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*

4   *Authors: Dubuc, A[1,2],*, Waltham, N.[1,2], Baker, R.[3], Marchand, C.[4], Sheaves M. [1,2]*

5   *[1] College of Science and Engineering, James Cook University, Townsville, Queensland, Australia*

6   *[2] TropWATER (Centre for Tropical Water & Aquatic Ecosystem Research), James Cook University,*

7   *Townsville, Queensland, Australia*

8   *[3] Department of Marine Sciences, University of South Alabama, Dauphin Island Sea Lab, Alabama,*

9   *United Sates of America*

10   *[4] ISEA (Institute of Exact and Applied Sciences), University of New Caledonia, Noumea, New*

11   *Caledonia*

12   ** Corresponding author*

13   *E-mail: alexia.dubuc1@my.jcu.edu.au (AD)*

14 Abstract (300 words max)

15   Mangrove forests are important habitats for fish. However, their utilisation by fish,

16   and the specific values they confer, are still not fully understood. This study

17   describes how fish use mangrove forests in an Indo-Pacific mangrove-coral reef

18   seascape. Sampling was conducted using underwater video cameras (UVCs) to

19   describe spatial and temporal variations in fish assemblages across a small-scale (~

20   2.5 km^2) system, and over the tidal and lunar cycle. UVCs were deployed in the two

21   main component habitats of mangrove forests: at the mangrove forest edge, and

22   inside the forest (5 m from the forest edge), to establish patterns of utilisation of fish

23   across the tidal and lunar cycle. Proximity to coral reefs had a strong influence on

24   the mangrove fish community, as most fish recorded were reef-associated. Juveniles

1

25   of 12 reef species were observed, including two species classified as vulnerable on

26   the IUCN list, and one endemic species. Fish assemblages on the mangrove edge

27   differed significantly from those inside the forest. Most fish utilised the forest edge,

28   with few species making regular use of in-forest habitats, supporting the contention

29   that most fish species remain on the edge and potentially retreat into the forest for

30   opportunistic feeding, or when threatened by larger predators. Species-specific

31   patterns of utilisation varied across the tidal and lunar cycle. Small differences in

32   depth profiles and substrate across the small-scale system had a significant effect on

33   fish assemblages, highlighting the importance of accounting for spatial heterogeneity

34   in these factors. These data provide important information for managers to

35   implement adequate conservation strategies that include broader interconnected

36   habitat mosaics.

37   ## Introduction

38   Mangrove systems are part of a mosaic of productive coastal habitats [1] that

39   provide a variety of services to fish and human populations [2, 3]. Mangrove forests

40   are a fundamental component habitat of mangrove systems [4], and confer many of

41   the attributes that make them highly valuable fish habitats [5-9]. However, studies

42   have shown varying degree of mangrove forest utilisation, with for instance a higher

43   contribution of reef fish species to mangrove fish assemblages in the Caribbean

44   compared to several places in the Indo-Pacific [10-21]. These observations suggest

45   that not all mangrove forests provide equivalent values to fish. Moreover, recent

46   work in mesotidal Australia suggests that few fish penetrate beyond the forest

47   boundary [15], suggesting that the use of mangrove forests is spatially

48   heterogeneous. This new evidence raises the question relating to the specific ways

49   in which mangrove forests are utilised by fish. More studies are needed to

50   characterise fish assemblages in mangrove forests with different settings (coastal,

51   estuarine, island, embayment), different tidal ranges (micro-, meso- or macrotidal),

52   proximity of other high value habitats such as seagrass beds and coral reefs, or

53   climatic zones [21-24]. A better understanding of how mangrove forest utilisation

54   varies spatially and temporally would provide new insights to help explaining the

55   contrasting results found in the literature.

56   In many parts of the Indo-Pacific, the tidal range is greater than in the

57   Caribbean, where mangrove forests are usually continually available to fish [3].

58   Intertidal mangrove forests are challenging environments, most notably because

59   they are only available to most aquatic organisms while they are flooded at high tide

60   [1, 24, 25]. The intermittent availability of mangrove forests may explain the low use

61   by fish in the Indo-Pacific [23]. Indeed, tidal variation (extent, duration and frequency

62   of flooding) generates a range of constraints for fish utilising mangrove forests. Most

63   evident is the decrease in water depth and eventual drainage of the forest as the tide

64   ebbs, forcing fish out of intertidal mangrove forest zones. Several studies have

65   indeed demonstrated that fish undertake regular migrations in tidally driven

66   mangrove systems, with different patterns of mangrove use according to fish

67   species, lunar cycle (neap vs spring tide) and tidal phase (flooding vs ebbing) [15,

68   26-29]. Migration of fish in response to tidal movements results in substantial

69   connectivity between the three major tropical coastal habitats: coral reefs, seagrass

70   beds and mangrove forests [25, 30], giving rise to the idea that mangrove forests are

71   part of a wider interconnected habitat mosaic [1]. Therefore, investigating tidal and

72   spatial variations in fish assemblages in mangrove forests is a crucial step towards

73   fully appreciating the value and functioning of the whole tropical coastal ecosystem.

74   The difficulty of sampling these habitats goes a long way towards explaining

75   the paucity of information available on fish assemblages inside mangrove forests

76   [20, 31]. The use of conventional techniques such as underwater visual censuses or

77   netting techniques is restricted across much of the Australasian region where

78   saltwater crocodiles (*Crocodylus porosus*) are common, and where dense mangrove

79   forests reduce the efficiency of most net-based approaches [15]. Recently,

80   underwater video has been successfully applied to study in-forest fish assemblages

81   [15, 32, 33], most notably because it overcomes a lot of sampling issues,

82   substantially reduces field labour intensity, and allows for high-temporal and -spatial

83   resolution data collection simultaneously in different habitats, such as the edge and

84   the inside of a mangrove forest [34].

85   In this study we deployed underwater cameras on the edge and inside a

86   mangrove forest [15, 26] coupled with high frequency depth loggers to record spatio-

87   temporal variations in fish assemblages in a microtidal Indo-Pacific mangrove-coral

88   reef seascape. We identified fish species that use the mangrove forest, and used an

89   array of exploratory data analyses and modelling techniques to describe how fish

90   utilisation changes between the forest edge and in-forest habitats, and how fish

91   assemblages vary across the tidal cycle.

92   # Materials and methods

93   ## Study site

94   Our study focused on a relatively pristine mangrove forest in Bouraké, South

95   Province of New Caledonia (21° 56.971S, 165° 59.481E; Fig 1). New Caledonia is

96   an archipelago located in the South West Pacific, 1,500 km east of Australia. New

97 Caledonia has the largest lagoon in the world, partly registered on the UNESCO

98 World Heritage list. New Caledonia experiences a semi-arid to tropical climate with

99 annual total rainfall of 1,000 mm, and a mixed semi-diurnal microtidal regime

100 (maximum 1.8 m tidal range). Bouraké receives little freshwater inflow with no

101 defined drainage.

102 The area comprises approximately 2.5 km² of mangrove forest dominated by

103 *Rhizophora stylosa* on the seaward edge and *Avicennia marina* on the landward

104 margin, with a large semi-enclosed central lagoon (1.2 km long, 60 m wide, 1-2 m

105 depth). A channel (20-70 m wide, 2-6 m depth, 700 m long) connects the main

106 lagoon to the coastal waters of Pritzbuer Bay (~ 20 km^2). The channel comprises two

107 sheltered inlets (approximately 0.01 km² each), and a shallow (1-2 m depth) coral

108 reef platform that extends from the middle of the channel to the edge of the

109 mangrove forest. Corals could be seen right on the edge of the forest in some

110 places. We chose a study location where coral reefs occur in close proximity to

111 mangrove forests (Fig 1), effectively a seascape comparable to the Caribbean

112 coastline [35], so we could relate our findings to this other ecoregion [36] where the

113 tidal range is smaller.

114

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

120

121 ## Data collection

122   Fish using the mangrove forest were examined on an inland/offshore gradient

123   along the channel (Fig 1). To assess differences in fish assemblage composition

124   between edge and inside the forest, 4 paired sampling were conducted (sites 1 to 8).

125   Each paired sampling consisted of two sites within 5-7 m distance; the even site

126   number of the paired sampling was located on the mangrove forest edge (defined as

127   the boundary between mangrove prop-roots and bare substrate), and the odd site

128   number located about 5 m inside the forest. Site 9 (considered an edge site in the

129   analyses) was located on the reef platform of the innermost bay, at the edge of

130   scattered mangrove trees slightly away from the main forest. The substrate at sites 1

131   and 9 consisted of dead corals, small live coral boulders and sand, while on other

132   edge sites it comprised mainly dead corals and small and larger live coral boulders.

133   The substrate was homogeneous and consisted of silt material at in-forest sites.

134   Fish assemblages were sampled using underwater video cameras (UVCs;

135   Model ATC9K Oregon Scientific) to investigate tidal variations in fish assemblages

136   simultaneously on the edge and inside the forest. Unbaited UVCs mounted on stable

137   bases were deployed at each site during neap (21 to 23 February 2017) and spring

138   tides (28 February to 1 March 2017). A sampling day consisted of cameras first

139   deployed at sites early in the morning (first light), continuing until the battery was

140   discharged, and, with a replacement battery, again deployed mid-afternoon at all

141   sites until the battery was discharged (recording lasted between 2h and 2.5h). Four

142   sampling days were completed (two during neap tides and two during spring tides).

143   Cameras were positioned around 7 cm above the substrate, facing towards the

144   channel. A marker mounted on a flexible rod (3 mm diameter, 0.5 m long) was

145   placed 0.5 m in front of the camera lens as a visibility indicator to ensure a minimum

146   visibility of 0.5 m was achieved in all videos. Visibility was very good and consistent

147   during the sampling period, and fish could be identified confidently up to

148   approximately 2 m from the UVCs in all videos. As depth is one of the main limiting

149   factors to mangrove accessibility, tidal variations in water depth (cm) were measured

150   every 15 minutes at each site with depth loggers (In-Situ Inc. Rugged Troll 100

151   model). James Cook University issued a permit for a limited impact research to

152   deploy underwater cameras in New Caledonia (no endangered or protected species

153   were involved as no collection of any specimen was conducted). The study area

154   does not benefit from any special protection, therefore, access and activities are not

155   restricted, and no specific permit was required to sample.

Data extraction from videos

156

157   While UVCs allow large amounts of data to be gathered quickly in the field,

158   considerable time is required to process these videos. Therefore, we subsampled

159   the acquired video footage. From the two neap tide sampling days, one day was

160   randomly selected and videos at all sites were processed for that day. For the

161   remaining sampling day, all videos were processed from five sites; being the reef

162   platform (site 9) and two pairs of in-forest and forest edge sites (sites 5-8). These

163   sites were selected so one replicate for a site located on the reef platform, and two

164   replicates of paired sites not located on the reef-platform were available. Considering

165   this selection, the sites were then randomly chosen. The same selection was applied

166   to the two sampling days conducted during spring tides.

167   Once sediments had settled after camera deployment (typically 2-3 min),

168   videos were viewed using VLC media player (VideoLAN, 2001) and subdivided in 5-

169   min intervals to follow tidal variations in fish assemblages. The occurrence of each

170   fish taxon in each 5-min interval was recorded. Only presence/absence data were

7

171 recorded to avoid biases induced by count data when using UVCs [15]. Fish were

172 identified to the lowest possible taxonomic level. Features useful in discriminating

173 species within some genera or families such as *Plectorhinchus* spp.*,* Mugilidae spp.,

174 or Gobiidae spp. were difficult to distinguish in videos, therefore these taxa were

175 identified to genus or family level only. When possible, juvenile fish were identified

176 based on colour patterns and body shape. Any activity such as feeding, hiding,

177 cruising or escaping was also noted. All fish identifications were validated by two

178 additional experts. For each 5-min interval video processed, the information

179 concerning the date of sampling, site, time of day, habitat (edge vs in-forest), lunar

180 phase (neap vs spring), tide direction (flooding vs ebbing), and corresponding water

181 depth was recorded (Appendix S1).

182 **Data analyses**

183 An index depending on observation per unit effort, similar to the catch per unit

184 effort index (CPUE) when dealing with fishing techniques, was developed to

185 calculate frequencies of occurrence of taxa from the video data. The frequency of

186 occurrence of each taxon was calculated per site (the total number of 5-min intervals

187 in which a taxon was observed at a site was divided by the total number of 5-min

188 intervals recorded at this site). Only taxa with a frequency of occurrence ≥ 0.05 at

189 one or more sites were retained for analyses (referred to as "common taxa"). Taxa

190 with a frequency of occurrence < 0.05 (referred to as "rare taxa") were excluded from

191 analyses.

192 Non-metric multidimensional scaling (nMDS) was used as an exploratory

193 analysis to assess differences in fish assemblages among sites during spring and

194 neap tides. The frequency of occurrence of each common taxon was calculated per

195   site per lunar phase. Data were square root transformed (SQRT) to decrease the

196   impact of extreme values, and an nMDS analysis based on Bray-Curtis

197   dissimilarities, the most appropriate distance measure when using abundance data

198   [37], was conducted. Clusters within the nMDS were determined by conducting an

199   overlay cluster analysis at 40% and 45% similarity on the dissimilarity matrix of all

200   frequencies of occurrence. A two-way analysis of similarity (ANOSIM) was used to

201   test whether there were significant differences in fish assemblages between sites

202   and lunar phase. Pearson correlations exceeding $R > 0.7$ between the ordination

203   and taxa were used to fit vectors on the nMDS plot. All analyses were performed

204   using PRIMER 6 software [38]. Additionally, frequencies of occurrence of each

205   common taxon at in-forest and edge sites were calculated and plotted using

206   horizontal bar plots to further investigate differences in fish assemblage composition

207   between the two habitats.

208   To investigate the factors impacting fish presence/absence, a General Linear

209   Mixed Model (GLMM) was conducted using the package "glmm" in R [39]. The

210   GLMM was conducted on all the 5-min intervals recorded (Appendix S1) with

211   presence/absence of any common taxa for each 5-min interval (1 if any common

212   taxa were observed in the 5-min interval, or 0 if no common taxa were observed) as

213   the response variable, "Depth", "Habitat" (edge vs in-forest), "Lunar phase" (neap vs

214   spring), and "Time of day" (morning vs afternoon) as the fixed factors, and "Site",

215   "Date", "Tide direction" (flooding vs ebbing) and a nested effect of "Site" within

216   "Habitat" as the random factors, using a Bernoulli distribution and a logit link function.

217   Cumulative depth frequency curves were plotted for each site to highlight

218   differences in temporal dynamics. To further understand how fish utilisation varies

219   across depth, variations of SQRT frequencies of occurrence across depth, over

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220 flooding and ebbing tide on the edge and in-forest were assessed using a General

221 Additive Mixed Model (GAMM). Each 5-min interval was allocated to a class of water

222 depth of 10 cm (from 10-20 cm to 120-130 cm) according to the water depth value

223 recorded, and the SQRT frequencies of occurrence of each common taxon was

224 calculated per class of water depth during flooding and ebbing tide per habitat (the

225 total number of 5-min intervals in which a taxon was observed at a class of depth

226 during flooding and ebbing tide per habitat was divided by the total number of 5-min

227 intervals recorded for this same sample unit). Frequencies of occurrence were SQRT

228 to reduce the impact of extreme values. To avoid false absence recordings, taxa

229 never recorded in the habitat of interest were not considered (i.e. if a taxon was

230 never recorded in-forest during the study it was not included in the in-forest

231 analysis). To run the GAMM, SQRT frequencies of occurrence were used as the

232 response variable, "Depth" as a smooth term, and "Habitat" and "Tide direction" as

233 parametric terms using a Gaussian distribution and an identity link function. "Habitat"

234 was included in the model to avoid any nesting issue. The model was built using the

235 package "mgcv" in R [40]. Patterns of variations of SQRT frequencies of occurrence

236 were then investigated graphically using boxplots to examine the variations of

237 average SQRT frequencies of occurrence among taxa at each depth interval, and a

238 LOESS curve was fitted to the data to analyse the general pattern of habitat use.

239 Patterns of mangrove habitat use for each taxon were then plotted using a LOESS

240 curve and individually assessed graphically to examine similarities and classify

241 patterns of fish occurrence across depth. Taxa were grouped in similar patterns if

242 their maximum average occurrence was observed at a similar tidal stage. Three

243 equivalent tidal stages were defined for this purpose: Low tide (between 10-20 and

244 40-50 cm); Mid tide (between 50-60 and 80-90 cm); High tide (between 90-100 and

245 120-130 cm).

246 # Results

247 ## Fish composition

248 Fifty-six video deployments were analysed (totalling more than 118h of video).

249 Seventy-two taxa from 29 families were recorded, with 36 common taxa (frequency

250 of occurrence ≥ 0.05 on at least one site) retained for further statistical analyses

251 (Table 1). Most species recorded were marine and reef-associated [41] including fish

252 of families Scaridae, Chaetodontidae, Pomacanthidae, Siganidae, Acanthuridae,

253 Lutjanidae, or Labridae.

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

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

11

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

256 Taxa highlighted in bold represent the common taxa (frequency of occurrence ≥ 0.05
257 on at least one site) that were kept for statistical analyses. Taxa highlighted with a *
258 represent the 10 most common taxa. Taxa or families underlined mean that juveniles
259 were potentially observed for that taxon or for at least one taxon within the family that
260 could not be identified. The superscript number corresponds to the pattern of
261 mangrove habitat utilisation across depth followed by the taxon as described in Fig
262 6: 1) High-tide users; 2) Mid-tide users; 3) Low-tide users; 4) Generalist users.

263

264 Fish composition varied significantly among sites (ANOSIM: R = 0.793, p <

265 0.001), with distinct assemblages generating three and four different clusters at 40 %

266 and 45 % similarity respectively on the nMDS plot (Fig 2). At 40 % similarity, the 1st

267 cluster comprised all the samples conducted in-forest. The samples were

268 characterised by a lower taxonomic richness (23 common taxa; Fig 3) dominated by

269 *Fibramia lateralis* and all the taxa belonging to the Gobiidae family (except

270 *Cryptocentrus leptocephalus* and *Asterropteryx* spp.), that were the only taxa

271 recorded almost exclusively at in-forest sites (Fig 3). The 2nd cluster comprised all

272 the samples conducted on the edge but site 7 at spring tide. The samples were

273 characterised by a higher taxonomic richness (34 common taxa; Fig 3), among

274 which 10 taxa, mostly reef-associated, significantly contributed to the fish

275 assemblage composition at edge sites (Fig 2). Site 7 at spring tide was an outlier

276 and made the 3rd cluster driven by the abnormally high occurrence of

277 *Neopomacentrus* spp. (Fig 2). Interestingly at 45 % similarity, another cluster was

278 generated, separating deep edge and shallow edge sites (Fig 4, Fig 2). Three

279 species of snappers, *Lutjanus fulviflamma, Lutjanus argentimaculatus* and *Lutjanus*

280 *russellii* were the only three species not showing apparent preference for edge or in-

281 forest sites as they were almost evenly recorded on the two habitats (Fig 3), and

282 therefore did not significantly characterised any of the two habitats (Fig 2). Replicate

283 samples plotted close to each other and were grouped in the same clusters (Fig 2).

284 Lunar phase did not significantly influence fish assemblages (ANOSIM: R = 0.2, p >

285 0.2).

286 **Fig 2. nMDS analysis performed on square root transformed frequencies of**
287 **occurrence for each taxon per site per tide.** Edge sites are represented by
288 squares and in-forest sites by circles. Sites sampled at neap tide are coloured in
289 deep pink, and sites sampled at spring tide in navy blue. Solid green and dotted blue
290 ellipses represent overlay clusters determined at 45 and 40 % similarity respectively.
291 Vectors represent taxa with a Pearson correlation with the ordination R > 0.7.

292

293 **Fig 3. Proportion of time spent by each of the common taxa on the edge**
294 **versus inside the forest.** edge=green and in-forest=brown. Proportions range from
295 0 to 1, 1 corresponding to a taxon exclusively recorded on the edge or in-forest and
296 0.5 corresponding to a taxon recorded on the edge as frequently as in-forest.

297

298 "Habitat" (GLMM: z = -2.637; p < 0.005), "Lunar phase" (GLMM: z = -9.406; p

299 < 0.001) and "Depth" (GLMM: z = -2.118; p < 0.05) significantly influenced the

300 presence/absence of taxa. However, "Time of day" (GLMM: z = -1.519; p > 0.1), date

301 of sampling (GLMM: z = 1.555; p > 0.05), "Tide direction" (GLMM: z = 0.991; p > 0.1)

302 and sites within a same habitat (GLMM: z = 1.394; p > 0.05) did not significantly

303 influence presence/absence of taxa. Further data exploration following the GLMM

304 results showed that at edge sites there was a higher proportion of 5-min intervals in

13

305   which a taxon was observed compare to in-forest sites. Similarly, during neap tides,

306   there was a higher proportion of 5-min intervals in which a taxon was observed

307   compare to spring tides (Appendix S2).

308   Tidal variations in fish assemblages

309   Average depth was substantially shallower at in-forest than edge sites (neap

310   tides (mean ± SE): 34 ± 0.57 and 55 ± 0.66 cm respectively; spring tides: 48 ± 1.11

311   and 71 ± 1.23 cm respectively), as was maximum depth (95 cm and 133 cm

312   respectively; Fig 4). Moreover, in-forest sites were exposed (i.e. not flooded) for 4-5

313   h per day during neap tides, and 2-3 h per day during spring tides, while sites on the

314   edge were always submerged. Sites could be classified into three groups according

315   to depth profiles (Fig 4): deep edge sites (sites 3, 5, 7; maximum depth 133 cm);

316   shallow edge sites (sites 1 and 9; maximum depth: 107 cm); in-forest sites (sites 2,

317   4, 6, 8; maximum depth: 95 cm; Fig 4).

318   **Fig 4. Site-specific cumulative depth frequencies.** Each colour represents a
319   paired edge and in-forest site, and edge sites are represented by dashed lines and
320   in-forest sites by solid lines. The dashed dark line indicates the mean cumulative
321   depth frequencies across all edge sites. The solid black line indicates the mean
322   cumulative depth frequencies across all in-forest sites. An example is provided to
323   help interpret the figure (for 25 % of the recorded time depth was on average equal
324   or below 37 cm at edge sites).

325

326   As the GLMM showed that depth had a significant effect on presence/absence

327   of taxa, a GAMM was used to further explore the response of frequencies of

328   occurrence of fish across increasing and decreasing depth (equivalent to flooding

329   and ebbing tide) and by habitat. SQRT frequencies of occurrence of fish significantly

330   varied across depth (GAMM: $F = 6.756$; $p < 0.001$; Appendix S3), and significantly

331   differed between "Habitat" (GAMM: $F = 39.792$; $p < 0.001$) and "Tide direction"

332   (GAMM: $F = 9.056$; $p < 0.005$). Magnitude of variations in SQRT frequencies of

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333   occurrence across depth was higher at edge than in-forest sites (Figs 5a and 5b,

334   Appendix S3). However, the patterns were similar between the two habitats, with

335   overall frequencies of occurrence highest at mid-tide, especially mid-ebb tide, and

336   lowest at extreme depth values (low or high tide; Figs 5a and 5b, Appendix S3).

337   **Fig 5. Boxplots of average square root transformed frequency of occurrence of**
338   **common taxa across depth on a) edge sites; b) in-forest sites.** The blue line is
339   the LOESS curve representing the general pattern of habitat use for all common taxa
340   considered. Shaded area around the LOESS curve represents the 95% confidence
341   interval. On Fig 5b, interval 90-80 cm has been removed as no data were recorded.

342

343   Similarities in mangrove forest utilisation among common taxa clearly

344   determined 4 main patterns of utilisation: 1) taxa with higher frequencies of

345   occurrence at high tide (90-130 cm; High-tide users); 2) taxa with higher frequencies

346   of occurrence at mid-tide (50-90 cm; Mid-tide users); 3) taxa with higher frequencies

347   at low tide (10-50 cm; Low-tide users); 4) taxa with similar frequencies of occurrence

348   across depth (Generalist users); Fig 6, Appendix S4).

349   **Fig 6. Patterns of mangrove habitat utilisation across the depth profile.** The
350   curves represent the LOESS curves constructed with the square root transformed
351   frequencies of occurrence of fish across depth. Common taxa followed four main
352   patterns of mangrove habitat utilisation across depth: 1) taxa using mangrove
353   habitats at high tide (High-tide users); 2) taxa using mangrove habitats at mid-tide
354   (Mid-tide users); 3) taxa accessing and leaving mangrove habitats at low tide (Low-
355   tide users); 4) taxa without any apparent preferences for depth (Generalist users).
356   Table 1 identifies the taxa allocated to each category.

357

Discussion

359   Understanding the spatial and temporal variations in the use of mangrove

360   habitats by fish is important when considering conservation and resource

361   management to protect mangrove ecosystems from human and natural

362   disturbances. This study highlights that the edge and inside of mangrove forests, the

15

363 two major component habitats of mangrove forests, featured distinct taxonomic

364 diversity and fish assemblage composition. Fish assemblages varied significantly

365 across the tidal cycle, with species-specific patterns of mangrove habitat utilisation.

366 Spatial differences in water depth among sites within a same habitat also seemed to

367 influence fish assemblages across this mangrove/coral system. While only a small

368 portion of the species observed on nearby coral reefs were recorded in Bourake, we

369 found that this mangrove forest does have a role in supporting reef fish species,

370 emphasising the importance of Indo-Pacific mangroves as valuable fish habitats.

371   The setting of this tropical mangrove/coral system influenced the nature of the

372 fish assemblages recorded. At least 72 taxa made use of this relatively small

373 mangrove/coral system, with most species classified as tropical marine and reef-

374 associated [41]. Most taxa recorded have not been identified as mangrove-

375 associated in previous studies in coastal mangroves in the west Pacific [15, 16, 42],

376 suggesting that their presence is linked to the proximity of coral reefs, further

377 supporting the contention that mangrove-coral habitats are interconnected.

378 Conversely, many fish families important in other Indo-Pacific mangrove systems

379 remote from coral reefs, such as Leiognatidae, Ambassidae, Sillaginidae,

380 Terapontidae, or Toxotidae [15, 16, 28, 43] were not recorded in Bouraké. Most

381 individuals observed were at a sub-adult stage, however, juveniles where

382 occasionally recorded for several taxa. Juveniles of at least 12 reef fish species were

383 commonly recorded (*Lutjanus fulviflamma*, *Lutjanus argentimaculatus, Lutjanus*

384 *russellii*, *Lethrinus* spp. (2 species), *Bolbometopon muriculatum*, *Siganus lineatus*,

385 *Caranx* sp., *Epinephelus caeruleopunctatus*, *Scarus* sp., *Acanthurus* sp.,

386 *Neopomacentrus* sp.). Additionally, relatively small individuals of *Epinephelus*

387 *lanceolatus* and *Acanthopagrus akazakii* were observed. Thus, the fish community

16

388   using this system consisted of a substantial number of juvenile reef species,

389   including juveniles of two species classified as vulnerable on the IUCN list (*E.*

390   *lanceolatus* and *B. muricatum*), and one endemic species (*A. akazakii*) [44]. These

391   findings highlight that near-coral mangrove habitats in the Central Indo-Pacific, such

392   as Bouraké, have a role in providing habitats for juvenile reef fish in parallel to the

393   situation in the Tropical Atlantic [12, 45, 46].

394   While early studies concluded that high connectivity between coral reefs and

395   mangroves had little influence on mangrove fish assemblages [18, 28, 47], recent

396   evidence suggest that in many instances there is a high occurrence of reef-

397   associated fish in mangroves adjacent to reefs [10, 19, 20, 48]. While supporting this

398   idea, the current study emphasises that the utilisation and value of mangrove forests

399   vary locally and cannot be generalised from one system to another [10, 15, 21].

400   This study highlighted clear spatial variations in fish assemblages across the

401   two different habitats mangrove edge and mangrove in-forest. Indeed, fish

402   assemblages were distinctly different between the mangrove edge and just a few

403   meters inside the mangrove forest. Most fish were recorded cruising on the edge of

404   the mangrove forest, while sightings inside the mangrove forest were sparser. Two

405   main hypotheses, namely increased food supply and providing shelter, have been

406   suggested to explain why fish use mangrove forests. However, neither of these two

407   hypotheses were confirmed by the current study as few foraging activities were

408   recorded and few individuals were observed actively sheltering among mangrove

409   prop-roots. In fact, few species made regular use of the mangrove forest, supporting

410   the idea that most fish species simply remain on the edge and potentially retreat into

411   the forest for opportunistic feeding, or to escape presence of larger predators [7].

412   This result aligns with the observations in estuarine mangrove forests of northern

413   Australia where few species made regular use of the in-forest habitat [15]. These two

414   habitats (edge and in-forest) probably confer different values to fish, however, fish

415   could benefit from most attributes that physically attract them in mangrove systems

416   [8] by using the mangrove fringe without venturing into the forest. This result

417   supports the idea that high tidal range leading to forest drainage limits the use of

418   mangrove forests in the Indo-Pacific compare to the Caribbean. Accessing the forest

419   could be disadvantageous because of increased risk of becoming trapped after the

420   tide falls, but could also be linked to adverse water quality such as low dissolved

421   oxygen that develops at low tide [49].

422   Fish assemblages exhibited small-scale spatial (dozens of meters)

423   heterogeneity, particularly along the forest edge compared to in-forest sites. There

424   was a clear distinction in terms of fish assemblages in the nMDS plot between sites

425   1 and 9, and sites 3, 5 and 7. This pattern could be explained by water depth profile

426   and substrate differences, with sites 1 and 9 featuring dead corals, small live coral

427   boulders and sand, and shallow depth, while other edge sites also had dead corals,

428   along with small and larger live coral boulders but lacked sand, and experienced

429   deeper depth. Conversely, all the in-forest sites were quite similar in terms of fish

430   assemblages, suggesting that they provide a homogeneous habitat with similar

431   substrate and depth profile throughout the system. Johnston and Sheaves (2007)

432   [50] also identified species-specific responses to different small-scale habitats

433   according to their depth and substrate composition. The importance of accounting for

434   spatial heterogeneity of fish assemblages when characterising the habitat value of a

435   system, or when using fish assemblages as a bio-indicator of ecological change or

436   ecosystem health [51], was highlighted by Becker et al. (2012) [52] who observed

437   the influence of small spatial scale changes in water depth and substrate

438   composition on fish assemblages at seagrass beds in South Africa.

439   Fish assemblages varied temporally across the tidal cycle. Tide-induced depth

440   variations have been linked to changes in fish assemblages [26, 28, 52, 53]. This

441   result was corroborated here as fish assemblages varied across depth, with more

442   fish observed during mid-tides, especially at mid- ebbing tides, and most species

443   generally avoiding extreme shallow or deep water. In fact, fish displayed species-

444   specific responses to depth with four main patterns identified: 1) taxa using

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

446   mid-tide (Mid-tide users); 3) taxa accessing and leaving mangrove habitats at low

447   tide (Low-tide users); 4) taxa without any apparent preferences for depth (Generalist

448   users). Patterns 3 and 4 mainly comprised taxa that frequently used mangrove

449   habitats such as *Fibramia lateralis*, *Lutjanus argentimaculatus*, *Siganus lineatus*,

450   *Gerres oyena*, or taxa belonging to the Gobiidae family [15], while the other two

451   profiles comprised mainly marine and reef-associated species. In essence, rather

452   than accessing mangrove habitats as soon as they become available, many species

453   seem to use mangrove habitats only for a restricted period of time. Other studies that

454   looked at variations in fish assemblages across the tidal cycle also reported species-

455   specific responses to the depth profile and highlighted that species using mangrove

456   habitats extensively were accessing them at a shallower depth than other less

457   frequently observed species [26, 52-56]. Factors driving these tidal migrations are

458   not fully understood, and the fact that species do not enter mangrove habitats as

459   soon as they become available may suggest that these patterns could be the result

460   of behavioural adaptations to avoid adverse water conditions such as low dissolved

461   oxygen that can occur early or late in the tide [49]. Species using extensively

19

462   mangrove habitats could be adapted to tolerate lower depth and adverse dissolved

463   oxygen conditions compare to species that would occasionally use mangrove

464   habitats when they are more suitable. More studies are needed to link tidal fish

465   migrations with dissolved oxygen conditions in mangrove habitats because dissolved

466   oxygen is likely to be a critical environmental factor determining the value of these

467   habitats.

468   Lunar phase was another influential factor responsible for temporal variations

469   in mangrove habitats utilisation by fish. More fish were detected during neap tide

470   than spring tide, however, taxonomic richness and fish assemblage composition

471   were similar. These data oppose previous studies that observed more fish at spring

472   tide than neap tide [57-59]. These authors suggest that spring tides result in more

473   habitats available and for longer duration, attracting more fish. We firstly thought this

474   was an artefact of the methodology, with fish disappearing from the field of view as

475   water became too deep. However, we compared fish occurrence within the same

476   depth intervals between neap and spring tides, and fish presence was still

477   substantially lower during spring tides, which suggests that there may be another

478   explanation. One explanation could be that at spring tides fish can access more

479   intertidal habitats, reducing the probability of encounter with the UVCs. We also

480   observed very strong currents in the channel and along the mangrove edge during

481   spring tides that could reduce the time fish can benefit from using mangrove habitats

482   as the energy needed to remain on the mangrove edge may be too high.

483   **Conclusion**

484   The results here provide further support that within a mangrove forest, the

485   inside and edge of the forest are two distinct habitats characterised by different fish

486 assemblages. The study mangrove forest plays a role in maintaining a substantial

487 number of fish species. However, the habitats use was species-specific, suggesting

488 that utilisation and value need to be considered species-by-species if we want to fully

489 understand the role mangrove systems play in maintaining fish communities. The

490 high spatial and temporal heterogeneity of fish assemblages complicates the

491 characterisation of mangrove forests value and utilisation, suggesting that results

492 from one location are unlikely to be applicable to other systems more broadly. This is

493 an important conclusion for managers when considering to adapt conservation

494 strategies from other locations, to local-specific habitat mosaics.

Acknowledgements

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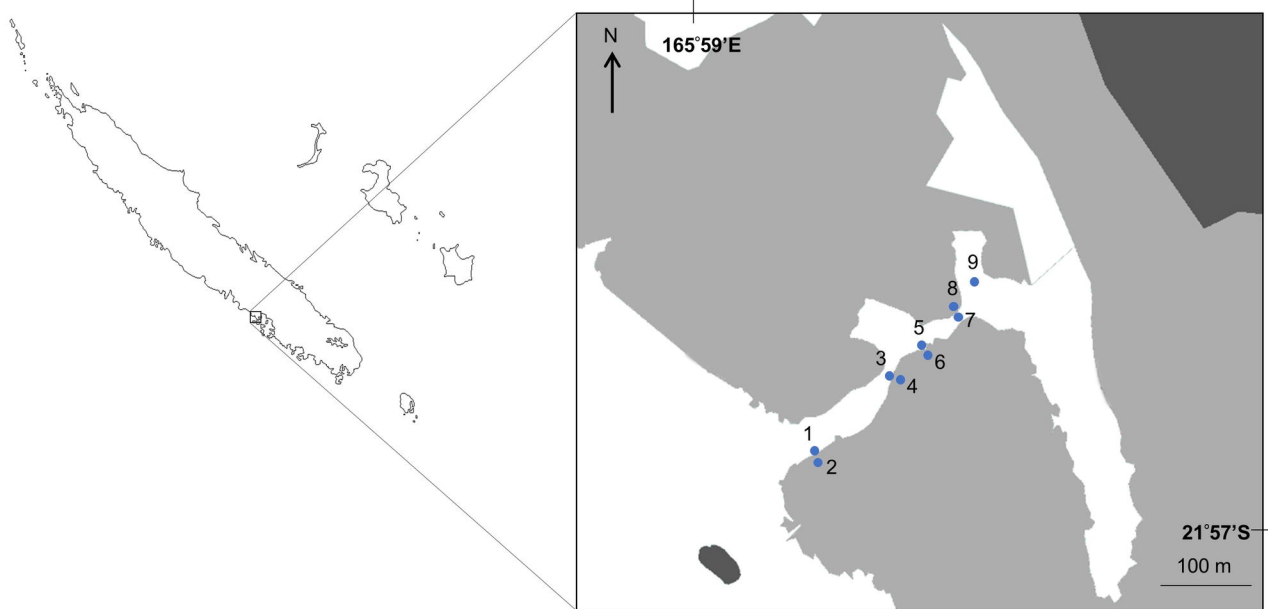660   2011;78(1):344-54.
661

662 # Supporting information

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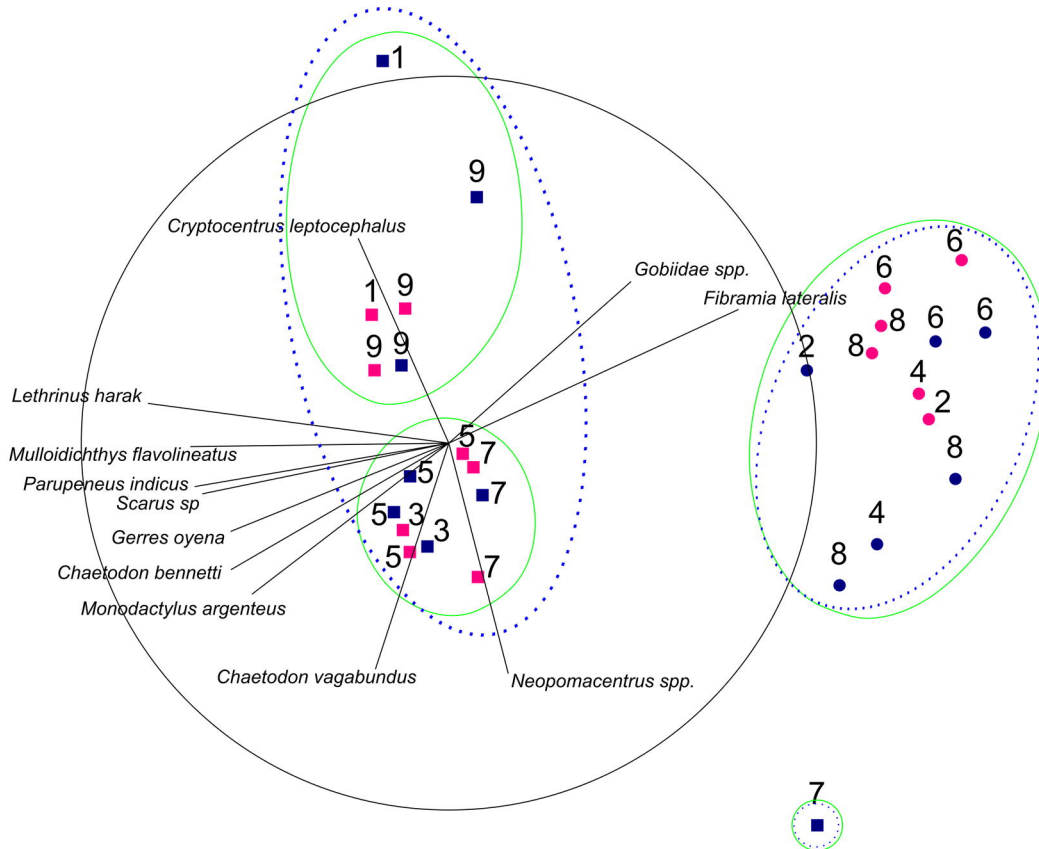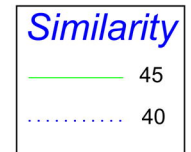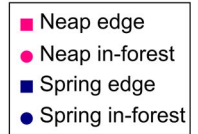664 **recorded during the study.**

665 **S2 Appendix. Percentage of 5-minutes intervals with no common taxa**
666 **observed at a) neap tide vs spring tide and b) edge vs in-forest habitats.**

667 **S3 Appendix. General Additive Mixed Model for a) edge sites and b) in-forest**
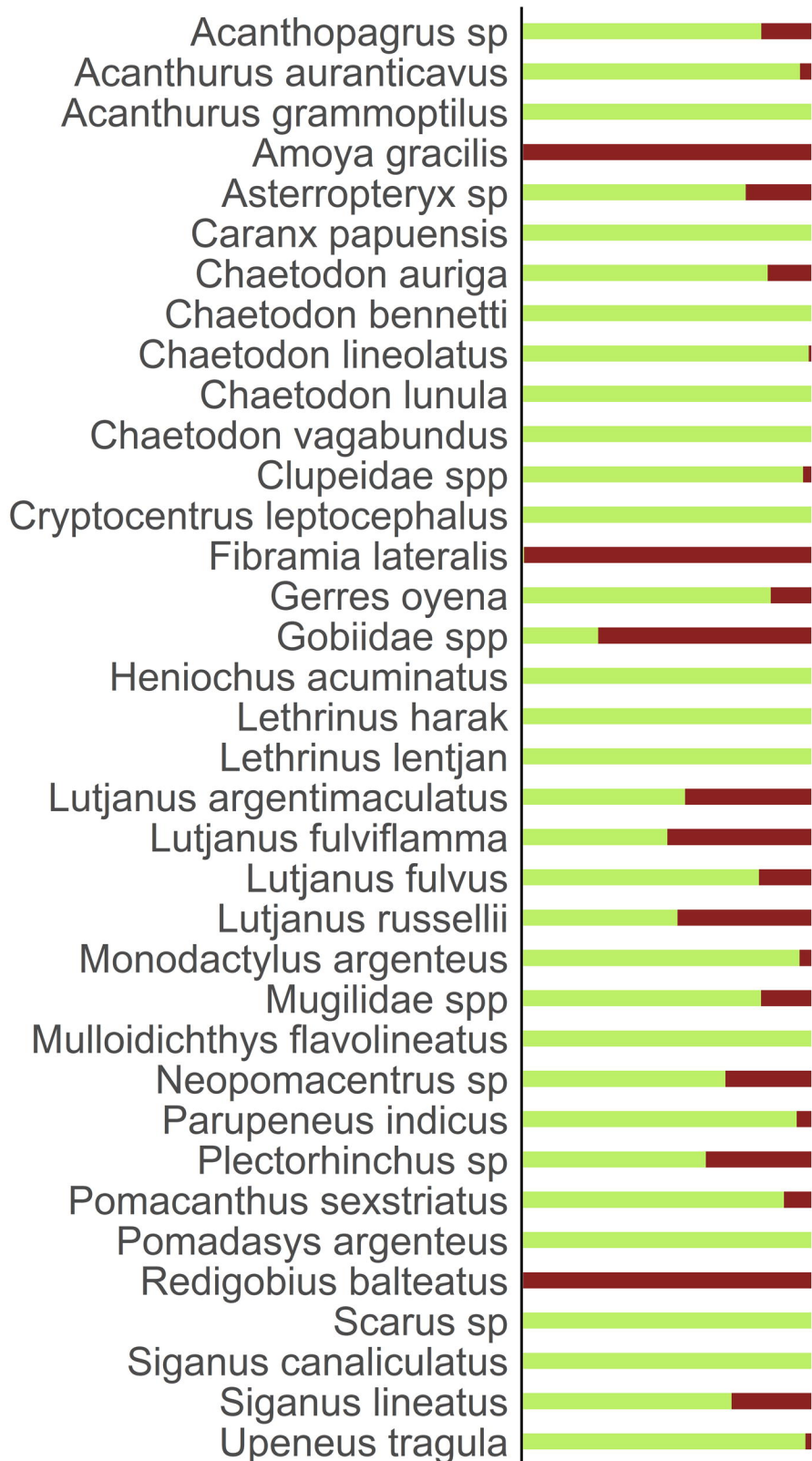668 **sites.**

669 **S4 Appendix. Similarities in species-specific patterns of mangrove utilisation**
670 **across depth: a) High-tide users; b) Mid-tide users; c) Mid-tide users (continue)**
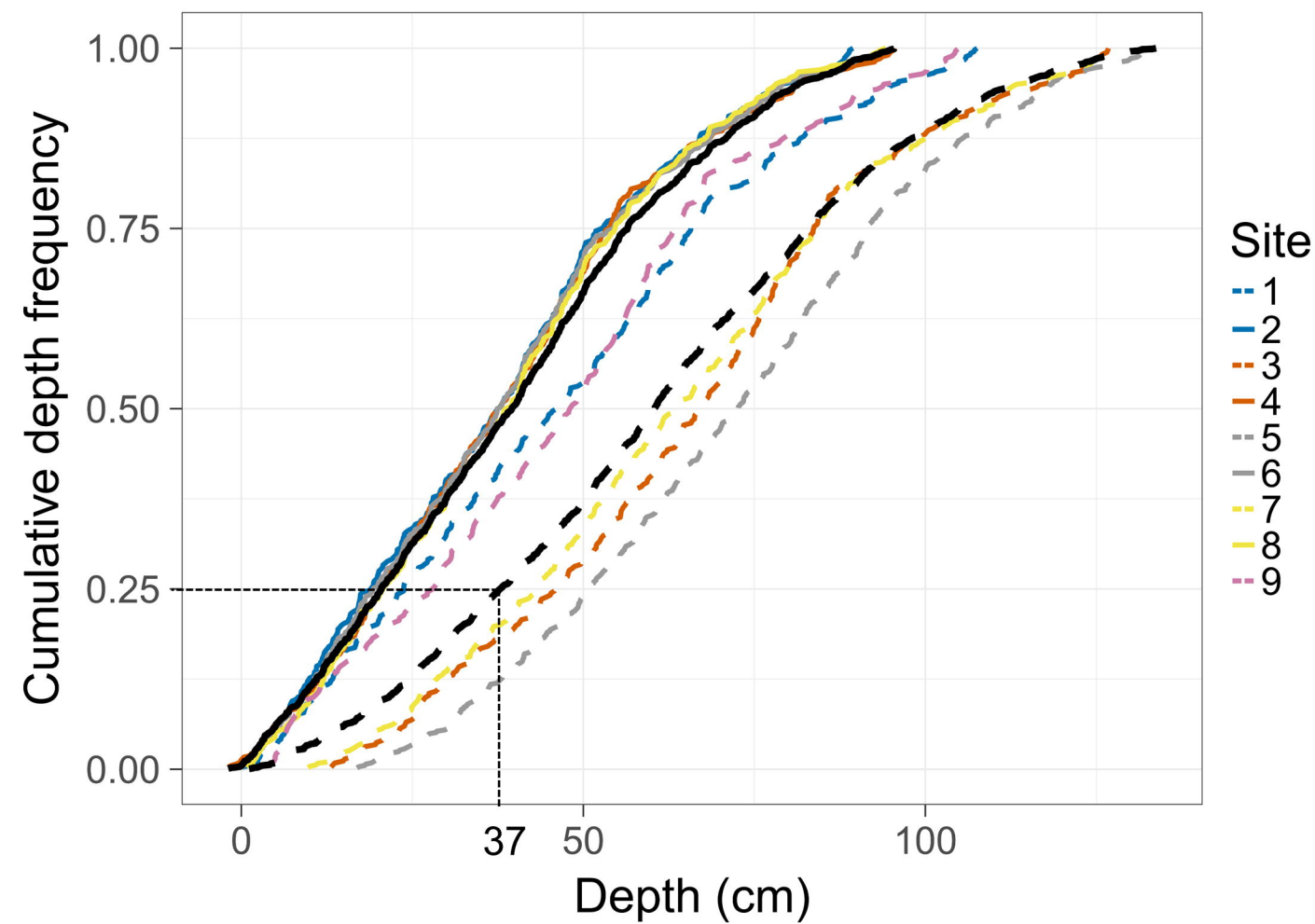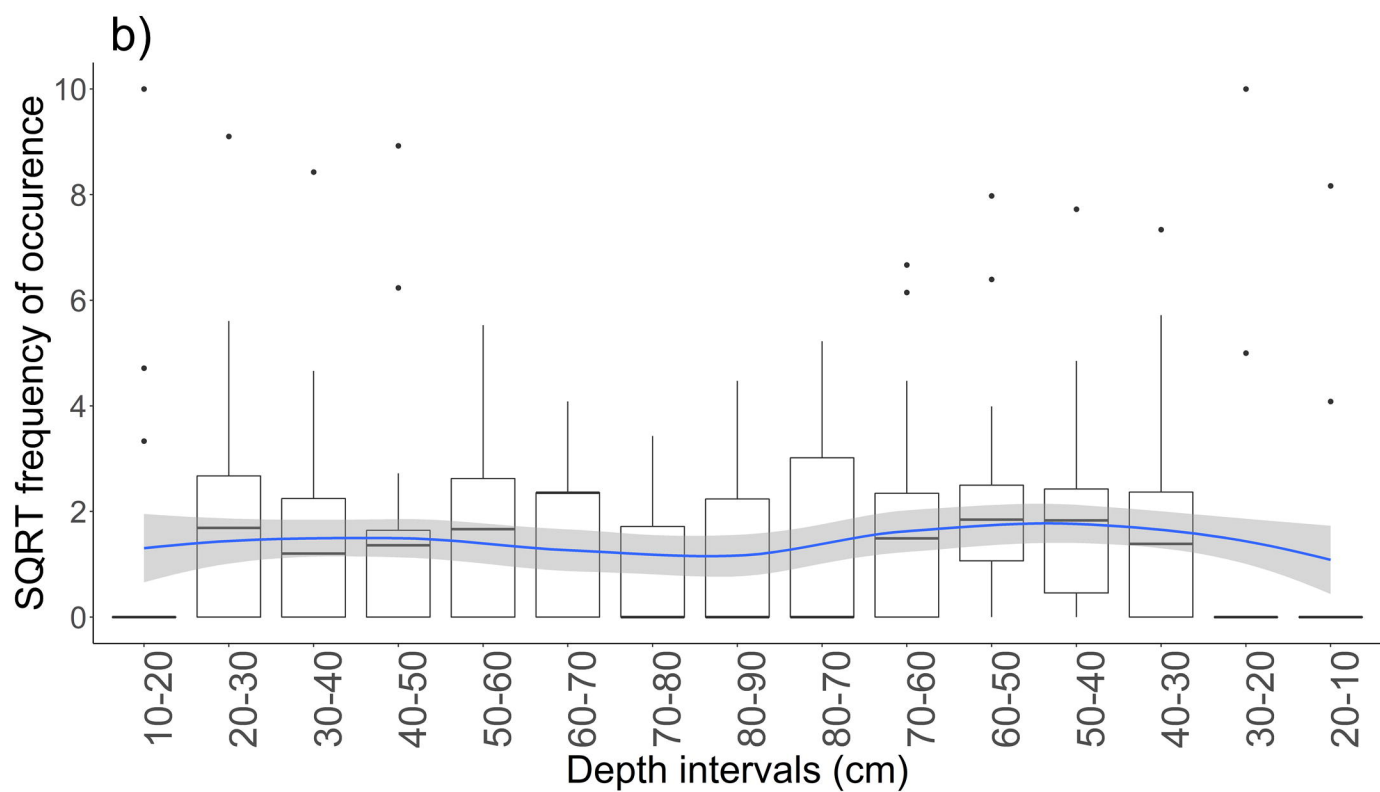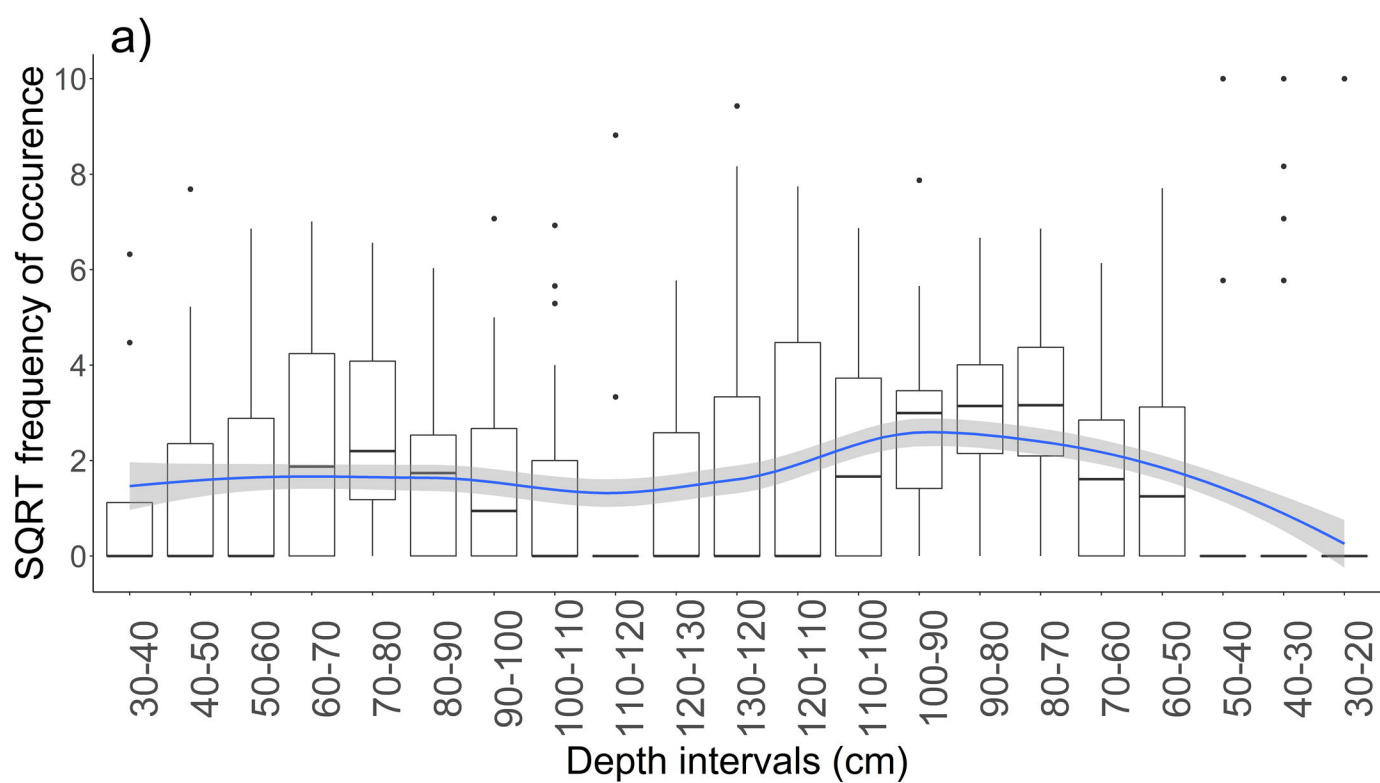671 **d) Low-tide users; e) Generalist users.**

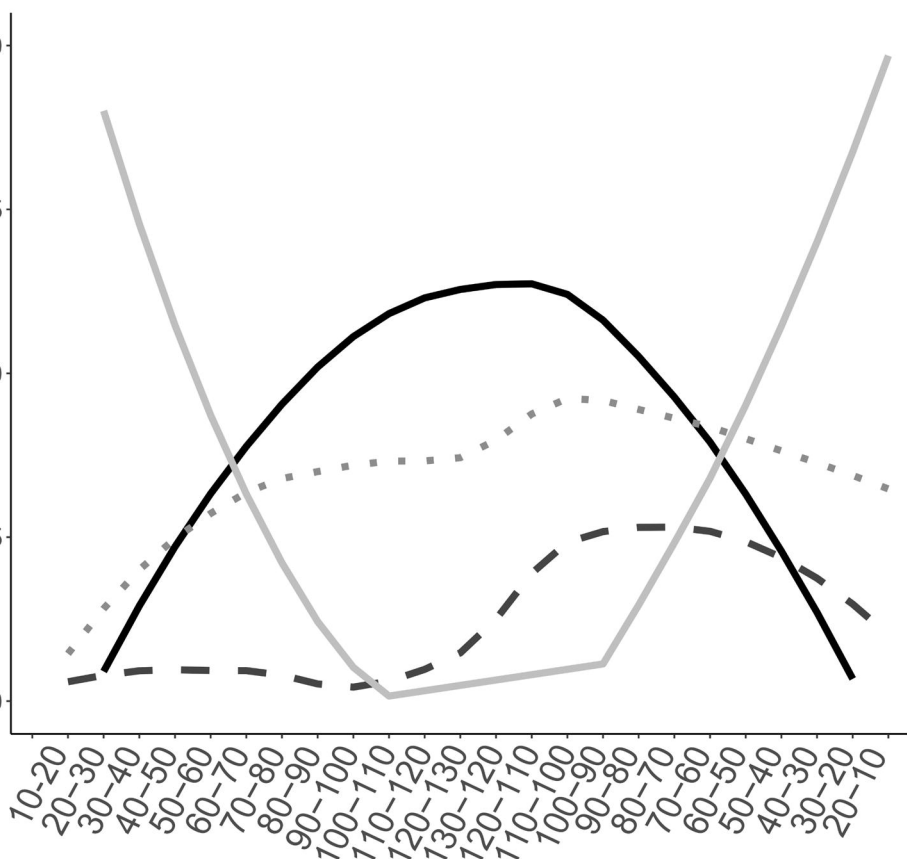Transform: Square root
Resemblance: S17 Bray Curtis similarity

Legend:
- Neap edge (pink square)
- Neap in-forest (pink circle)
- Spring edge (navy square)
- Spring in-forest (navy circle)

Similarity
- —— 45
- ···· 40

Species labels:
- *Cryptocentrus leptocephalus*
- *Gobiidae spp.*
- *Fibramia lateralis*
- *Lethrinus harak*
- *Mulloidichthys flavolineatus*
- *Parupeneus indicus*
- *Scarus sp*
- *Gerres oyena*
- *Chaetodon bennetti*
- *Monodactylus argenteus*
- *Chaetodon vagabundus*
- *Neopomacentrus spp.*

2D Stress: 0.1