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1 **Title: Within and between day variability in coral reef fish assemblages:**  
2 **implications for fish community surveys**

3 **Short running title: Short-term variability in fish communities**

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11

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## 19 **Data availability statement**

20 All data is available on Figshare: 10.6084/m9.figshare.16606442.

21 **Keywords:** reef fish, monitoring, survey, coral, community assemblage, temporal  
22 variability, diurnal patterns

## 23 **Summary**

24 Coral reef ecosystems are under increasing anthropogenic pressures making it ever  
25 more important to monitor changes in fish communities to implement appropriate  
26 management. In contrast to long-term spatial and temporal variation which has been  
27 extensively documented, little work has been carried out to identify variability in fish  
28 assemblages on short time scales, with few studies testing patterns of fish  
29 assemblages between and within days.

30 Here we investigated the diurnal changes in species richness, relative abundance and  
31 assemblage composition in a shallow coral reef fish community in Egypt. To do so, a  
32 section of coral reef was filmed during the morning (0600 hrs), midday (1000 & 1400  
33 hrs) and afternoon (1800 hrs) over eleven days.

34 Dusk (0600 hrs) and dawn samples (1800 hr) showed higher species richness  
35 compared to late morning (1000 hr) and mid-day samples (1400 hr) and borderline  
36 significantly higher numbers of total individuals, likely associated with feeding  
37 activity and predator avoidance. Assemblage composition varied across days and  
38 time-of-day, showing greater variability during dusk and dawn associated with a  
39 transition between day-time and night-time assemblages.

40 Our results have implications for designing coral reef fish surveys, emphasising that  
41 short-term changes in fish communities should be considered when designing  
42 experiments to monitor fish assemblages over time. Where possible, we suggest  
43 increasing replication within sites and time scales or randomising data within a  
44 specific time window at all sites, looking to exclude dusk and dawn.

## 45 **Introduction**

46 Anthropogenic impacts alter coral reef fish assemblages, affecting ecosystem  
47 processes (B. J. Harvey, Nash, Blanchard, & Edwards, 2018; Hoegh-Guldberg &  
48 Bruno, 2010; Hughes et al., 2017; Rice, Ezzat, & Burkepile, 2019) and functions.  
49 Knowledge of the spatial and temporal variability of coral reef fish assemblages is  
50 crucial in order to implement effective monitoring and conservation measures,  
51 preserving ecosystem processes and functions (Bellwood, Hughes, Folke, & Nyström,  
52 2004; Hughes et al., 2017; Lindenmayer & Likens, 2010). This depends on robust  
53 ecological studies and monitoring programmes that detect spatial and temporal changes  
54 in fish assemblages (Goldsmith, 2012; Ormerod, 2003; Thomas, 1996).

55 However, the spatial and temporal heterogeneity characterizing fish  
56 communities makes understanding ecological causes for changes in fish assemblage  
57 composition challenging (Levin, 1992). This requires the implementation of sampling  
58 designs that minimise sampling variance due to processes occurring at scales that are  
59 not of interest, such as within or between days (Underwood, 1991; Underwood &  
60 Chapman, 2003; Winer, 1962).

61 The spatial variability in coral fish assemblages has been studied in great detail  
62 worldwide at multiple spatial and temporal scales, including across continents  
63 (Ahmadi, Tornabene, Smith, & Pezold, 2018), regionally (Almany, 2004; Friedlander,  
64 Brown, Jokiel, Smith, & Rodgers, 2003; I. D. Williams et al., 2015, 2008), locally  
65 between (Friedlander et al., 2003; Friedlander & Parrish, 1998a; Hixon & Beets, 1993)  
66 and within coral reef systems (Dollar, 1982; Friedlander & Parrish, 1998b; Friedlander,  
67 Sandin, DeMartini, & Sala, 2010) on short (Birt, Harvey, & Langlois, 2012; Bond et  
68 al., 2018; Santos, Monteiro, & Gaspar, 2002) and longer time scales (Santos, Monteiro,  
69 & Lasserre, 2005; Jan, Chen, Lin, & Shao, 2001). The large majority of studies

70 published on fish assemblages at large and medium scales are on based sampling with  
71 a single survey effort per site at one time during the day or at night (Choat, Ayling, &  
72 Schiel, 1988; Gust, Choat, & McCormick, 2001; Santos et al., 2002; Willis, Millar, &  
73 Babcock, 2000). Finer-scale temporal variability, in particular daytime changes,  
74 remaining less well understood.

75         The environmental conditions within coral reefs can fluctuate dramatically  
76 throughout the day (Guadayol, Silbiger, Donahue, & Thomas, 2014; Potts & Swart,  
77 1984; Santos et al., 2002), impacting behaviour and subsequent distribution of coral  
78 reef assemblages (Bond et al., 2018; González-Sansón, Aguilar, Hernández, Cabrera,  
79 & Curry, 2009; Hammerschlag, Heithaus, & Serafy, 2010). Much of the prior work on  
80 finer-scale temporal variability in fish assemblages has focussed on shifts in behaviour,  
81 distribution and reef fish abundance between diurnal (daylight hours) and nocturnal fish  
82 assemblages, documenting well-defined crepuscular change over periods (Colton &  
83 Alevizon, 1981; Rooker & Dennis, 1991; Starck & Davis, 1966). In contrast, variability  
84 within and between days has attracted less attention (Colton & Alevizon, 1981; Rooker  
85 & Dennis, 1991; Starck & Davis, 1966), despite its potential to confound abundance  
86 and density estimates in reef fish surveys (Spyker & Van Den Berghe, 1995). Studies  
87 investigating diurnal fish assemblage changes found evidence for differences in the  
88 abundance of some fish species within days, but generally not between days (Colton &  
89 Alevizon, 1981; Rooker & Dennis, 1991; Santos et al., 2002). Willis (2006) found  
90 diurnal differences in the density of some fish species, but not in assemblage  
91 composition. Diurnal variation is likely the result of behavioural adaptations, including  
92 foraging (Hammerschlag et al., 2010; Ogden & Buckman, 1973), predator avoidance  
93 (R. J. Fox & Bellwood, 2011; Wolf, 1985) and spawning (Colin, 1978; Samoilys,  
94 1997). Feeding times in fish vary diurnally (Polunin & Klumpp, 1989), in particular in

95 herbivorous species, which exhibit marked feeding activities associated with time  
96 periods when algae have the greatest nutritional value (Hobson, 1973; Zemke-White,  
97 Choat, & Clements, 2002), and in zooplanktivorous species, associated with currents  
98 delivering plankton (Bray, 1980; Kingsford & MacDiarmid, 1988). This evidence  
99 suggests that diurnal, rather than between-day variation impacts fish assemblage  
100 composition.

101 Here, we used video imagery surveying a coral reef in Egypt to investigate  
102 whether species richness, number of individuals and community composition varied  
103 within and between days. Based on prior work (e.g. Colton & Alevizon, 1981; Santos  
104 et al., 2005; Rooker & Dennis, 1991; Spyker & Van Den Berghe, 1995; Willis et al.,  
105 2006), we predicted that there will be differences in fish assemblage composition within  
106 days, but less so between days, with certain groups of species such as herbivores species  
107 showing diurnal patterns in relative density.

## 108 **Materials and methods**

109 This study was conducted at three sites at the house reef at the Roots Camp,  
110 approximately 13km north of the town of El Quseir, Egypt (26.2062°N, 34.2195°E) in  
111 July 2014. The three sampling sites, characterised by similar benthic composition,  
112 featuring south sloping reef walls enclosing a central sandy inlet allowing inshore  
113 access dominated by *Acropora* and *Pocillopora* at a depth of 5-7m, similar to reefs  
114 described in the area prior (Alexandroff, Zuschen, & Kroh, 2016). The sites were  
115 located south of the entry point along the reef line at a distance of 250m from each  
116 other, representing a typical section of the reef.

## 117 **Experimental design and data collection**

118 Data was collected using video at 0600-0700 hrs, 1000-1100 hrs, 1400-1500 hrs  
119 and 1800-1900 hrs. Sampling day was included as a factor to account for between-day

120 variability in community composition. Thus, the experimental design was a three-factor  
121 design including day (integer) and time-of-day (categorical, four levels: 0600, 1000,  
122 1400 and 1800 hrs) and site (categorical, three levels). At the time that the study was  
123 carried out, sunrise was approximately 0454 hr and sunset was approximately at 1834  
124 hr at the start of the sampling period.

125         The video system deployed consisted of a mount using 50mm diameter PVC  
126 pipe holding a GoPro (Hero 3+ Black) camera at a 90-degree angle approximately 15cm  
127 above the sandy bottom of the reef at an average depth of six meters. Defining the area  
128 or volume that is ultimately sampled using video recordings is a key challenge (E. S.  
129 Harvey & Shortis, 1998; Willis & Babcock, 2000). To avoid over or underestimating  
130 the sampling area, the camera was positioned two metres away from the reef wall on  
131 the sandy bed, allowing us to confidently identify species in the naturally enclosed  
132 sampling area of a volume of approximately 8.38m<sup>3</sup>. On each day for 11 days, one  
133 surveyor placed the camera onto the mount and started recording. Different sites were  
134 recorded each day (n=8), after being randomly selected. Once recording began it was  
135 left *in situ* for 30 minutes; the first 10 minutes of footage were excluded to allow any  
136 disturbed fish to settle and the 20 minutes of footage after this was then used for the  
137 analysis.

138         The video footage was subsequently downloaded to a computer and trimmed to  
139 exclude any unwanted footage such as deployment. Where possible the individuals  
140 were identified down to species level by two researchers. In order to eliminate repeat  
141 counts of fish in the field, maximum number of individuals of the same species  
142 appearing in the field of view (MaxN) over the whole 20 min of filming was recorded,  
143 providing a conservative estimate of fish density recorded (Cappo, Harvey, Malcolm,  
144 & Speare, 2003; E. S. Harvey, Cappo, Butler, Hall, & Kendrick, 2007).

## 145 **Statistical analysis**

146           Levene's test (J. Fox, 1997) was used to analyse sample variance for the total  
147 number of individuals and species richness for the factors time-of-day and site using  
148 the `levene.test` function in the `car` package in `r` (J. Fox, 1997). Multivariate dispersions  
149 between groups, a multivariate equivalent of Levene's test for homogeneity in variance  
150 (Anderson, 2001), were analysed using the `betadisper` routine in the `vegan` for  
151 assemblage composition (Oksanen et al., 2013). Permutational multivariate analysis of  
152 variance (PERMANOVA with 9999 permutations) was used to analyse differences in  
153 fish assemblage composition at the four time intervals, between days and sites using  
154 the `adonis2` function in `vegan`, based on square-root transformed assemblage  
155 composition data (Anderson, 2001) following the three factor design described above.  
156 Permutational distance-based approaches are appropriate for analysing abundance data  
157 that have many zero counts and are highly skewed (Anderson, 2001; Watson, Harvey,  
158 Anderson, & Kendrick, 2005). The data were square-root transformed and analysed  
159 using a Bray-Curtis dissimilarity matrix adding a dummy variable. Pairwise tests were  
160 run between the significant groups using permutation tests of group mean dispersions  
161 (Anderson, 2006; Anderson, Ellingsen, & McArdle, 2006) in `vegan`.

162           Univariate analyses were conducted on species richness, the total number of  
163 individuals and the relative abundance of individual species using the `adonis2` function  
164 on Euclidean distance (see above) square-root transformed.

165           Differences in community composition were assessed using a non-metric  
166 multidimensional scaling plot (NMDS) for all videos using Bray-Curtis dissimilarity  
167 index on square-root transformed abundance data (Kruskal, 1964). The overlaid vectors  
168 indicate significant correlations among the relative abundances of species on the two  
169 axes of the NMDS using the `vegan` package (Oksanen et al., 2013; Oksanen, Kindt,



170 Simpson, & Oksanen, 2018). Vectors of species contributions to beta diversity (species  
171 contribution to beta diversity) were computed, providing an insight into which species  
172 contributed most to changes in beta diversity across samples (Legendre & Cáceres,  
173 2013; Legendre & Gallagher, 2001) in the package *adespatial* (Dray et al., 2018) in R  
174 with 999 permutation on Hellinger-transformed species abundance data. Changes in  
175 relative abundance of the five most abundant species and the five most important  
176 species contributing to beta diversity were analyzed using an ANOVA according to the  
177 three-factor design described above.

## 178 **Results**

179 A total of 4,258 individuals from 70 species were recorded during the study  
180 period. The five most abundant species were *Zebrasoma desjardini* (763 individuals  
181 recorded), *Ctenochaetus striatus* (682 individuals recorded), *Siganus luridus* (383  
182 individuals recorded), *Acanthurus sohal* (293 individuals recorded) and *Siganus*  
183 *argenteus* (292 individuals recorded) (Table 1).

184 [Table 1 here]

### 185 **Number of individuals and species richness**

186 Levene's Test for Homogeneity of Variance indicated that there were no  
187 significant differences in variances for the total number of individuals between time-  
188 of-day ( $F_{3,20}=1.005$ ,  $P=0.411$ ) or site ( $F_{2,21}=1.524$ ,  $P=0.241$ ), nor for species richness  
189 across time-of-day ( $F_{3,20}=1.054$ ,  $P=0.391$ ) and site ( $F_{2,21}=0.470$ ,  $P=0.632$ ).

190 Univariate analysis indicated that there were no significant differences in the  
191 total number of individuals across days, time-of-day or between sites (Table 2a, Figure  
192 1a). Permutational analysis on untransformed species richness data suggested  
193 significant differences between time-of-day, but not days, the day and time-of-day  
194 interaction or sites (Table 2b). Pairwise tests indicated that species richness was

195 significantly lower at 1400 hrs compared to 0600 hrs ( $P=0.004$ ) and 1800 hrs ( $P=0.04$ ).

196 There models indicated borderline statistical significance that was indicative of greater

197 species richness at 0600 hrs compared to 1000 hrs ( $P=0.095$ ) (Figure 1b).

198 [Figure 1 here]

199 [Table 2 here]

## 200 **Fish assemblage composition**

201 When analyzing the fish assemblages, betadisper indicated heterogeneity in

202 assemblage composition between factors in time-of-day ( $F_{3,20}=5.39$ ,  $P=0.003$ ), but

203 homogeneity in multivariate dispersions for site ( $F_{2,21}=0.56$ ,  $P=0.589$ ). Pairwise

204 comparisons of mean dispersions indicated lower variability in assemblage at 1000 hrs

205 and 1400 hrs (but no significant pairwise difference), compared to significantly higher

206 variability at 0600 and 1800 hrs (but no significant pairwise difference).

207 There were significant differences in community assemblage composition for

208 day and time of day, but not for the interaction between day and time-of-day or site

209 (Table 3). Pairwise tests indicated significant differences in community assemblage for

210 the groups 0600 and 1400 hrs ( $P=0.044$ ), and between 1400 and 1800 hrs ( $P=0.021$ ).

211 Ordination plots emphasized high time-of-day variability. The 1000 and 1400 hrs

212 groups tended to cluster fairly closely; while group 0600 and 1800 hrs showed greater

213 scatter, indicating more variable community assemblages and a separation between

214 midday and crepuscular times (0600 and 1800 hrs) (Figure 2).

215 [Table 3 here]

216 [Figure 2 here]

217 We investigated effects of day and time-of day on the five most abundant

218 species *Zebrasoma desjardinii*, *Ctenochaetus striatus*, *Siganus luridus*, *Acanthurus*

219 *sohal* and *Siganus argenteus*, as well as the five species which showed the greatest

220 species contributions to beta diversity (SCBD, mean for each species across samples),  
221 including *Abudefduf vaigiensis* (mean SCBD: 0.0838), *Siganus argenteus* (also fifth  
222 most abundant species, mean SCBD: 0.0872), *Siganus luridus* (also third most  
223 abundant species, mean SCBD: 0.0786), *Zebrasoma desjardinii* (also most abundant  
224 species, SCBD: 0.0617) and *Ctenochaetus striatus* (second most abundant species,  
225 SCBD: 0.0348). Between and within-day variation was absent or stochastic, with no  
226 significant differences between sites for *Ctenochaetus striatus* ( $F_{1,14}=0.69$ ,  $P=0.419$ ;  
227  $F_{3,14}=0.43$ ,  $P=0.737$  and  $F_{2,14}=312$ ,  $P=0.206$  respectively), *Siganus luridus* ( $F_{1,14}=0.74$ ,  
228  $P=0.405$ ;  $F_{3,14}=0.20$ ,  $P=0.893$  and  $F_{2,14}=0.44$ ,  $P=0.651$  respectively), *Acanthurus sohal*  
229 ( $F_{1,14}=4.07$ ,  $P=0.063$ ,  $F_{3,14}=2.29$ ,  $P=0.123$ ,  $F_{2,14}=0.22$ ,  $P=0.803$ , respectively) and  
230 *Siganus argenteus* ( $F_{1,14}=3.78$ ,  $P=0.072$ ;  $F_{3,14}=1.76$ ,  $P=0.201$  and  $F_{2,14}=0.05$ ,  $P=0.953$   
231 respectively)

232       Between day variation in relative abundance was significant but not within-day  
233 variation or site in *Zebrasoma desjardinii* ( $F_{1,14}=9.31$ ,  $P=0.009$ ,  $F_{3,14}=1.46$ ,  $P=0.268$ ;  
234  $F_{2,14}=0.25$ ,  $P=0.781$ , respectively). Similarly, *Abudefduf vaigiensis* showed significant  
235 differences between days, but not within days and across sites ( $F_{1,14}=23.83$ ,  $P=0.001$ ,  
236  $F_{3,14}=1.26$ ,  $P=0.326$ ,  $F_{2,14}=4.03$ ,  $P=0.042$ , respectively).

## 237 **Discussion**

238       Few studies have quantified short-term (between and within-day) variability in  
239 fish assemblages in sampling or monitoring programmes investigating medium spatial  
240 and temporal variation (i.e. in the order of seasons or years) (Hare & Mantua, 2000;  
241 Lazzari et al., 1999). Yet, spatial patterns are potentially confounded by within or  
242 between-day variation due to sampling at different times (Gray, 1996; Willis et al.,  
243 2006). This study provides a valuable snapshot exploring variation in species richness  
244 and composition within and between days.

245 Species richness (i.e. mean number of species) showed significant differences  
246 within days, but not between days or sites. Species richness was greatest at dawn (0600  
247 hrs) and dusk (1800 hrs) and there was some indication (approaching marginal  
248 significance given  $P=0.063$ ) that the total number of individuals was highest during  
249 dusk and dawn (Figure 1a). This is in contrast to Birt et al. (2012), who found significant  
250 differences in species richness between, but not within days. Feeding activity has been  
251 shown to be highest during dusk and dawn and coral reef species show a pronounced  
252 day-night changeover (Azzurro, Pais, Consoli, & Andaloro, 2007; Collette, 1972),  
253 likely contributing to the patterns observed.

254 Overall, assemblage composition was similar of that reported by Kochzius  
255 (2007), who investigated community structure using visual census in El Wuadim Bay  
256 (El Queseir). In line the results of this study, they found that the families Acanthuridae,  
257 Labridae and Pomacentridae dominated the community in terms of relative abundance,  
258 with the exception of Anthiinae (subfamily of Serranidae), which were not common in  
259 our study or others studies in the Red Sea (Khalaf & Kochzius, 2002; Rilov &  
260 Benayahu, 1998). It is worth noting that species richness in this coral reef was relatively  
261 low compared to other sites in the Red Sea , sites with greater species richness might  
262 show different patterns.

263 Our study found significant between and within-day variability in fish  
264 assemblage composition, unlike other studies (Colton & Alevizon, 1981; Rooker &  
265 Dennis, 1991; Santos et al., 2002; Spyker & Van Den Berghe, 1995; Willis et al., 2006).  
266 Pairwise-comparisons indicated that assemblage composition differed significantly  
267 between 0600 & 1400 and 1400 & 1800 hrs, likely associated with a transition between  
268 day-time and night-time assemblages. This is supported by the significant within-day  
269 heterogeneity evidenced by PERMDISP, suggesting greater variability in fish

270 assemblage composition during dusk and dawn. These results are associated with the  
271 emergence and retreat of diurnally or nocturnally active fish during dawn and dusk  
272 (Colton & Alevizon, 1981; Hobson, 1965; Rooker & Dennis, 1991). Moreover, reef  
273 species are more active in morning and evening associated with peaks in feeding  
274 activity in many species, predator avoidance during the day (Rickel & Genin, 2005)  
275 and a pronounced day-night changeover (Azzurro, Pais, Consoli, & Andaloro, 2007;  
276 Collette, 1972). We also found evidence for significant changes in assemblage  
277 composition between days. This may be associated with some temporal variability that  
278 is more subtle operating at between-day scales, including reproductive behaviour (e.g.  
279 spawning) (Tolimieri, Sale, Nemeth, & Gestring, 1998; D. M. Williams, 1983),  
280 schooling and feeding behaviour (Milazzo, Badalamenti, Fernández, & Chemello,  
281 2005; Ogden & Buckman, 1973), tidal or current state (Kingsford & MacDiarmid,  
282 1988).

283       Variation in abundance of individual species within daylight hours reflects  
284 feeding, habitat use and activity levels, and is likely species-specific (Holbrook,  
285 Schmitt, & Brooks, 2008). Prior knowledge of such species-specific foraging behaviour  
286 and activity facilitates the design appropriate surveys, in particular if they are aimed a  
287 specific group of species (e.g. economically important targeted species). For example,  
288 diurnal variability in relative abundance will be lower in sedentary or territorial species  
289 such as *Paracirrhites arcatus* than that of larger, highly mobile species such as groupers  
290 (Holbrook, Schmitt, & Brooks, 2008). Here, we investigated changes in relative  
291 abundance in six species, finding little to no evidence for a change in abundance with  
292 time-of-day. *Zebrasoma desjardini*, *Ctenochaetus striatus*, *Siganus luridus*,  
293 *Acanthurus sohal* and *Siganus argenteus* often occur in roaming schools (Bos, Cruz-  
294 Rivera, & Sanad, 2017; Bouchon-Navaro & Harmelin-Vivien, 1981; Lundberg &

295 Lipkin, 1979) introducing variability that may make it difficult to distinguish between  
296 or within-day patterns. Despite exhibiting significant variation in their behavior and  
297 feeding ecology, surgeonfishes (including *Zebrasoma desjardini*, *Ctenochaetus*  
298 *striatus* and *Acanthurus sohal*) tend to be the dominant herbivores on coral reefs  
299 (Barlow, 1974; Fouda & El-Sayed, 1996; Robertson, 1983). Herbivores been shown to  
300 exhibit definite diurnal patterns in abundance, associated with either predator avoidance  
301 during dusk and dawn and/or the increasing nutrient peak of algae during midday (Hay  
302 et al., 1988; Hobson, 1973; Zemke-White, Choat, & Clements, 2002). *Abudefduf*  
303 *vaigiensis* is a generalist omnivore feeding on pelagic copepods, algae and sessile  
304 invertebrates (Clarke & Bishop, 1948; Frédéricich, Fabri, Lepoint, Vandewalle, &  
305 Parmentier, 2009; Rowe, Figueira, Raubenheimer, Solon-Biet, & Machovsky-Capuska,  
306 2018), exhibiting diurnal feeding activities (Emery, 1973). While surprising that these  
307 species showed significant within-day changes in abundance, our results are in line with  
308 other studies (Andrew & Jones, 1990; Azzurro et al., 2007; Birt et al., 2012; Choat &  
309 Clements, 1993; Howard, 1989). The plasticity and flexibility of feeding habits has  
310 been highlighted in Siganidae (such as *Siganus luridus* and *Siganus argenteus* (Fox,  
311 2012), which might have contribute to the lack of significant within and between-day  
312 patterns. Furthermore, temporal bias might arise from variability in fish or be an  
313 sampling or statistical effect. Birt et al. found significant differences between and  
314 within-days in their four-day study, arguing that rare species may be responsible for  
315 these observed differences in combination with the Bray Curtis resemblance matrix,  
316 which can be particularly sensitive to rare species and their use of bait. Indeed, any  
317 sampling technique will influence the observations, including video (Watson et al.,  
318 2005) or visual counts (Hay et al., 1988; Zemke-White, Choat, & Clements, 2002).  
319 Observations are therefore snapshots, providing an indication of assemblage

320 composition, rather than a definite picture (Sale, 1997), and are influenced by the high  
321 variability of particular mobile species (such as planktivores) and schooling species.

322 Our results suggest that between and within-day variation in fish assemblage  
323 composition requires serious consideration. The changes in fish assemblage  
324 composition across daylight and hours and between days have the potential to affect  
325 abundance estimates of species and individual numbers (Casey & Myers, 1998; Galzin,  
326 1987; Hobson, 1965; D. M. Williams, 1983). Sampling is a trade-off between  
327 increasing replication within one site or increasing the number of sampling sites (i.e.  
328 spatial units) (Thompson & Mapstone, 2002). To avoid this source of bias whilst  
329 dealing with logistical constraints, investigators should aim to randomize sampling with  
330 respect to time across all sampling sites including a range of microhabitats, accounting  
331 for variability in depth, rugosity and exposure (Milazzo et al., 2005; Thompson &  
332 Mapstone, 2002) and considering specific sampling windows. It might be useful to  
333 avoid dusk and dawn sampling times when community turnover is highest.

334 Here, we focussed solely on diurnal patterns in fish assemblage composition.  
335 However, change in fish assemblage composition is driven by other factors including  
336 salinity (Allen, 1982), temperature (Marshall & Elliott, 1998), lunar cycle (Polunin &  
337 Klumpp, 1989), turbidity (Abou-Seedo, Clayton, & Wright, 1990), currents and tidal  
338 state (Polunin & Klumpp, 1989), all of which are correlated. In particular tidal state is  
339 another important variable associated with changes in fish abundance related to change  
340 in directional movement of fish (e.g. sheltering) (Polunin and Klumpp, 1989) or  
341 heterogeneity of available prey resources (such as plankton) (Bray, 1980; Polunin and  
342 Klumpp, 1989). Due to the difficulty in sampling at consistent tidal states, this issue  
343 can only be minimised by sampling across the range of tidal cycles and increasing

344 replication where required. During our study, tidal influences were minimised using  
345 stratified sampling, which is a feasible solution for other surveys.

346 Diurnal variation in community composition is nested within larger scale  
347 temporal variation. Seasonal effects on fish assemblage composition have been  
348 reported previously and are the result of changes in environmental variables, life history  
349 characteristics and species interactions (Ogden & Quinn, 1984; Pessanha & Araújo,  
350 2003; Tolimieri, Sale, Nemeth, & Gestring, 1998). This variation at greater temporal  
351 scales has important impacts on small-scale diurnal patterns. Changes in abiotic and  
352 abiotic conditions at larger temporal scales impact diurnal patterns and variability in  
353 fish assemblage composition and should be taken into consideration. This may be more  
354 important in temporal fish assemblages, where seasonal shifts in abiotic conditions are  
355 more pronounced. This is an area that should be investigated in the future.

356 Despite the knowledge of changes in coral fish assemblages, diurnal changes in  
357 assemblage composition have received little attention when designing experiments or  
358 investigating ecological hypotheses. Here we argue that diurnal variability in fish  
359 assemblages, in particular, associated with a transition in community assemblage  
360 between dusk and dawn should be considered designing studies. Variation in  
361 abundances at short time scales has the potential to be misinterpreted as error or changes  
362 in population size and assemblage composition. Randomisation and replication are  
363 useful to deal with this variability in the light of common constraints faced by many  
364 research projects.

#### 365 **Author contributions**

366 LB and BS designed the experiment; BS collected the data in the field; LB analysed the  
367 data; LB wrote the paper. All authors read and approved the final manuscript.

#### 368 **Conflict of interest**



369 The authors declare no conflict of interest.

370

371 Tables

372

373 Table 1. Total species recorded during the survey.

Family	Species	Number of individuals
Acanthuridae	<i>Acanthurus sohal</i>	293
	<i>Acanthurus nigrofuscus</i>	2
	<i>Ctenochaetus striatus</i>	682
	<i>Naso elegans</i>	123
	<i>Naso unicornis</i>	30
	<i>Zebrasoma desjardini</i>	763
	<i>Zebrasoma xanthurum</i>	106
Balistidae	<i>Balistapus undulatus</i>	7
	<i>Rhinecanthus assasi</i>	1
	<i>Sufflamen albicaudatus</i>	58
Carangidae	<i>Caranx melampygus</i>	4
Chaetodontidae	<i>Chaetodon auriga</i>	61
	<i>Chaetodon austriacus</i>	108
	<i>Chaetodon fasciatus</i>	56
	<i>Chaetodon paucifasciatus</i>	46
	<i>Chaetodon semilarvatus</i>	8
	<i>Chaetodon trifascialis</i>	8
	<i>Heniochus intermedius</i>	3
Cirrhitidae	<i>Paracirrhites forsteri</i>	6
Dasyatidae	<i>Taeniura lymma</i>	8
Diodontidae	<i>Diodon hystrix</i>	2
Fistulariidae	<i>Fistularia commersonii</i>	2
Holocentridae	<i>Neoniphon sammara</i>	5
	<i>Sargocentron caudimaculatus</i>	9
	<i>Sargocentron diadema</i>	1
	<i>Sargocentron diadema</i>	1
Labridae	<i>Anampses meleagrides</i>	1
	<i>Bodianus anthioides</i>	18
	<i>Chelio inernis</i>	10
	<i>Cheilinus lunulatus</i>	24
	<i>Coris aygula</i>	21
	<i>Epibulus insidiator</i>	16
	<i>Gomphosus caeruleus</i>	31
	<i>Halichoeres hortulanus</i>	26
	<i>Halichoeres iridis</i>	1
	<i>Novaculichthys taeniourus</i>	14
	<i>Oxycheilinus digramma</i>	6
	<i>Thalassoma rueppellii</i>	72
<i>Labridae sp.</i>	19	
Lethrinidae	<i>Lethrinus mahsena</i>	16

Lutjanidae	<i>Lutjanus bohar</i>	1
Monacanthidae	<i>Amanses scopas</i>	7
Mullidae	<i>Mulloidichthys flavolineatus</i>	44
	<i>Parupeneus cyclostomus</i>	1
	<i>Parupeneus forsskali</i>	84
Nemipteridae	<i>Scolopsis ghanam</i>	45
Ostraciidae	<i>Ostracion cyanurus</i>	1
Pinguipedidae	<i>Parapercis hexophthalma</i>	21
Pomacanthidae	<i>Pygoplites diacanthus</i>	25
Pomacentridae	<i>Abudefduf vaigiensis</i>	162
	<i>Amblyglyphidodon indicus</i>	7
	<i>Dascyllus trimaculatus</i>	1
	<i>Pomacentrus sulfureus</i>	40
Scaridae	<i>Calotomus viridescens</i>	2
	<i>Cetoscarus bicolor</i>	3
	<i>Chlorurus sordidus</i>	39
	<i>Hipposcarus harid</i>	29
	<i>Scarus ferrugineus</i>	5
	<i>Scarus fuscopureus</i>	2
	<i>Scaridae sp.</i>	363
Scorpaenidae	<i>Pterois miles</i>	3
	<i>Pterois radiata</i>	1
Serranidae	<i>Cephalopholis argus</i>	7
	<i>Diploprion drachi</i>	2
	<i>Grammistes sexlineatus</i>	2
Siganidae	<i>Siganus argenteus</i>	292
	<i>Signatus luridus</i>	383
	<i>Signatus stellatus</i>	1
Tetraodontidae	<i>Arothron diadematus</i>	8
	<i>Arothron hispidus</i>	2
	<i>Canthigaster margaritata</i>	8

374

375

376 **Table 2.** PERMANOVA results based on Euclidean dissimilarity matrix on the (A)  
 377 total number of individuals (square root transformed) and (B) total number of species  
 378 (untransformed).

379

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**(A) Total relative number of individuals**

Source	df	SS	MS	Pseudo-F	P(perm)
Day	1	7.75	7.75	3.03	0.100
Time-of-day	3	23.05	7.68	3.02	0.063
Site	2	0.84	0.84	0.33	0.562
Day*Time-of-day	3	5.51	1.84	0.72	0.554
Residuals	15	38.32	2.56		

---

Total	23	75.46			
<b>(B) Species richness</b>					
<b>Source</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>Pseudo-F</b>	<b>P(perm)</b>
Day	1	53.25	53.25	3.75	0.072
Time-of-day	3	205.47	68.49	4.82	<b>0.018</b>
Site	2	5.09	2.55	0.18	0.828
Day*Time-of-day	3	25.34	8.45	0.60	0.639
Res	14	198.80	14.20		
Total	23	487.96			

380

381 **Table 3.** PERMANOVA based on Bray Curtis dissimilarity matrix of the relative  
 382 number of individuals (square root transformed with one dummy variable).  
 383 Significant values are highlighted bold.

384

<b>Source</b>	<b>df</b>	<b>SS</b>	<b>Pseudo-F</b>	<b>P(perm)</b>
Day	1	0.03	2.58	<b>0.001</b>
Time-of-day	3	0.04	1.50	<b>0.022</b>
Site	1	<0.01	5	0.508
Day*Time-of-day	3	0.03	1.09	0.330
Res	15	0.15		
Total	23	0.26		

385

386 **List of figure captions**

387

388 **Figure 1.** Mean number of individuals ( $\pm$  SE, n=24) (A). Significant differences are  
389 indicated using letters, and species richness (average number of species per video,  $\pm$   
390 SE, n=24) at time-of-day: 0600, 1000, 1400 and 1800 hrs (B).

391

392 **Figure 2.** Nonmetric multidimensional scaling ordination (NMDS) of community  
393 structure. Dashed ellipse represents the 95% confidence interval for the centroid of each  
394 stratification group as calculated by ordiellipse (Oksanen, Kindt, Simpson, & Oksanen,  
395 2018). Points represent each video.

396

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