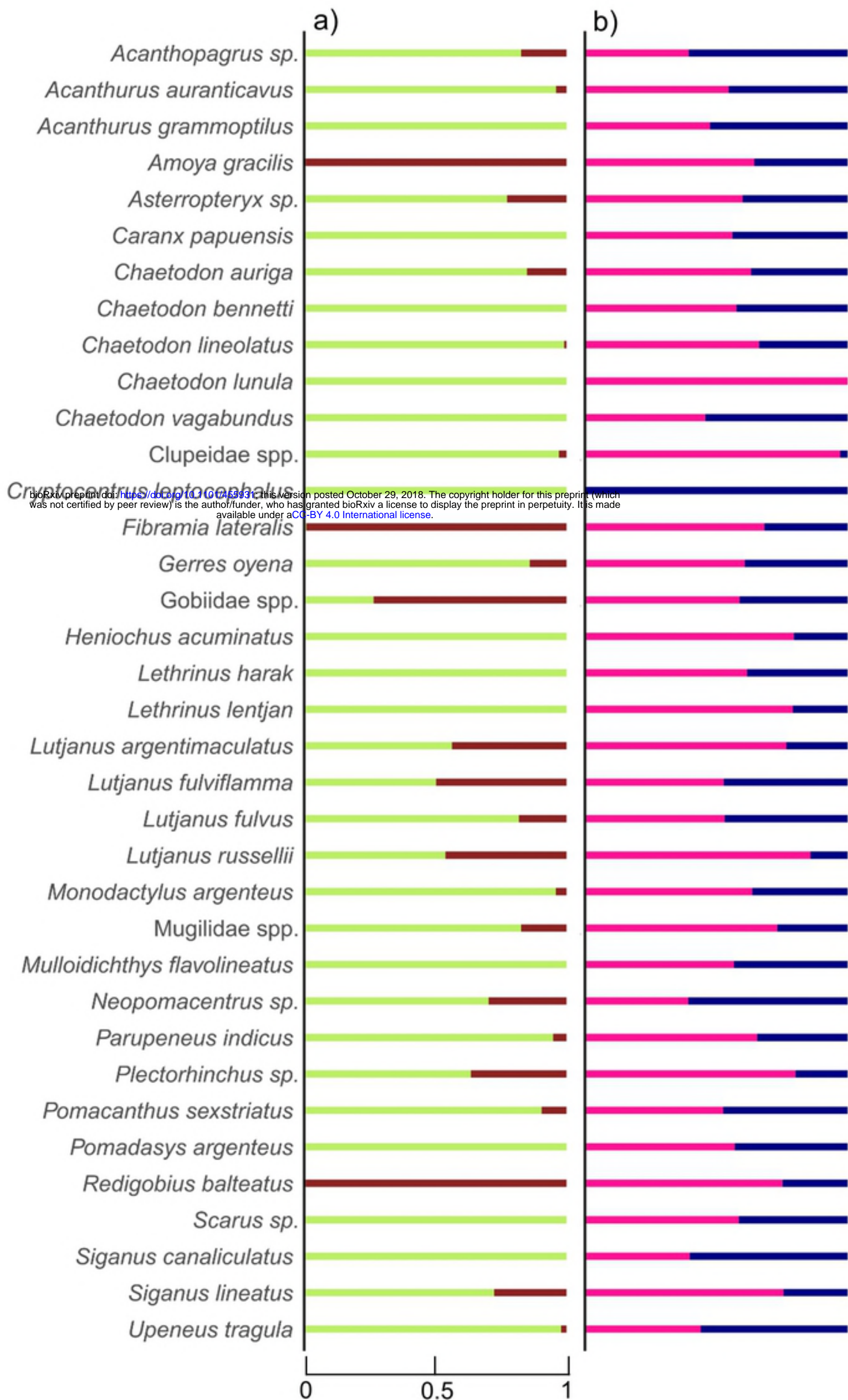


Fig 2

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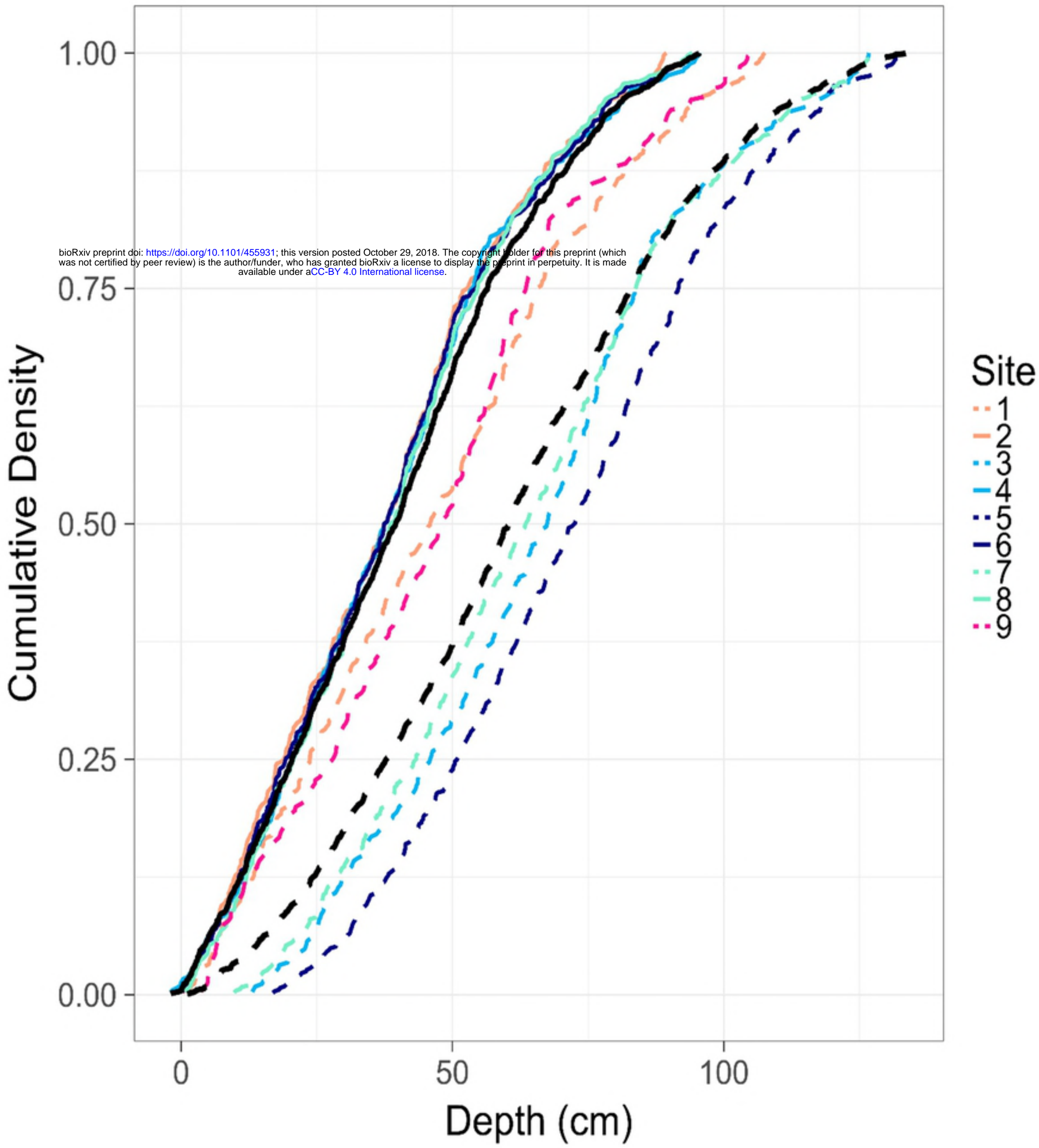


Fig 3

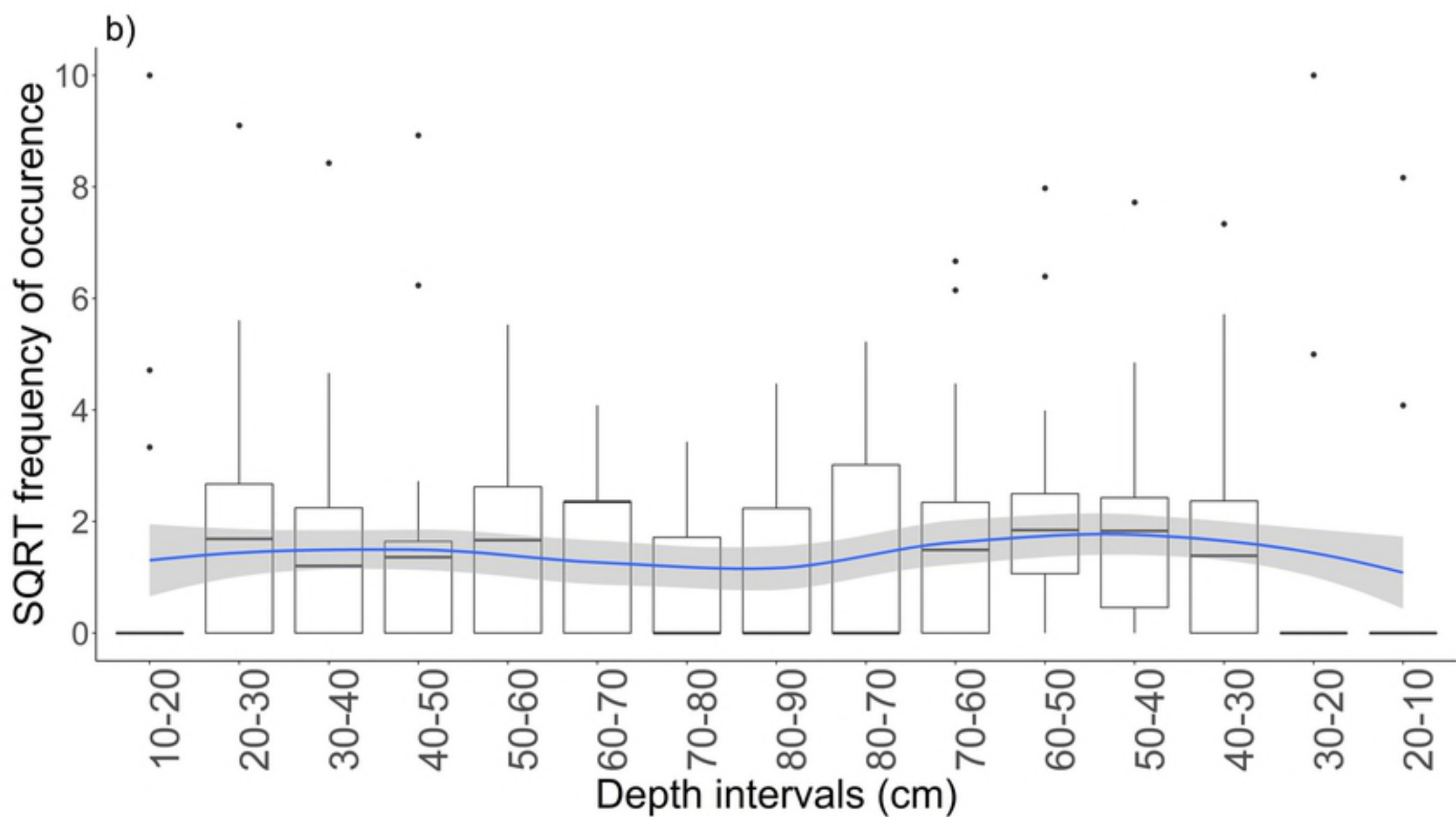
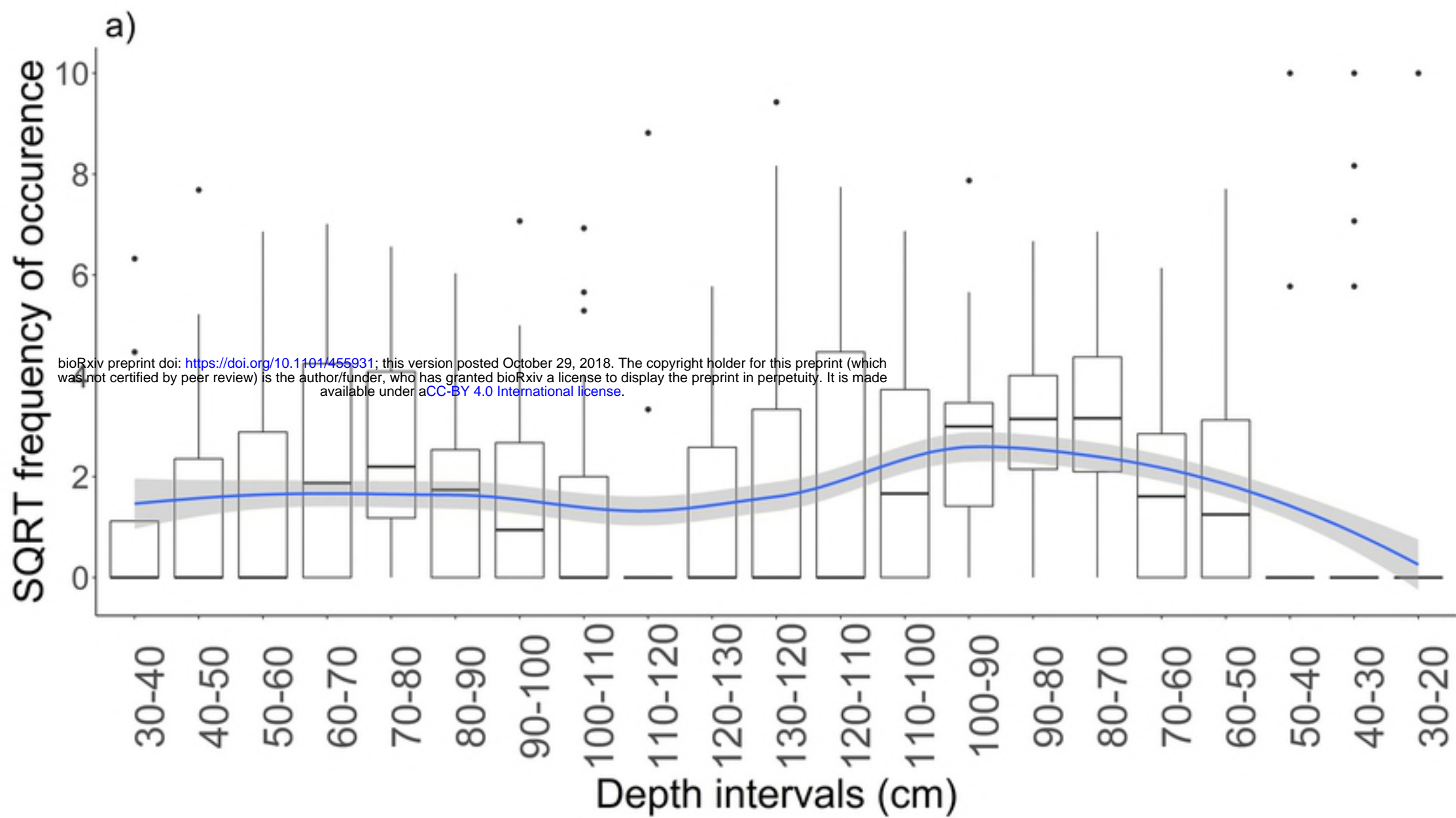


Fig 4

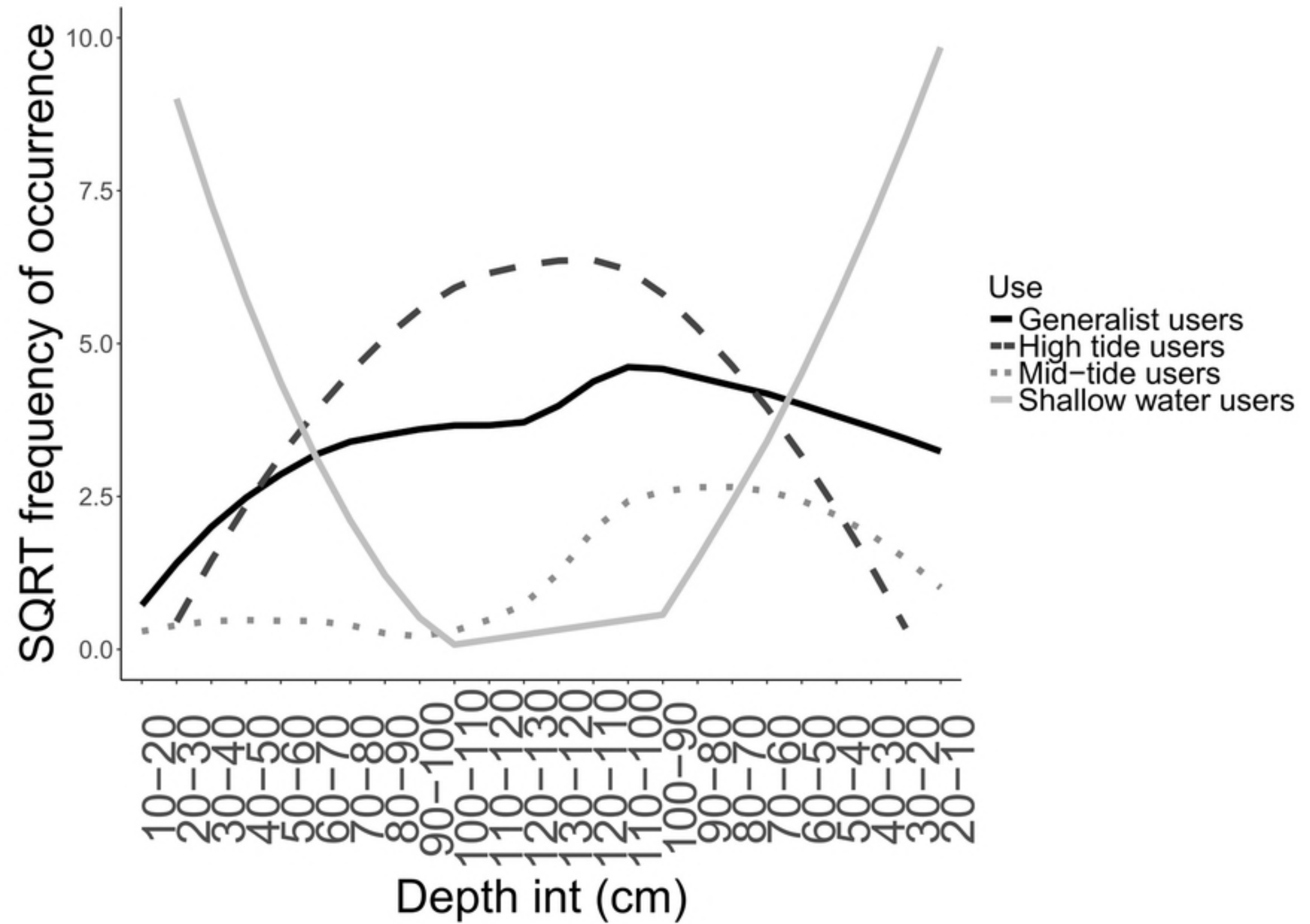


Fig 5

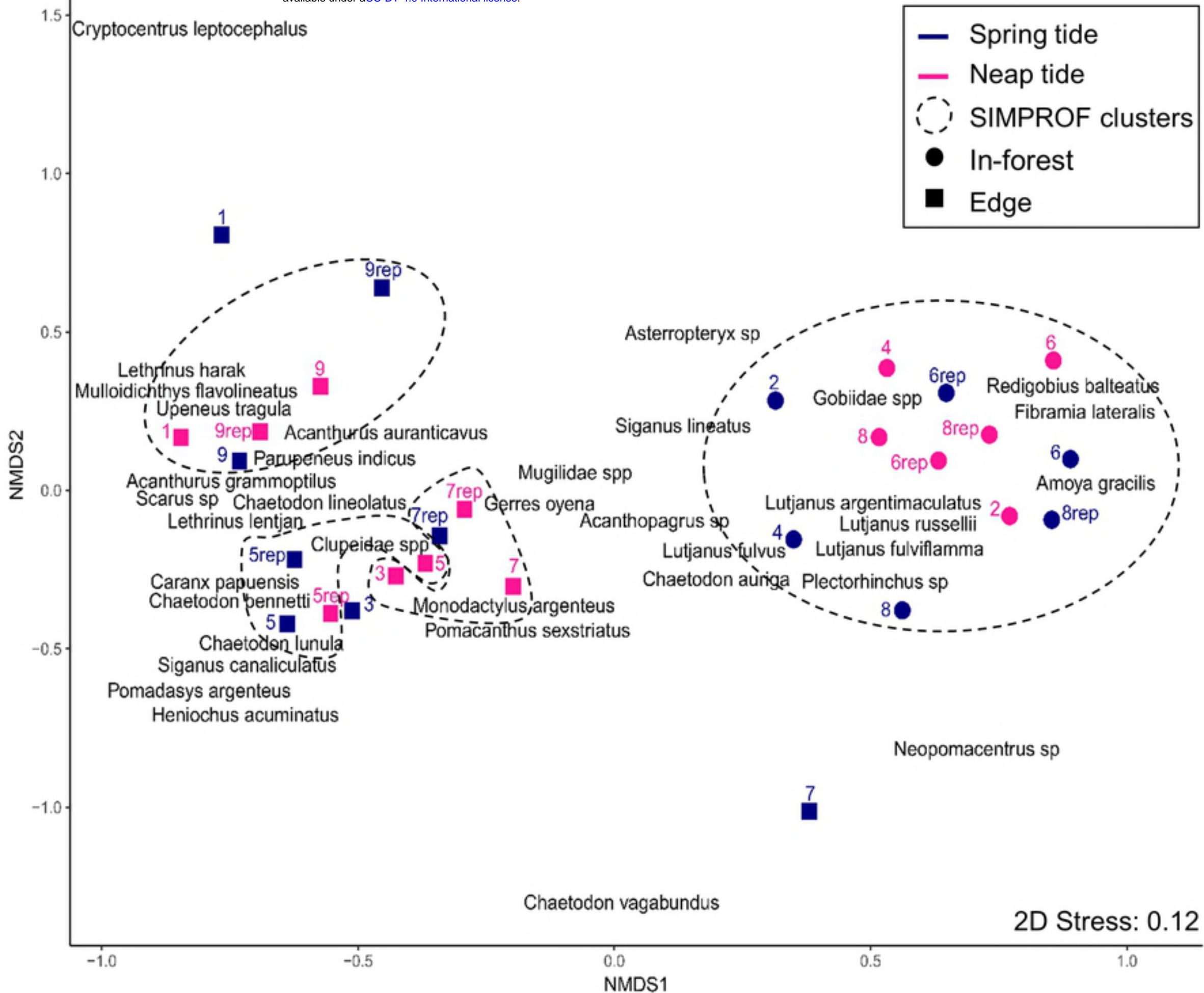


Fig 6