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1 **Shelter use by large reef fishes: long-term occupancy and the impacts of**

2 **disturbance**

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Abstract

Large fishes often shelter beneath structures on coral reefs. While avoidance of UV radiation has been proposed as the main driver of this behaviour, sheltering behaviour has only been studied during the day and over short timeframes. Here we applied passive acoustic telemetry techniques to continuously monitor shelter usage patterns by large reef fishes over a period of seven months. For three sweetlip species (Haemulidae), one snapper species (Lutjanidae) and one surgeonfish species (Acanthuridae), diurnal shelter use was remarkably consistent, with occupation of shelters throughout the day, and under all weather conditions, suggesting that factors other than UV avoidance may be important in driving shelter use. Large-scale observations revealed that all fish species appeared to undertake long-distance migrations (>1 km) away from their shelter sites each night. With the exception of the surgeonfish *Acanthurus dussumieri*, all fishes returned to the same areas to shelter for the entire study period. Individuals of *A. dussumieri*, however, failed to return on the night of a severe tropical cyclone. They never reappeared at the shelter sites. The disappearance of this species suggests that *A. dussumieri* probably forage at night in a different location to the carnivorous haemulids and lutjanids. Overall, this study highlights the long-term importance of shelter structures for fish that may range over large areas of coral reefs.

Introduction

Large coral-reef fishes (>250 mm) often shelter beneath structures such as tabular corals, overhangs, tunnels and bommies (Samoilys 1997; Kawabata et al. 2011). Of these structures, large reef fishes appear to prefer tabular corals, which may harbour the highest biomass of fishes observed anywhere on coral reefs (Kerry and Bellwood 2012, 2015a, 2016). While these shelters are evidently important to the fishes, we are only beginning to understand the drivers of shelter use by large reef fishes. Recent studies have identified a

49 peak in shelter use by fishes at times when solar irradiance is highest, suggesting that

50 sheltering behaviour is driven primarily by UV avoidance (Kerry and Bellwood 2015b).

51 However, given the competition for space among sheltering fishes, it is likely that there are

52 other factors at play (Kerry and Bellwood 2016). To better understand the drivers of shelter

53 use, the spatial and temporal occupation patterns of large reef fishes needs further

54 investigation.

55   While avoiding solar irradiance appears to be a primary driver of diurnal shelter use

56 by large reef fishes (Kerry and Bellwood 2015b), other possible drivers may include

57 predation avoidance (Hixon and Beets 1993; Khan et al. 2016), energetic benefits by

58 avoiding hydrodynamic action (Johansen et al. 2007, 2008; Kawabata et al. 2010) or

59 behavioural adaptations to maintain social and reproductive hierarchies (Afonso et al. 2008;

60 Nanami 2015; Kerry and Bellwood 2016). Many of these potential benefits of shelter use are

61 likely to continue after dark (e.g. avoiding currents and predators). However, our knowledge

62 of shelter use is restricted to diurnal observations over a short temporal period (days to

63 weeks). For a more thorough understanding of shelter use in fishes, there is a clear need to

64 monitor shelter use over the entire 24-h circadian cycle, as well as over extensive time

65 periods, to evaluate the consistency of species' shelter occupancy patterns.

66   Tabular corals are the preferred shelter sites for large reef fishes yet these corals are

67 also highly vulnerable to disturbances including bleaching, acidification, corallivory and

68 dislodgement (Marshall and Baird 2000; Madin and Connolly 2006; Fabricius et al. 2011;

69 Goatley and Bellwood 2011; Hughes et al. 2012). The loss of tabular corals may therefore

70 have far-reaching impacts on local fish populations and on their contribution to the broader

71 ecosystem, arising from the foraging activities of day-sheltering large reef fishes. To reveal

72 broader patterns of shelter use by large reef fishes and its use in relation to foraging

73 movements, detailed 24-h long-term data are required, posing a problem for the application

74   of conventional observational field methods such as videography. A possible solution is high-

75   resolution long-term spatial data collection using passive acoustic telemetry (Heupel et al.

76   2006). In this study, therefore, we used a novel application of recent acoustic telemetry

77   techniques to investigate patterns of shelter use by large reef fishes, day and night, over an

78   extended period (7 months), which included a disturbance by a severe tropical cyclone.

79   Specifically, we sought to determine the nature and extent of shelter use in large reef fishes

80   and patterns of habitat use when not sheltering.

81

82   **Methods**

83   *Study site*

84   The two components of this study were conducted over 12 months from February

85   2015 to January 2016 in the lagoon at Lizard Island, a mid-shelf, granitic island in the

86   northern Great Barrier Reef (GBR), Australia (14°40'S 145°280'E). We focussed on an area

87   of sheltered coral reef and sand bounded by Lizard, South and Palfrey islands (Fig. 1). The

88   reef margin varied in depth from 1 to 5 m and consisted of a defined reef crest, extended reef

89   flat and no clear reef slope. The reef crest and front flat were dominated by massive *Porites*,

90   interspersed with tabular and branching *Acropora* and soft corals (Hughes et al. 2012).

91   Within this area we identified three main shelter structures which harboured mixed-species

92   aggregations of large reef fishes (Figs. 1b, 2a). These three structures were the most heavily

93   used shelter sites in the study area. There were no other large tabular corals (>40 cm

94   diameter) or crevices that housed comparable fish densities. The locations of these structures

95   were marked using a handheld GPS and they were used as focal sites for the long-term study.

96

97   *Acoustic telemetry*

98   A total of 35 individual fish were caught at the three focal sites by divers using barrier

99   nets. Five species from three families were caught and tagged: 10 *Lutjanus carponotatus*

100   (total length [TL] 250–335 mm) (Lutjanidae); 10 *Plectorhinchus lineatus* (TL 370–540 mm);

101   5 *P. gibbosus* (TL 425–500 mm*); 2 P. chaetodonoides* (TL 570–580 mm) (Haemulidae); and

102   8 *Acanthurus dussumieri* (290–390 mm) (Acanthuridae). The first four species are probably

103   carnivorous (Randall et al. 1997; Frisch et al. 2014), while the latter is nominally

104   herbivorous/detritivorous (Choat et al. 2004; Clements et al. 2009; Cheal et al. 2012). These

105   fishes were selected as they are commonly found sheltering under tabular structures (Kerry

106   and Bellwood 2015a) and the number of fishes tagged reflected their relative abundances in

107   the focal shelter sites. Visual estimates suggested that these numbers represented

108   approximately 10% of *L. carponotatus*, 70% of *P. lineatus*, 75% of *P. chaetodonoides,* 50%

109   of *P. gibbosus* and 70% of *A. dussumieri* individuals using the shelters.

110   Fish were transported to Lizard Island Research Station and held in 3600-L holding

111   tanks. Individual fish were then anaesthetised using MS-222 (tricaine methanosulphonate;

112   0.12 g L^{-1}), and a small acoustic transmitter (Vemco V7-4x, random delay interval 190–290

113   s, power output 146 dB re 1 μPa at 1 m) was inserted into their peritoneal cavity through a

114   small incision. The incision was closed with a single surgeon's stitch using absorbable

115   sutures and treated with povidone iodine antiseptic to prevent infection. Tagged fish were

116   held for at least 12 h after tagging to ensure recovery before being released at their capture

117   location. Surgical procedures followed Welsh and Bellwood (2012).

118   For the first seven months of the study, an array of 18 passive acoustic receivers

119   (Vemco VR2W, 16 kHz) was deployed to monitor shelter use by the fishes. In this array, 13

120   receivers were placed close to or within shelter structures along the reef crest. The remaining

121   five receivers were positioned on the sand parallel to the reef crest, roughly 20 m from the

122   reef edge (Array One; Fig 1b). After seven months, data downloaded from the receivers

123   indicated very few nocturnal detections on any receiver. To better investigate the nocturnal

124   spatial ecology of the fishes, the acoustic array was redeployed for a further 5 months in a

125   broader configuration encompassing the study site and the large adjacent reef flat (Array

126   Two; Fig. 1c). One receiver from Array One was not redeployed as it malfunctioned during

127   the preceding months. Three receivers were left in their original positions at each of the main

128   shelter sites to continue to record patterns of diurnal shelter use.

129

130   *Verification of telemetry results*

131   To test the utility of passive acoustic telemetry techniques for monitoring fine-scale

132   movement patterns we tested the ranges of the acoustic receivers in Array One, then verified

133   these results using visual and video censuses of fishes on the reef. First, to compare detection

134   ranges between shelters and sand habitats, a standard range-testing protocol was implemented

135   following Welsh et al. (2012; see electronic supplementary material, ESM). Second, to

136   determine the extent to which fishes remained under or near the shelters, fish were counted

137   around the reef edge shelters and on the adjacent sand habitat. A series of 20×5-m transects

138   were conducted at multiple shelter sites within the array. The acoustic receiver at each shelter

139   site was used as the start point of each transect, and only fish in tagged families were

140   counted: Haemulidae (sweetlips and grunts); Acanthuridae (surgeonfishes) and Lutjanidae

141   (snappers). Transects were run over two habitat types from the focal shelter site: along the

142   reef; and perpendicular to the reef over the sand. All fish from the relevant families were

143   counted and the distance from the shelter recorded to the nearest metre. Transects were

144   undertaken by two divers on SCUBA. Starting at the focal receiver, the divers swam away

145   from the shelter site and focal receiver, with one diver recording any fish observed and their

146   distance along the transect, and the other laying the transect tape. In total, 28 transects were

147   conducted over the sand habitat, and 16 along the reef.

148   To quantify the nature and extent of shelter use without potential diver disturbance

149 (Dickens et al. 2011), cameras were used to record the extent of fish movement. The purpose

150 of filming was to examine whether the telemetry data corresponded with fish presence under

151 the shelters. Focal shelter structures were filmed using multiple GoPro cameras attached to

152 small dive weights. Shelters were filmed between 1000 and 1400 hrs over seven consecutive

153 days. The first hour of footage each day was excluded from any analysis to allow fish to

154 resume normal behaviour after being disturbed by camera deployment. The presence of

155 individual fishes of relevant species was then recorded along with the amount of time that

156 each individual spent in the shelter. Fish counts and video methods were used to provide

157 independent validation and accurate high-resolution estimates of fish position and shelter use

158 when they are within the detection range of a receiver.

159   Several studies have suggested that the ability of receivers to successfully detect an

160 acoustic signal can fluctuate in response to both the time of day and the moon phase (Payne

161 et al. 2010; Currey et al. 2015). This variation is most often attributed to an increase in

162 crustacean activity during nocturnal periods which causes interference with acoustic signals

163 (Payne et al. 2010). To account for diel and lunar variation in detection capability, three fixed

164 delay tags (Tag V7-4x, random delay interval 500–700 s, Vemco) were deployed within the

165 study site (one per main shelter site) in January 2016. These sentinel tags were then left to

166 transmit for six to nine months. Detection data from the sentinel tags was separated into the

167 average number of detections per hourly bin and was then used to standardise detections

168 throughout the study period, i.e. to allow for any time-of-day variation in detection

169 probability (Payne et al. 2010) (ESM).

170

171 *Data analysis*

Telemetry data and detection plots were inspected in Vemco VUE software (Vemco, Halifax, Canada), and any spurious detections were removed prior to analysis (Simpfendorfer et al. 2015). Three fishes (one *L. carponotatus*, one *P. chaetodonoides*, and one *A. dussumieri*) displayed a potential mortality event (PME) within the first 30 d of the study and were excluded from the analyses (Khan et al. 2016). To identify the daily activity of each fish over the first seven months (Array One) individual detection plots were examined in VUE. Daily detections were then separated into hourly bins, and averaged per species for each hour of the day across the seven months Array One was in place. To account for the slight differences in detection probability due to diel rhythm and tag collisions, standardised detection frequencies per hourly bin were calculated from the control (sentinel) tags and were used to standardise fish detections following Payne et al. (2010). The mean detection frequencies of each fish species were then compared between day (0600–1800 hrs) and night by summing the mean detection frequencies per hourly bin using chi-squared goodness of fit tests (Payne et al. 2010). VUE was then used to assess the distribution of nocturnal detections in Array Two. The nocturnal detections of each individual fish were examined; however, the limited data was insufficient for further, formal analysis. Only data from Array One was used for analysis of daily activity of each fish. Data from Array Two was used to explore the extent to which nocturnal behaviour occurred beyond the region covered by Array One. The nocturnal behaviour of the fishes and the nocturnal data collected in Array Two are discussed in more detail in the ESM.

Impacts of Tropical Cyclone Nathan

To assess the impact of Severe Tropical Cyclone Nathan, a category four cyclone that passed Lizard Island on 20 March 2015, we accessed wind speed and direction, temperature, and rainfall data from the Australian Institute of Marine Science weather station adjacent to

197   our study site in the lagoon at Lizard Island (www.aims.gov.au/docs/data/data.html). We then

198   compared the residency of shelters by tagged fishes before, during, and after this disturbance.

199

200   **Results**

201   *Acoustic telemetry and shelter use*

202   While the detection ranges of the receivers were larger than the shelters (working

203   detection range = 52.1 m across the sand, 30.5 m along the reef and 5.8 m across the reef flat;

204   ESM), the visual and video censuses revealed that the fish species tagged in this study were

205   rarely observed more than 2 m from a focal shelter (ESM). Specifically, monitored fishes

206   spent $74.5 \pm 8.7\%$ of the video observation period in a small field of view within shelter sites

207   (Fig. 2a; ESM). Therefore, we determined that fishes detected by receivers in any of the main

208   shelter sites were most likely to be close to or within the shelters.

209

210   *Diel patterns of shelter use and residency*

211   A total of 1,190,550 successful detections were recorded for the five species over the

212   12-month study period (using both array designs). In Array One, all five focal species

213   showed consistent diurnal shelter use, and all shared a similar pattern of hourly detections

214   over the 24-h period (Fig. 2b). All species had significantly higher mean detection rates

215   during the day than during the night (χ^2, $p < 0.001$ in all cases; ESM Table S1). One *P.*

216   *chaetodonoides* and one *L. carponotatus* suffered a PME after a very short period and were

217   excluded from the analyses. Also, all but one of the surgeonfish *A. dussumieri* were detected

218   only for the first 32 d of the study. This species is therefore excluded from the main analysis

219   and is discussed separately below.

220   For the four focal species (*L. carponotatus*, *P. lineatus*, *P. chaetodonoides*, and *P.*

221   *gibbosus*), the diurnal patterns were remarkably consistent over the monitored 7-month

period. By contrast, nocturnal detections were almost non-existent. Detections were particularly low during the night, with only 0–2 detections h^{-1} for all individuals of all four species combined (using both arrays). Over the seven months, 11.4% of detections were made during the night period in Array One, and 12.6% in Array Two. However, these nocturnal detections displayed no clear patterns in any species (ESM Table S2). Furthermore, 58% and 85% of all nocturnal detections in Arrays One and Two, respectively, were from the two main diurnal shelter sites (Fig. 3). Thus these 'nocturnal' detections are primarily the result of some fish occasionally remaining in the diurnal shelter locations for a short while in the early evening before they left for the night (ESM Table S2). The low overall number of nocturnal detections indicates that individuals were leaving the detection range of both arrays during this period (ESM).

All four species displayed a rapid increase in average hourly detections during the morning crepuscular period (0500–0700 hrs) followed by relatively consistent hourly detections throughout the day. All four species maintained high numbers of detections during the day with only minor variation. *Plectorhincus chaetodonoides* and *P. gibbosus* had their highest detection rates in the morning between 0600 and 0900 hrs, followed by a smaller peak in the late afternoon between 1500 and 1700 hrs. By contrast, *L. carponotatus* and *P. lineatus* displayed a similar pattern but with the highest peak in detection in the late afternoon, and second highest in the morning period (Fig. 2b). Notably, none of the fishes experienced their highest detection rates during the middle of the day. The pattern of hourly detections in the evening crepuscular period mirrored that of the morning; hourly detections rapidly declined between 1700 and 1900 hrs. There was minimal variation among individuals within each species in the pattern of detections throughout the day (ESM).

Acanthurus dussumieri and Tropical Cyclone Nathan

247 57,582 of the successful detections were for the eight *A. dussumieri* individuals. One

248 individual experienced an early PME and was discounted from the study. The remaining

249 seven individuals displayed high diurnal residency within shelter sites and quickly left the

250 array during the evening crepuscular period (Fig. 2b). This pattern was consistent among

251 individuals and similar to the other species examined. However, *A. dussumieri* individuals

252 tended to display slowly increasing detection rates from 2400 to 0500 hrs rather than the

253 rapid increases in the crepuscular period displayed by the other large reef-fish species.

254 Six of the seven individual *A. dussumieri* experienced PMEs after 32 d of the study.

255 This disappearance coincided with Tropical Cyclone Nathan passing over the lagoon (Fig. 4).

256 The fishes left the shelter at sunset as on previous days, but were not recorded the following

257 morning, nor at any time in either array over the following 11 months. On the night of the

258 cyclone, the highest intensity winds exceeded 180 km h^{-1} and were recorded at approximately

259 0300 hrs (Fig. 4b). While most *A. dussumieri* failed to return after the cyclone, the focal

260 shelter sites were not visibly damaged and remained in use by the four other species for the

261 remainder of the study period (Fig. 4). The one *A. dussumieri* detected in the array after the

262 cyclone had not been detected for 30 d prior to the cyclone and was only re-detected

263 sporadically after 18 d following the cyclone.

264

265 **Discussion**

266 ***Shelter use by large fishes***

267 The results identified a clearly defined long-term (7-month) diel pattern of shelter use

268 in large reef fishes. The diel patterns of shelter use are in partial concordance with the solar

269 irradiance hypothesis (Kerry and Bellwood 2015b) in that the abundance of large reef fishes

270 under shelters at night is very low. However, details in the diurnal use patterns suggest that

271 there may be other factors driving shelter use in addition to solar irradiance. All tagged

species displayed sedentary diurnal behaviour, which was initiated in the dawn crepuscular period. This suggests that avoiding solar irradiance is not the sole driver of shelter use, as irradiance is lowest in the early morning and late evening (Kerry and Bellwood 2015b). It is also evident that the large reef fishes examined are not likely to be responsible for the midday peak in fish abundance found by Kerry and Bellwood (2015b), as they are present throughout the day. This suggests that solar irradiance may be more important in other reef-fish species that opportunistically use shelters only during the middle of the day. It is possible that large tabular shelter structures provide multiple important services to different groups of reef fishes and, given their high rates of occupancy, large reef fishes may be particularly reliant on these structures for other services [such as hydrodynamic advantages or predation avoidance (Johansen et al. 2008; Kawabata et al. 2011)] during the entire diurnal period.

This strong association between large reef fishes and shelters was not found at night. Based on previous studies it was initially expected that large reef fishes would use shelters during the day and move to nearby sandy lagoonal foraging areas in the evening (Nagelkerken et al. 2000; Appeldoorn et al. 2009; Fox and Bellwood 2011). For example, at Lizard Island, rabbitfish *Siganus lineatus* remain stationary on the reef edge during the day, and forage on the adjacent sand habitat during the night (Fox and Bellwood 2011). Similarly, in the Caribbean, Beets et al. (2003) found that haemulids occupied reef shelters during the day then migrated to adjacent sand and seagrass habitats at twilight. Array One demonstrated that large reef fishes did aggregate in shelters during the day, but they did not use the adjacent sandy habitat at night. Not only were tagged fishes not detected away from shelter sites at night, they were not detected anywhere within the study site. The five sand receivers had a working detection range of more than 60 m out onto the sand, and a maximum detection distance of over 100 m (ESM Fig. S2). The working detection range of the receivers in Array One would thus have easily encompassed the entire home range previously

297 described for the nocturnal foraging *S. lineatus* at Lizard Island (Fox and Bellwood 2011)

298 (ESM Fig. S8. Thus, it can be reasonably assumed that if the tagged fishes were foraging

299 over sand anywhere within the study site they would have been detected.

300   The purpose of Array Two was to examine whether fish migrate away from sites

301 along the reef margin, use adjacent sand areas elsewhere in the lagoon, or if they move on to

302 the adjacent reef flat. There was no evidence that the tagged fishes exhibited any of these

303 behaviours. There are three possible explanations for the low nocturnal detections. First, it is

304 possible that noise from the environment interfered with the detections (Payne et al. 2010).

305 However, long-term range-testing indicated that there were no substantial differences in

306 detection probability between diurnal and nocturnal periods (ESM), which conforms to

307 previous findings on the GBR (Welsh et al. 2012). Second, it is also possible that these fishes

308 make crepuscular migrations to other locations within the lagoon, most likely to foraging

309 areas (Appeldoorn et al. 2009). However, the lack of tag detections indicating

310 consistent/recurrent crepuscular transit to other lagoonal sites suggests that these fishes do

311 not stay within the boundaries of the lagoon. A third possibility is that the fishes remain

312 within the study site but remain largely undetected, which implies that they are foraging on

313 the reef flat itself, and thus outside of the (reduced) detection range of receivers over this

314 habitat type. Detection patterns from Array Two showed that three individuals were

315 occasionally detected during the night at receivers on the reef margin outside of the initial

316 area of Array One (ESM). However, while Array Two had a larger proportion of nocturnal

317 detections compared to Array One, nocturnal detections were only a small fraction of those

318 recorded during the day. Overall, nocturnal detections did not reveal any clear patterns of

319 nocturnal behaviour other than the absence of tagged fishes from the study site, with no clear

320 evidence of repeated or directional movement along reef edges.

321   In the Caribbean, adult haemulids display twilight migrations of 100–300 m

322   (Appeldoorn et al. 2009), and on the GBR coral trout move up to 500 m during the day

323   (Zeller and Russ 1998). However, these distances are comparable to the areas covered by the

324   two arrays, suggesting that, if the study species moved in a similar manner to the fishes in

325   previous studies, they would have been detected by both Array One and Array Two

326   throughout the 24-h period. Thus, it appears that the large reef fishes in this study may be

327   covering a much larger area than previously thought. This has implications for management

328   of large reef species in a fisheries context. In addition, it also impacts our understanding of

329   the contribution of large reef fishes to biogeochemical fluxes on coral reefs in terms of the

330   spatial extent of their contribution to trophic networks or reef energy budgets. Given the

331   potentially important role of large, carnivorous, diurnally sheltering fishes in nutrient

332   dynamics on reefs (Shantz et al. 2015), further investigation of their nocturnal movements is

333   required.

334   Our nocturnal data represented only a small fraction of any given fish's nocturnal

335   activity (precluding formal analysis such as kernel utilization distributions). Furthermore,

336   most nocturnal detections occurred at two main shelter sites, as some fishes were slower to

337   leave than others in the early evening. The clearest result from our nocturnal detections,

338   therefore, is the lack of detections, i.e. these fishes demonstrably move away from the array

339   and must disperse over broader distances at night than previously thought (Fig. 3; details in

340   ESM Figs. S7, S8; ESM Table S2).

341

342   ***Impact of Tropical Cyclone Nathan***

343   Six of the seven *A. dussumieri* not only failed to return to their regular resting areas

344   after the cyclone, but were not detected again within the study site for the remainder of the

345   12-month study period. Interestingly, no other tagged species had similar responses to the

346 cyclone despite showing similar patterns of shelter use prior to the cyclone, suggesting

347 fundamental ecological differences between *A. dussumieri* and the remaining species.

348   The main difference between *A. dussumieri* and the other species in this study is that

349 *A. dussumieri* is a detritivore/herbivore and the rest are carnivores. How this characteristic

350 makes it more vulnerable to disturbances is not clear. However, it is notable that diurnal

351 surgeonfish species at Lizard Island concentrate their feeding in exposed reef crest locations

352 (Goatley and Bellwood 2010, 2012) and that the cyclone had the greatest impact on south-

353 eastern exposed reef crests of Lizard Island. If *A. dussumieri* undertake crepuscular

354 migrations to forage at night in these areas, it is possible that they would have experienced

355 the most severe wave action during the cyclone. While we do not know where *A. dussumieri*

356 go overnight, the evidence strongly suggests that the carnivorous Lutjanidae and

357 Haemulidae forage in different and potentially more sheltered areas than the nominally

358 herbivorous/detritivorous *A. dussumieri*.

359   The fate of the six *A. dussumieri* is not known. There are four main options: they may

360 have shifted to new shelters, or died, during or following the cyclone. As large mobile fishes,

361 it seems unlikely that they died during the cyclone. Displacement and/or delayed mortality

362 seem most likely. Given their size, the *A. dussumieri* may have the ability to move

363 considerable distances. Their nocturnal movement strongly suggests that they are foraging at

364 night, probably on detritus and microalgae (Clements et al. 2009, 2017). This is the first

365 evidence of potential nocturnal foraging in an acanthurid, although it closely mirrors the diet

366 and behaviour of the only other nocturnal nominal herbivore, the siganid *S. lineatus* (Fox and

367 Bellwood 2011). These species appear to have no difficulty traversing large distances,

368 including over open sand, at night. The reasons why *A. dussumieri* leave the study area, or

369 lagoon, at night remains unclear. Presumably the algal/microbial resources used by *S.*

370 *lineatus* are not suitable for *A. dussumieri*. If this is the case, then disruption of their feeding

areas outside the lagoon may have triggered *A. dussumieri* to migrate away in search of intact

nocturnal foraging grounds. Like the giant humphead parrotfish, *Bolbometopon muricatum*

(Bellwood and Choat 2011), *A. dussumieri* may be able to move between reefs and may have

relocated elsewhere on the GBR. If so, it is noteworthy that they never returned.

Alternatively, if the six *A. dussumieri* were disturbed by hydrodynamic activity during

the cyclone they may have simply been unable to navigate back to their diurnal resting

locations due to changes in visual, auditory or olfactory signals. It is unlikely that visual cues,

as used by other surgeonfishes (Mazeroll and Montgomery 1998), are important, as most of

the movement occurred during the night, and the cyclone had little impact on the landscape

of the lagoon. There is also little evidence to suggest that auditory cues are used for

navigation by adult fishes (Simpson et al. 2008). It appears most probable that if *A.

dussumieri* were unable to return to diurnal resting locations it was most likely due to

changed olfactory cues, which are used by numerous juvenile and adult reef fishes for

navigation and may be directly affected by changing hydrodynamics (Stobutzki and

Bellwood 1998; Leis et al. 2003; Simpson et al. 2008; Bellwood et al. 2016). Returning to a

known diurnal resting location is likely to be associated with lower mortality risk (e.g.

Dahlgren and Eggleston 2000; Forrester and Steele 2004; Yoder et al. 2004; Forrester et al.

2015). Therefore, even if *A. dussumieri* were able to successfully relocate to new diurnal sites

after the cyclone, these individuals may have been more vulnerable to predation by diurnal

and crepuscular predators (Kawabata et al. 2011; Khan et al. 2016).

Regardless of the mechanisms involved, the cyclone effectively removed *A.

dussumieri* from lagoon shelters despite these shelters remaining intact. This event

emphasises the potential extent of connectivity between reef areas and the key role that

shelters and disturbances may play in shaping patterns of habitat use in reef fishes, especially

these apparently nocturnal detritus/microalgal-feeding fishes.

396   A novel application of passive acoustic telemetry revealed strongly defined diel

397   movement patterns in large reef fishes over a 12-month period. Occupation of shelter sites

398   during all daylight hours suggests that drivers other than UV avoidance are also important in

399   maintaining sheltering behaviour. Negligible nocturnal detections in both arrays suggests that

400   many large reef fishes may travel distances of more than 1–2 km each night, much further

401   than previously observed for these fish families on the GBR. Our findings highlight that

402   single aggregation sites may affect fish communities and the services they provide over large

403   areas of reef, and conversely, that disturbances away from shelter sites may affect the fishes

404   that use these structures (as seen with the cyclone). These considerations are likely to be of

405   considerable value in the design and implementation of management approaches to protect

406   nocturnal fishes and the functions they provide.

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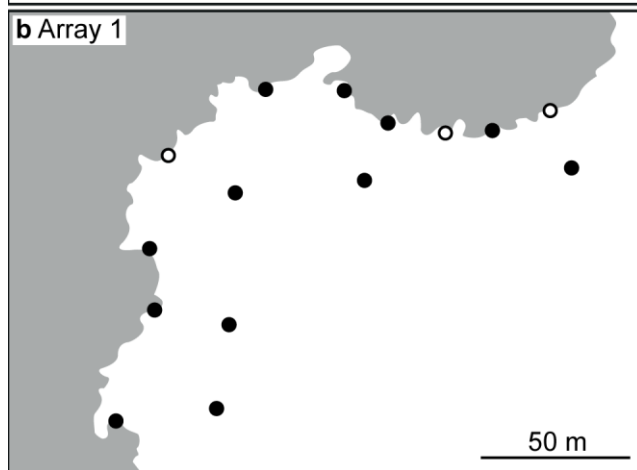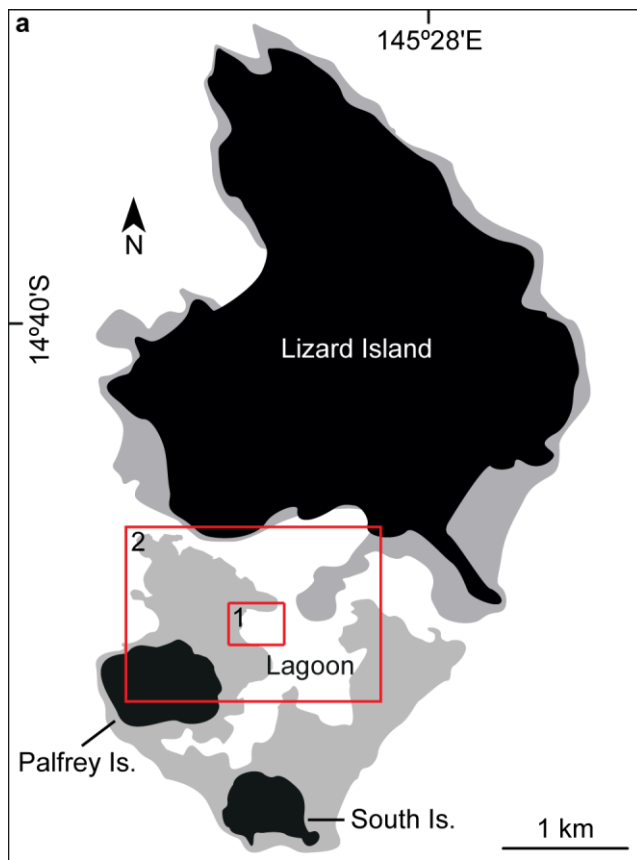
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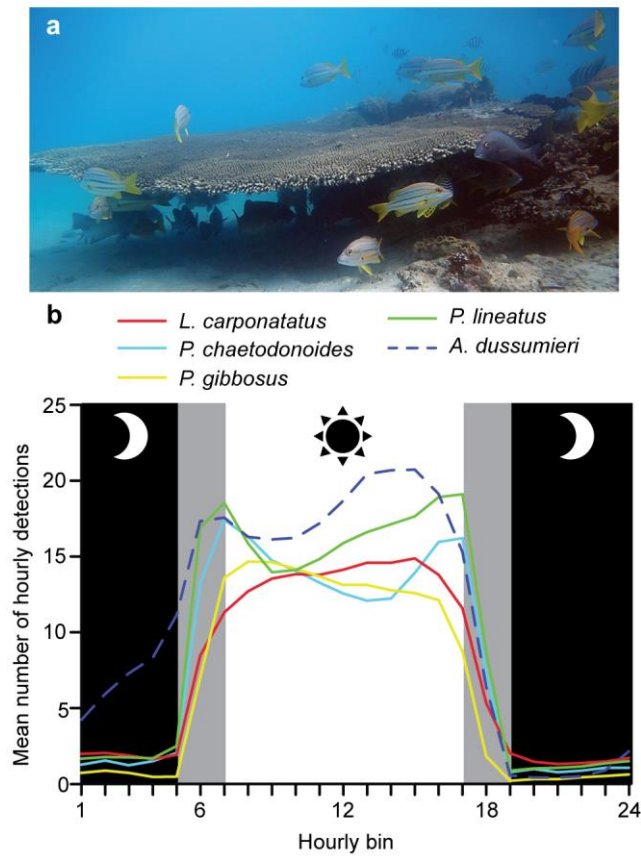
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Figures

558　**Fig. 1 a** Position of receiver in Arrays One and Two in relation to Lizard Island. **b** Positions

559　of the receivers in Array One and **c** in Array Two. *Open circles* represent the positions of the

560　three principal shelter sites. The extents of the two arrays are shown in *red*

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564　**Fig. 2 a** Reef fishes sheltering under a large plate coral in the lagoon at Lizard Island. **b** Diel

565　patterns of shelter use by five large coral-reef fishes

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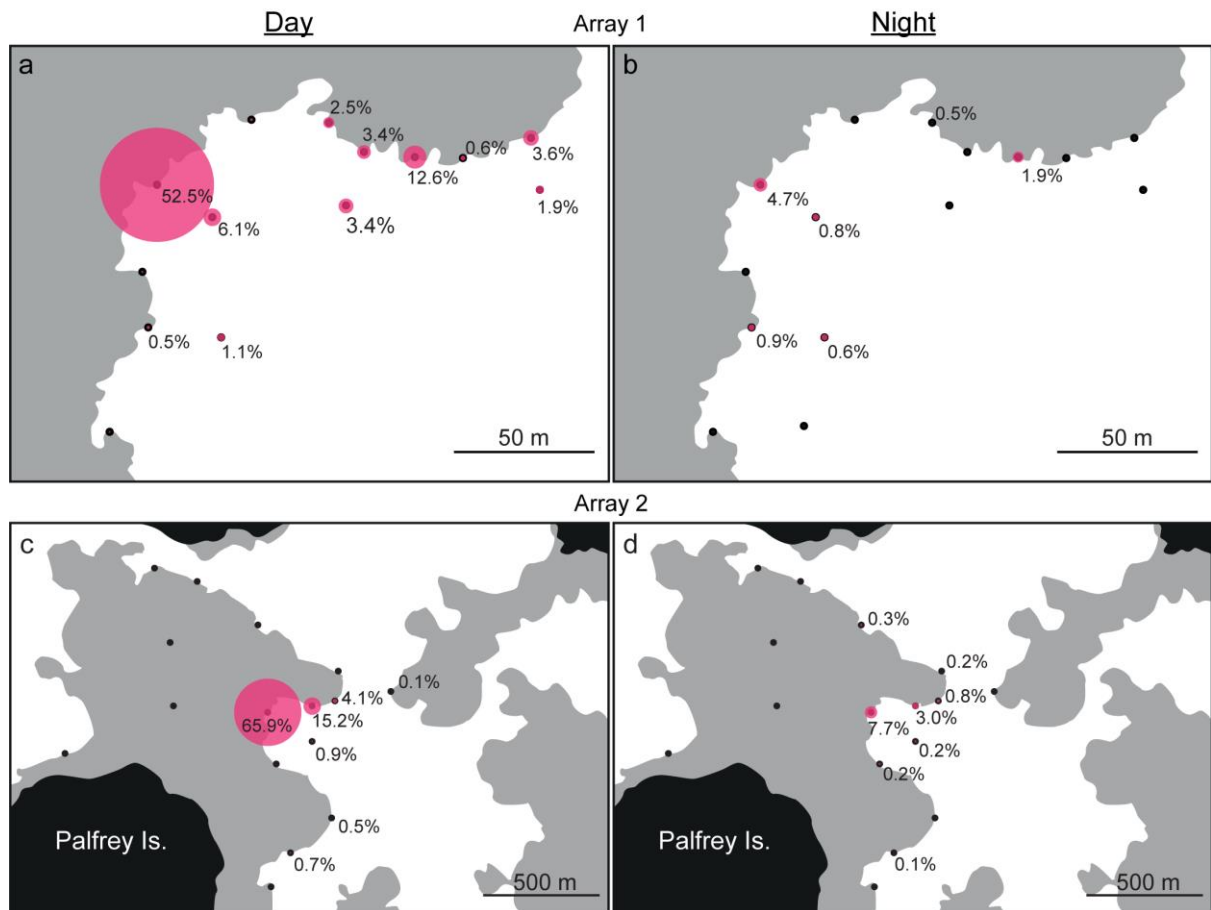
Fig. 3 Bubble plots (*pink shaded circles*) representing the proportion of total detections at each receiver (*solid black circles*) during the day (**a**) and the night (**b**) in Array One and the day (**c**) and night (**d**) in Array Two. The *size* of the circles reflects the percentage of total detections recorded at that receiver during day or night. Receivers without percentages recorded a proportion of total detections that was less than 0.5% (**a, b**) or 0.1% (**c, d**)
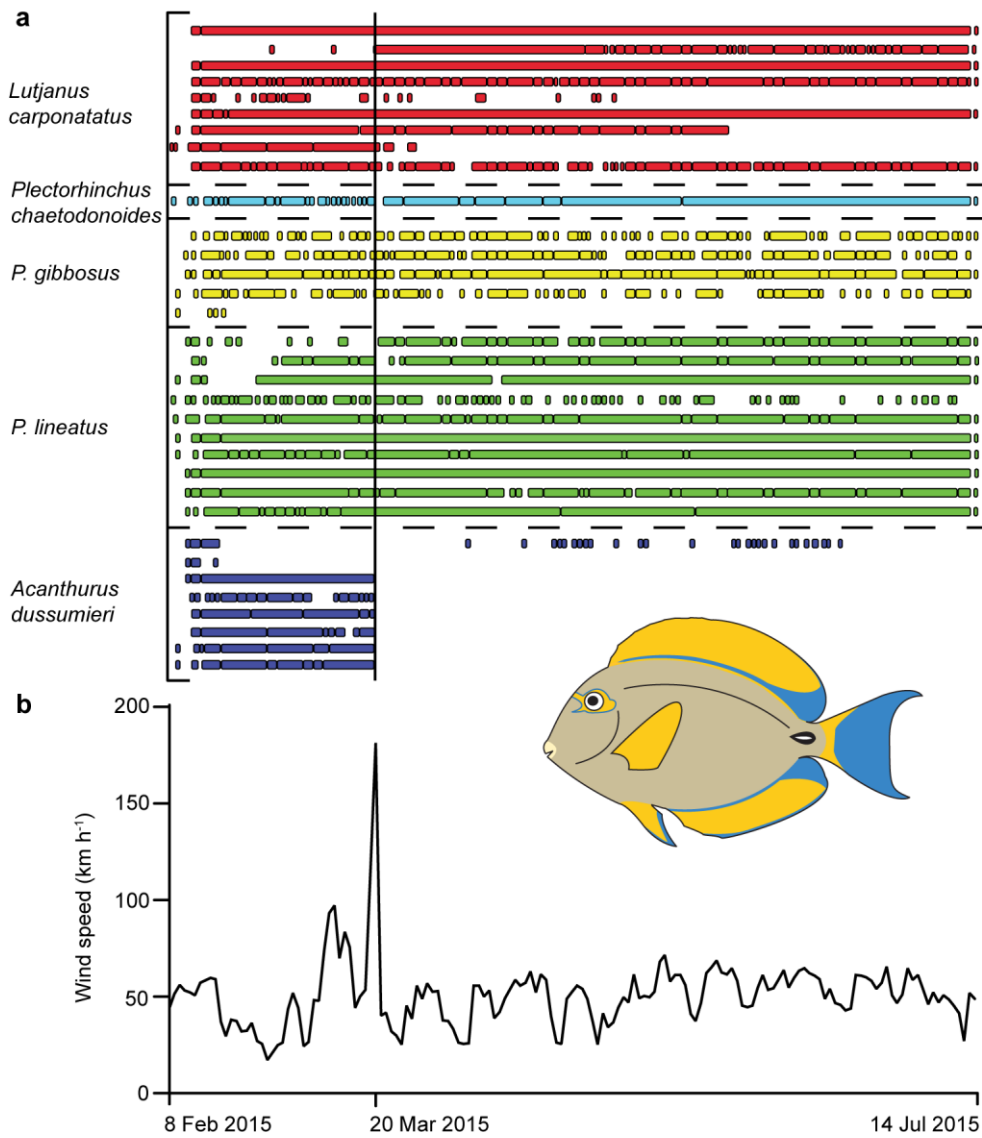
Fig. 4 a Long-term patterns in detections (from all receivers) of five large coral-reef fish species revealing the loss of *Acanthurus dussumieri* following the impact of Cyclone Nathan on 20 March 2015. **b** Maximum wind speed recordings from Lizard Island

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