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

Fish utilisation of a mangrove forest in New Caledonia

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

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

[2] TropWATER (Centre for Tropical Water & Aquatic Ecosystem Research), James Cook University, Townsville, Queensland, Australia

[3] Department of Marine Sciences, Dauphin Island Sea Lab, University of South Alabama, Dauphin Island Sea Lab, Alabama, United Sates of America

[4] IMPMC, Institut de Recherche pour le Développement (IRD), UPMC, CNRS, MNHN, Nouméa, New Caledonia, France

** Corresponding author*

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

Abstract (300 words max)

Mangrove forests are important habitats for fish. However, their utilisation by fish, and the specific values they confer, are still not fully understood. This study details how fish use mangrove forests in an Indo-Pacific mangrove-coral reef seascape. Sampling was conducted using underwater video cameras (UVCs) to describe spatial and temporal variations in fish assemblages across a small-scale (~ 2.5 km^2) system, and over the tidal and lunar cycle. UVCs were deployed in the two main component habitats of mangrove forests: at the mangrove forest edge, and inside the forest (5 m from the forest edge). The patterns of utilisation of fish were established across the tidal and lunar cycle. Proximity to coral reefs had a strong influence on the mangrove fish community, as most fish recorded were reef-associated. Juveniles of 12 reef

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

Introduction

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

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

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

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

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

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

Materials and methods

Study site

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

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

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

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

Data collection

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

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

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

Data analyses

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

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

The frequency of occurrence of each taxon was calculated per site (the total number of 5-min intervals in which a taxon was observed at a site was divided by the total number of 5-min intervals recorded at this site). Only taxa with a frequency of occurrence ≥ 0.05 at one or more sites were retained for analyses (referred to as “common taxa”). Taxa with a frequency of occurrence < 0.05 (referred to as “rare taxa”) 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
Acanthuridae	***Acanthurus auranticavus**** [1]
	Acanthurus grammoptilus [2]
	Acanthurus sp. cf blochii
	Ctenochaetus sp.
	Zebrasoma velifer
Apogonidae	***Fibramia lateralis**** [4]
	Ostorhinchus septemstriatus
Belonidae	*Belonidae spp.*
Blenniidae	*Blenniidae spp.*
Carangidae	*Caranx ignobilis*
	Caranx papuensis [1]
	Caranx sp.
Chaetodontidae	***Chaetodon auriga**** [3]
	Chaetodon bennetti [2]
	Chaetodon ephippium
	Chaetodon flavirostris
	Chaetodon lineolatus [2]
	Chaetodon lunula [2]
	Chaetodon melannotus
	Chaetodon speculum
	Chaetodon vagabundus [2]
	Heniochus acuminatus [1]

Table 1 (continued)

Family	Taxon
Haemulidae	*Plectorhinchus lineatus*
	Plectorhinchus spp. [2]
	Pomadasys argenteus [2]
Hemiramphidae	*Hyporhamphus sp.*
Labridae	*Choerodon graphicus*
	Labridae spp.
Lethrinidae	***Lethrinus harak**** [1]
	Lethrinus lentjan [1]
	Lethrinus obsoletus
Lutjanidae	***Lutjanus argentimaculatus**** [4]
	Lutjanus fulviflamma [3]
	Lutjanus fulvus [3]
	Lutjanus russellii [4]
Monodactylidae	***Monodactylus argenteus**** [1]
Mugilidae	***Mugilidae spp.**** [4]
Mullidae	***Mulloidichthys flavolineatus*** [2]
	Parupeneus ciliatus
	Parupeneus indicus [3]
	Upeneus tragula [1]
Pomacanthidae	***Pomacanthus sexstriatus*** [2]
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* [3]		*Epinephelus malabaricus*
Gobiidae	*Amblygobius linki*		*Epinephelus sp.*
	Amblygobius nocturnus	Siganidae	***Siganus canaliculatus*** [1]
	Amoya gracilis [4]		***Siganus lineatus**** [3]
	Asterropteryx sp. cf striata [3]		*Siganus punctatus*
	Cryptocentrus leptocephalus [4]	Sparidae	***Acanthopagrus sp. cf akazakii*** [2]
	Eviota sp.	Sphyraenidae	*Sphyraena barracuda*
	Exyrias puntang	Tetraodontidae	*Arothron hispidus*
	Gobiidae spp.* [4]		
	Gobiidae spp.2		
	Redigobius balteatus [4]		

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

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

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

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 ± 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.

We identified 4 main taxa-specific patterns of utilisation across the depth profile: 1) taxa using mangrove habitats at high tide (High tide users); 2) taxa using mangrove habitats at mid-tide (flood or ebb; Mid-tide users); 3) taxa without any apparent preferences for depth (Generalist users); 4) taxa accessing and leaving mangrove habitats at low depth (Shallow water users) (Fig 5).

Fig 5. Taxa-specific patterns of mangrove habitat utilisation across the depth profile. The curves represent the LOESS curves constructed with the square root transformed (SQRT) frequency of occurrence of fish across depth. Common taxa followed four main patterns of mangrove habitat utilisation across depth: 1) taxa using mangrove habitats at high tide (High tide users); 2) taxa using mangrove habitats at mid-tide (flood or ebb; Mid-tide users); 3) taxa without any apparent preferences for depth (Generalist users); 4) taxa accessing and leaving mangrove habitats at low depth (Shallow water users).

Fish composition varied greatly among sites, with distinct assemblages generating four different clusters on the nMDS plot (Fig 6). The 1st cluster comprised all the samples conducted in-forest, the 2nd cluster comprised 5 of the 6 samples conducted at shallow edge sites (Fig 3), the 3rd cluster comprised all the samples conducted at site 5, and the 4th cluster comprised 3 of the 4 samples conducted at site 7 and 1 sample conducted at site 3. The samples conducted on the first day (X) and the ones conducted on the following day (Xrep) during the same lunar phase plotted close to each other on the nMDS plot and were for most of them grouped in the same clusters. Three sites were outliers (1, 3 and 7) during spring tides and did not group into any cluster. This could be explained by the presence of sedentary species (*Cryptocentrus leptocephalus* at site 1, and *Neopomacentrus sp.* at site 7), thus if the camera was placed in front of their home, the same individual was most of the time recorded across the entire video driving the fish assemblage composition (*Neopomacentrus* spp. and). Lunar phase did not influence fish assemblages given

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

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

Discussion

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

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

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

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Supporting information

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

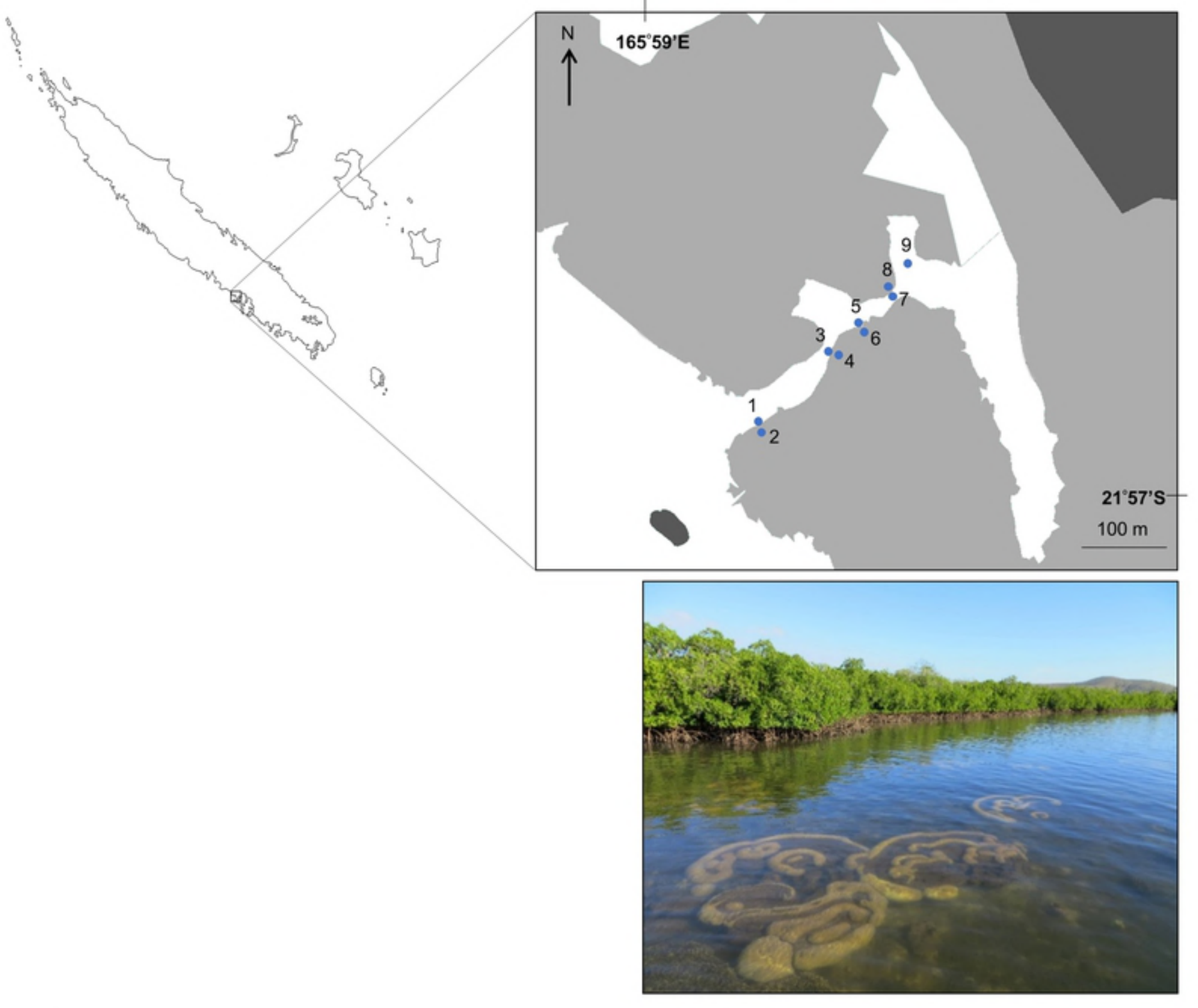


Fig 1

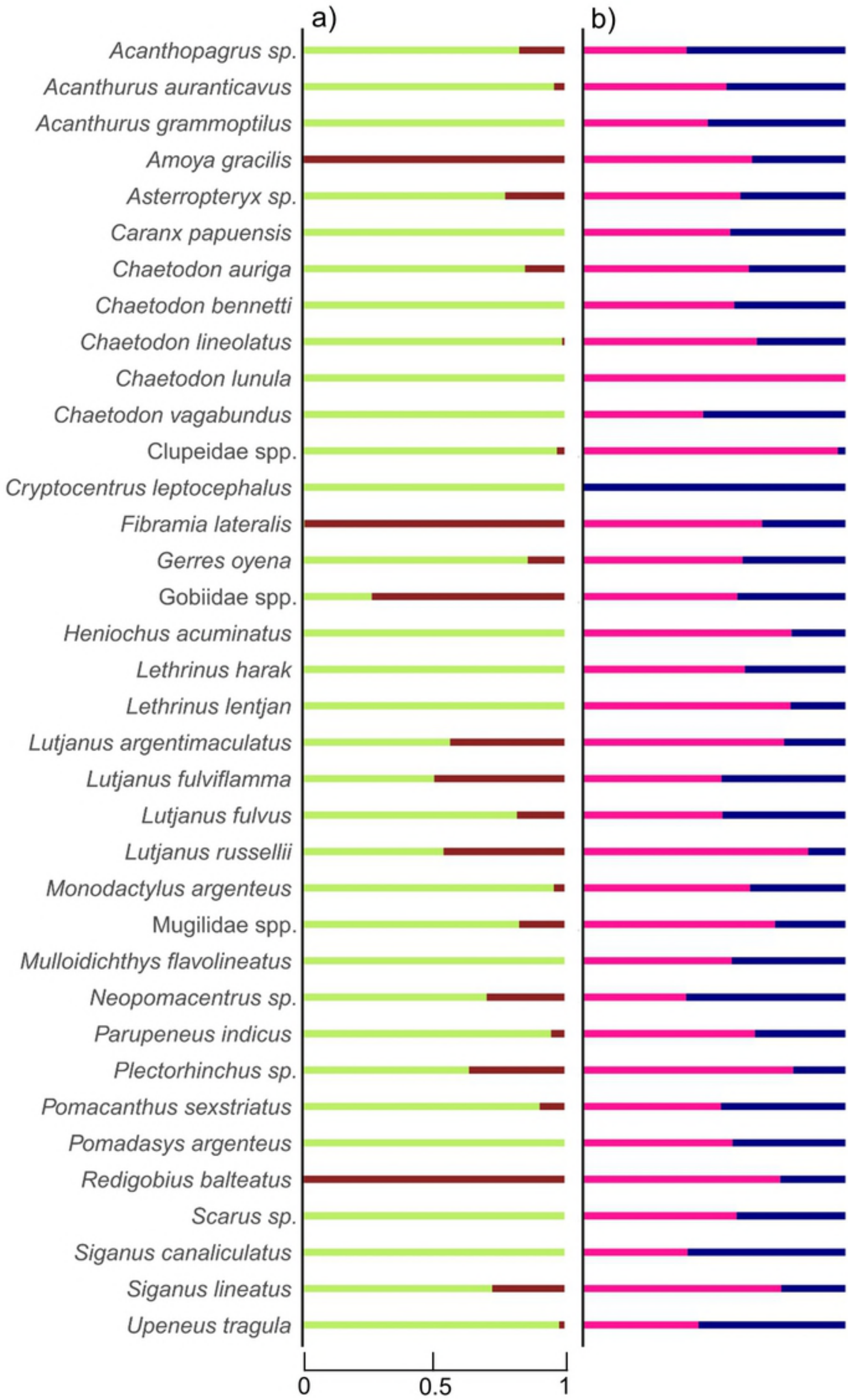

a)
b)
Acanthopagrus sp.
Acanthurus auranticavus
Acanthurus grammoptilus
Amoya gracilis
Asterropteryx sp.
Caranx papuensis
Chaetodon auriga
Chaetodon bennetti
Chaetodon lineolatus
Chaetodon lunula
Chaetodon vagabundus
Clupeidae spp.
Cryptocentrus leptocephalus
Fibramia lateralis
Gerres oyena
Gobiidae spp.
Heniochus acuminatus
Lethrinus harak
Lethrinus lentjan
Lutjanus argentimaculatus
Lutjanus fulviflamma
Lutjanus fulvus
Lutjanus russellii
Monodactylus argenteus
Mugilidae spp.
Mulloidichthys flavolineatus
Neopomacentrus sp.
Parupeneus indicus
Plectorhinchus sp.
Pomacanthus sexstriatus
Pomadasys argenteus
Redigobius balteatus
Scarus sp.
Siganus canaliculatus
Siganus lineatus
Upeneus tragula
0
0.5
1

Fig 2

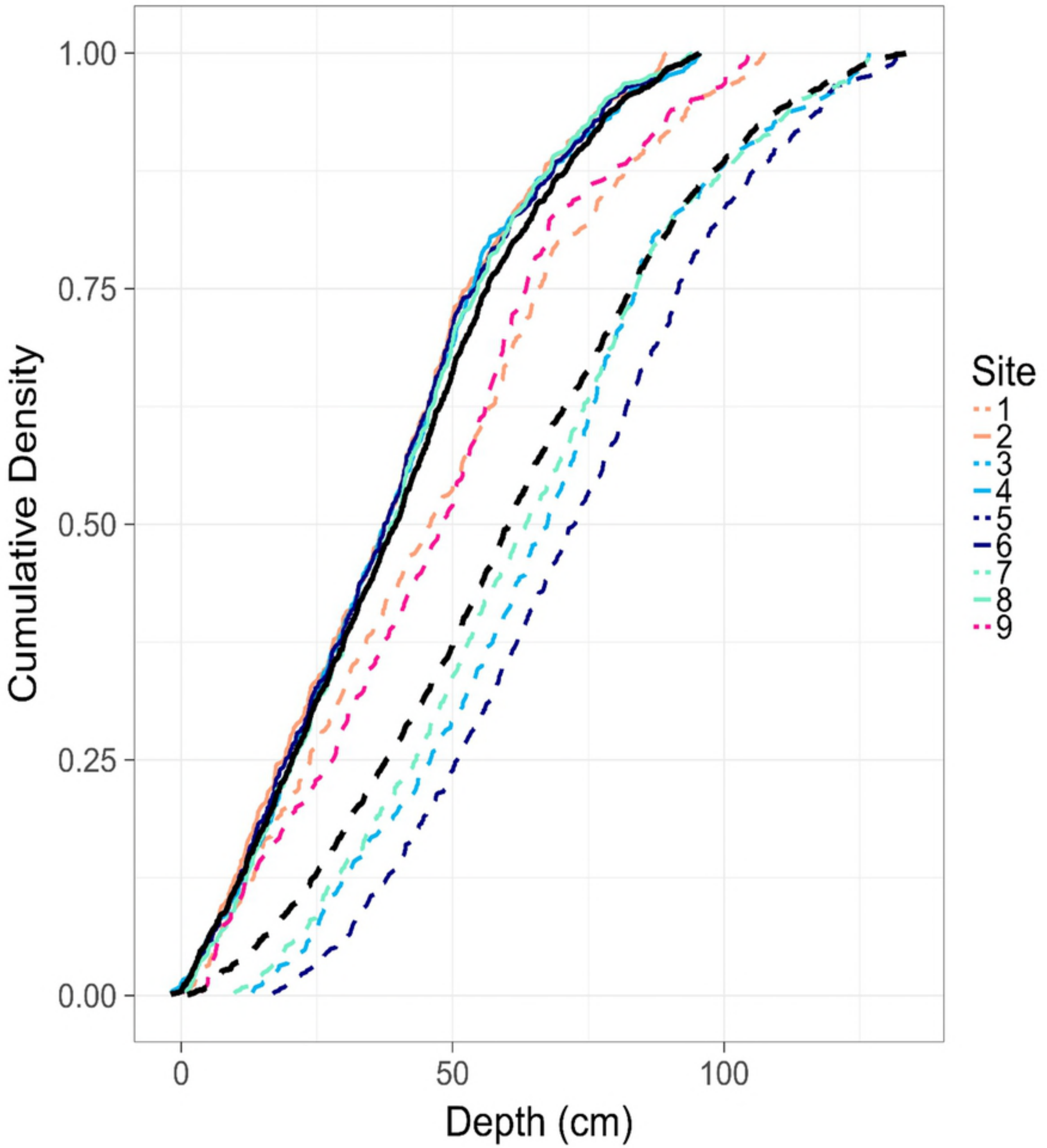
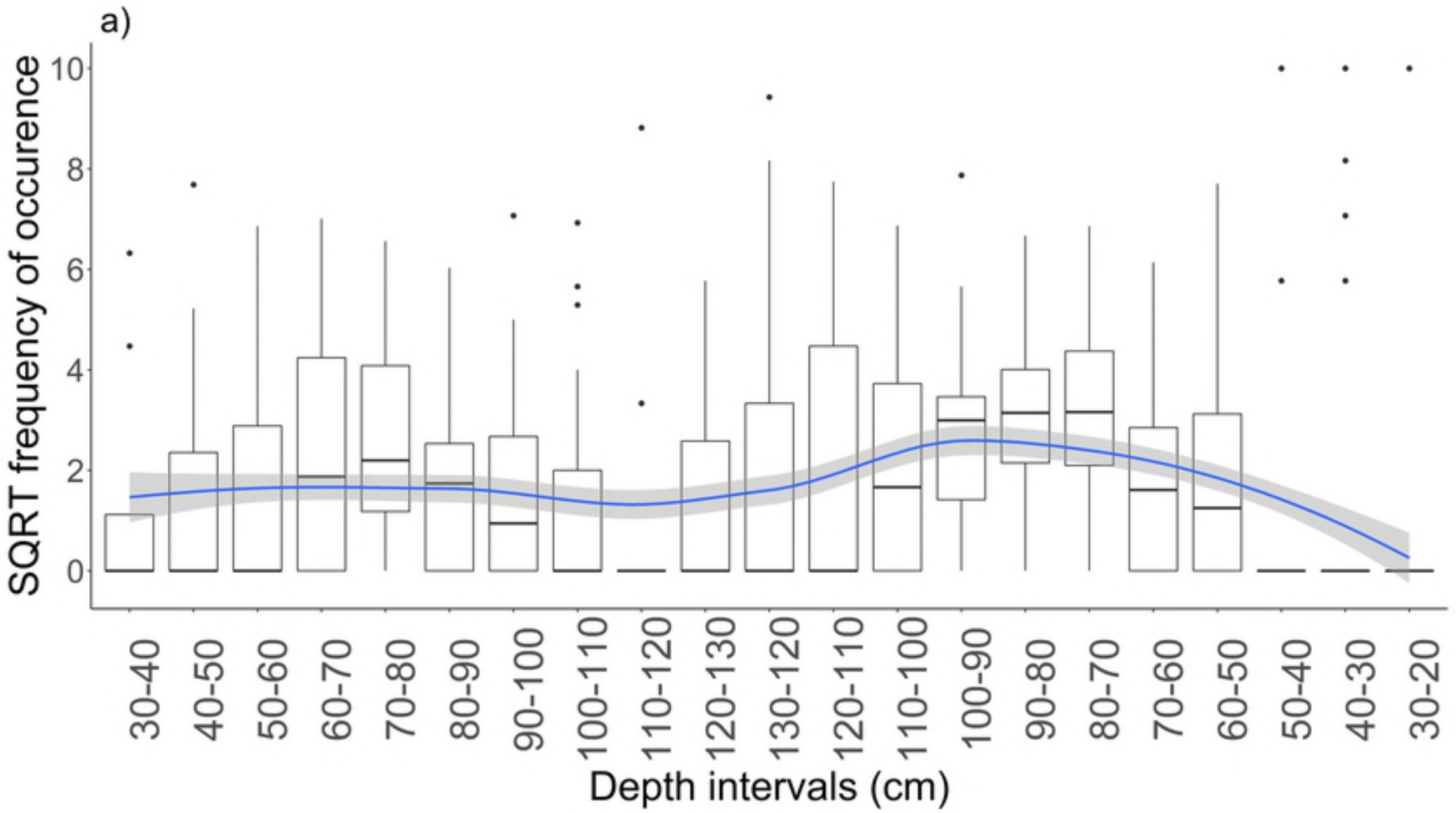

1.00
0.75
0.50
0.25
0.00
Cumulative Density
0
50
100
Depth (cm)
Site
1
2
3
4
5
6
7
8
9

Fig 3


a)
SQRT frequency of occurence
0
2
4
6
8
10
30-40
40-50
50-60
60-70
70-80
80-90
90-100
100-110
110-120
120-130
130-120
120-110
110-100
100-90
90-80
80-70
70-60
60-50
50-40
40-30
30-20
Depth intervals (cm)

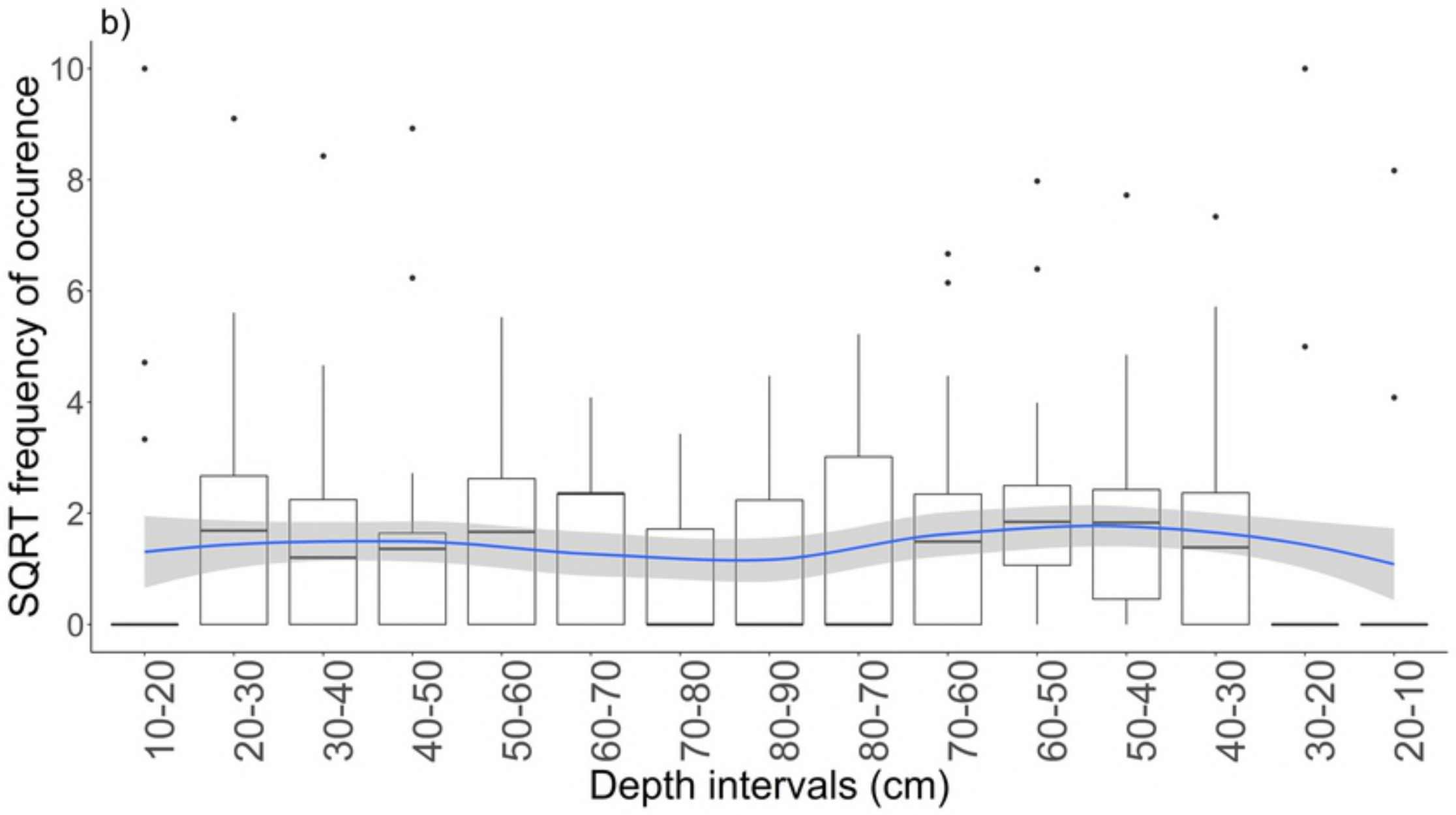

b)
SQRT frequency of occurence
0
2
4
6
8
10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
80-70
70-60
60-50
50-40
40-30
30-20
20-10
Depth intervals (cm)

Fig 4

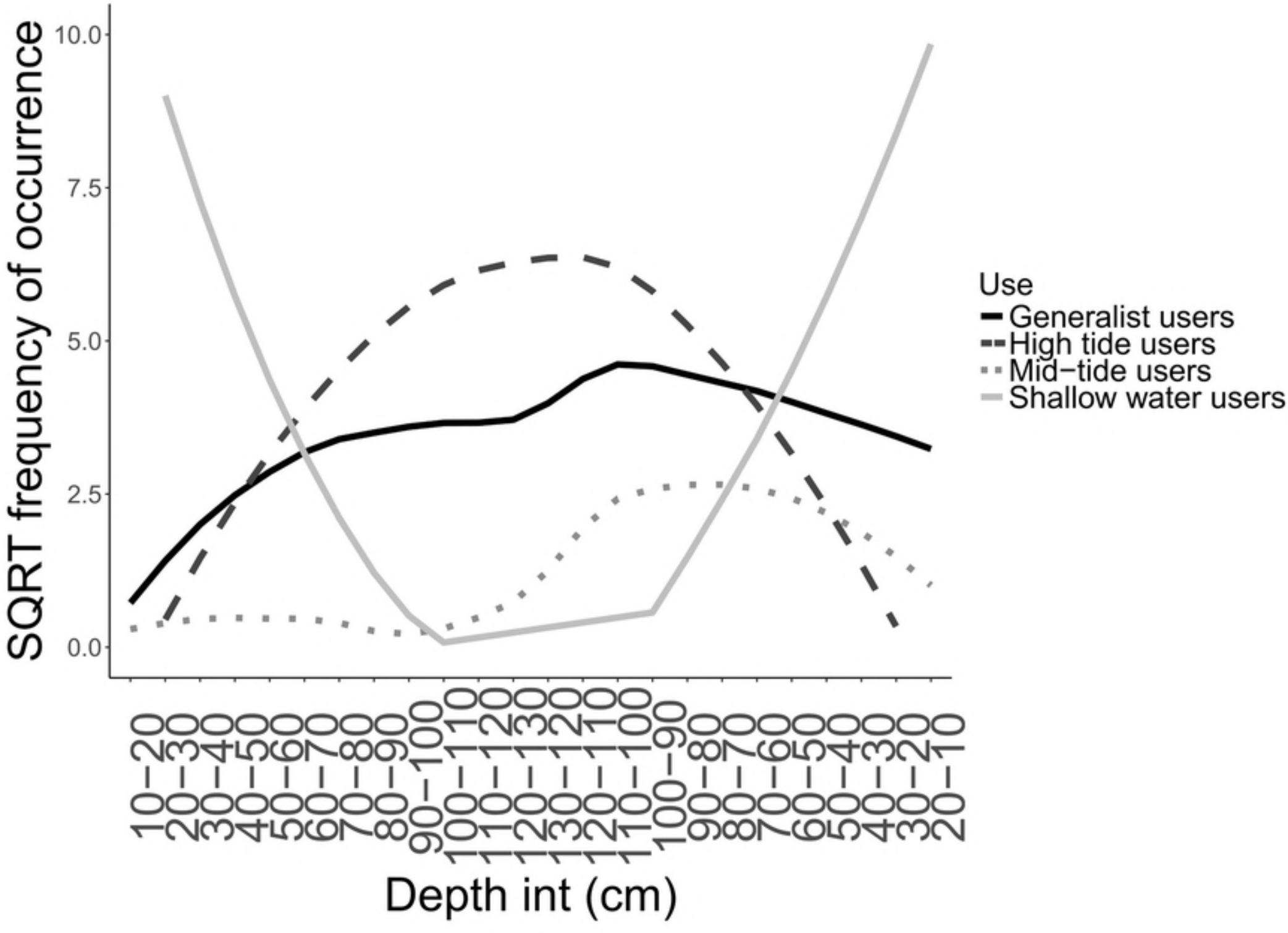

SQRT frequency of occurrence
10.0
7.5
5.0
2.5
0.0
Use
Generalist users
High tide users
Mid−tide users
Shallow water users
Depth int (cm)

Fig 5

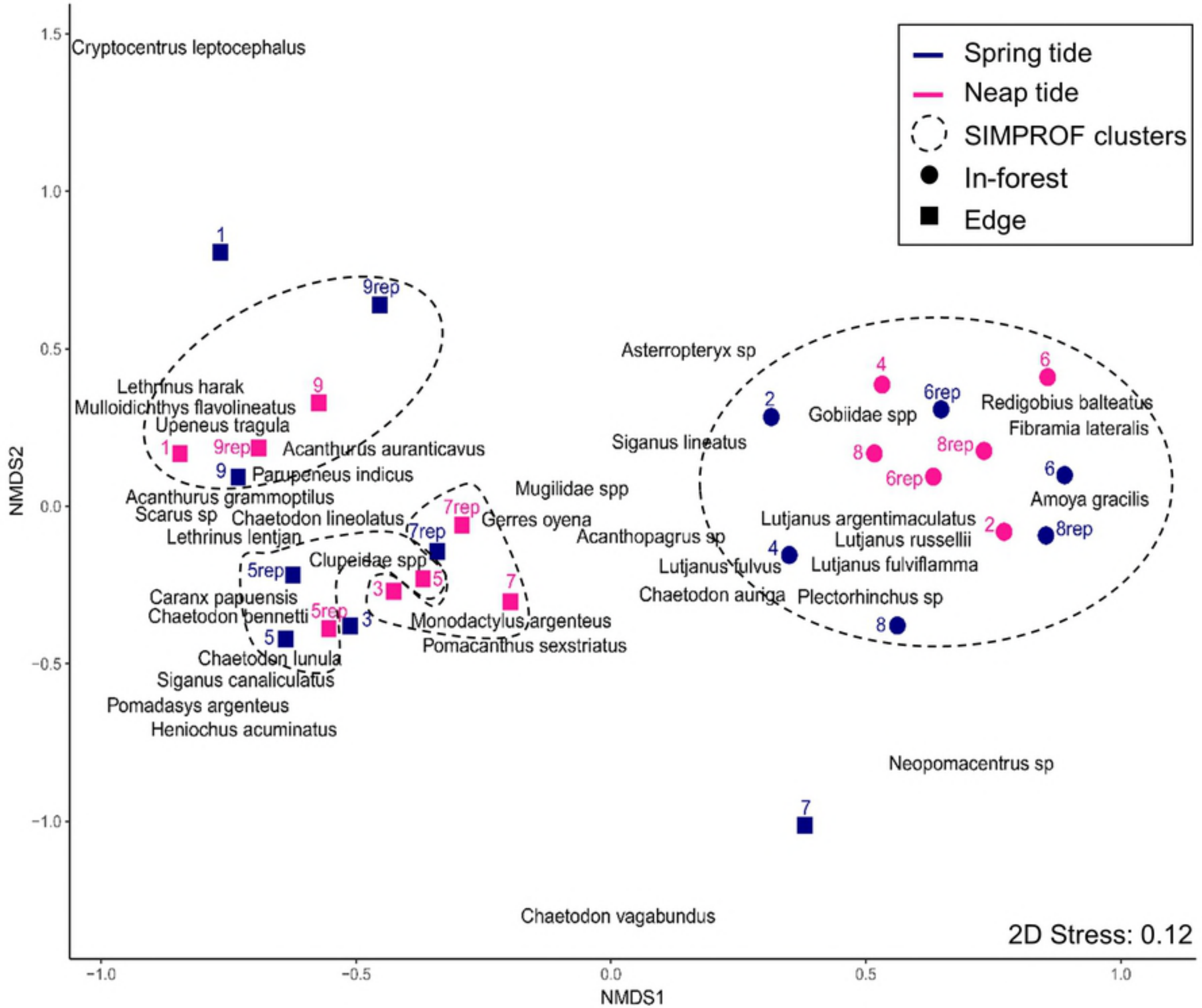

Spring tide
Neap tide
SIMPROF clusters
In-forest
Edge
Cryptocentrus leptocephalus
Asterropteryx sp
Lethrinus harak
Mulloidichthys flavolineatus
Upeneus tragula
Acanthurus auranticavus
Parupeneus indicus
Acanthurus grammoptilus
Scarus sp
Chaetodon lineolatus
Lethrinus lentjan
Mugilidae spp
Gerres oyena
Clupeidae spp
Caranx papuensis
Chaetodon pennetti
Chaetodon lunula
Siganus canaliculatus
Pomadasys argenteus
Heniochus acuminatus
Monodactylus argenteus
Pomacanthus sexstriatus
Gobiidae spp
Redigobius balteatus
Fibramia lateralis
Siganus lineatus
Amoya gracilis
Lutjanus argentimaculatus
Lutjanus russellii
Acanthopagrus sp
Lutjanus fulvus
Lutjanus fulviflamma
Chaetodon auriga
Plectorhinchus sp
Neopomacentrus sp
Chaetodon vagabundus
2D Stress: 0.12
NMDS1
NMDS2

Fig 6