



HAL
open science

Remote video surveys unveil the diurnal variability of trophic-based processes by fishes on coral reefs

Camille Magneville, Thomas Claverie, Sébastien Villéger

► **To cite this version:**

Camille Magneville, Thomas Claverie, Sébastien Villéger. Remote video surveys unveil the diurnal variability of trophic-based processes by fishes on coral reefs. *Coral Reefs*, 2023, 43 (2), pp.253-263. 10.1007/s00338-023-02436-x . hal-04645517

HAL Id: hal-04645517

<https://hal.science/hal-04645517v1>

Submitted on 10 Oct 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Remote video surveys unveil the diurnal variability of trophic-based**
2 **processes by fishes on coral reefs**

3

4 Camille Magneville ^{1,2*} (<https://orcid.org/0000-0003-0489-3822>)

5 Thomas Claverie ^{1,3,4} (<https://orcid.org/0000-0002-6258-4991>)

6 Sébastien Villéger ¹ (<https://orcid.org/0000-0002-2362-7178>)

7

8 ¹ MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Montpellier, France.

9 ² Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), Department of Biology, Aarhus

10 University, Ny Munkegade 114, DK-8000 Aarhus, Denmark

11 ³ Centre Universitaire de Formation et de Recherche de Mayotte, France.

12 ⁴ UMR ENTROPIE, Univ La Réunion, IRD, IFREMER, Univ Nouvelle-Calédonie, CNRS, Saint-Denis,

13 Réunion, France

14

15 * corresponding author (camille.magneville@gmail.com)

16

17

18

19

20

21 **Abstract**

22

23 Feeding activities by fishes are among the key ecological processes that sustain coral reef
24 functioning. Those trophic-based processes are known to vary across space and across seasons or
25 years. However, there is still little knowledge about their variability within and between days as well as
26 whether these processes are dominated by the same species across time. Using remote underwater
27 cameras, we quantified rates of three feeding activities (corallivory, herbivory and invertivory) for three
28 one-hour time slots (morning, midday, afternoon) over two days on two coral reefs around Mayotte
29 Island (Western Indian Ocean). Feeding activities were highly variable at within and between-day scales
30 and concentrated in a few pulses. Herbivory was the highest in the afternoon which aligns with previous
31 findings regarding activity of herbivorous fishes. Corallivory was the highest in the morning, which
32 highlights the advantage of long-duration benthic remote underwater videos to accurately assess all
33 trophic activities. Trophic-related processes were dominated by the same few species in both sites and
34 across time of the day. This study pinpoints the importance of including within-day and between-day
35 variations when studying ecological processes, as neglecting these variations may introduce biases
36 into our understanding of these processes.

37

38 **Keywords:** feeding activities, coral reef fishes, temporal variability, daily variability, species dominance

39 **Introduction**

40

41 A challenge for functional ecology is to understand how species are shaping ecological
42 processes which mediate energy and material flows occurring in the ecosystems (Brandl et al. 2019).
43 This question is of utmost importance on coral reefs, which are the most speciose marine habitat per
44 unit area (Knowlton and Jackson 2008) while being under increasing anthropogenic pressures
45 (Bellwood et al. 2004; Hughes et al. 2017). Among the eight ecological processes at the core of the
46 functioning of coral reefs, three are directly related to feeding activities of fishes: bioerosion, herbivory
47 and predation (Brandl et al. 2019). Despite the high diversity observed on coral reefs, several studies
48 have consistently shown that only a few species dominate these key trophic processes (Bellwood et al.
49 2003, 2006; Cvitanovic and Bellwood 2009; Hoey and Bellwood 2009; Bennett and Bellwood 2011;
50 Vergés et al. 2012). In addition, the identity of species dominating such ecological processes vary
51 spatially between reef habitats (Bellwood et al. 2006) and across reefs and regions (Schiettekatte et al.
52 2022). While some studies have also demonstrated temporal variation in species dominance at large
53 temporal scales, with certain species prevailing during specific times of the year (Lefèvre and Bellwood
54 2011), to our knowledge, no research has assessed such variations at shorter time scales, such as
55 within and between day variations.

56

57 In addition, as fish trophic roles cannot be inferred from species abundance (Fox and Bellwood
58 2008), surveys of feeding rates are needed to assess the contribution of each species. Such evaluation
59 of fish feeding activity, which involves quantifying the number of bites per individual over a specified
60 surface area and time unit, can be conducted by observing individual behaviors through space or
61 throughout the day using scuba-diving techniques (Zemke-White et al. 2002). To prevent potential bias
62 due to the presence of the diver, remote surveys using high-definition cameras have been increasingly
63 applied. However, some of these studies focusing on spatial variability used short-duration recordings
64 (<1h) within each site on a single day (e.g. Longo et al. 2019) which prevented accounting for intra-day
65 variability in fish activity. In addition, the few studies recording for several hours, ranging from half-day
66 (Rasher et al. 2013) to all daylight time, to assess overall fish activity within a microhabitat (Bellwood et
67 al. 2006), across micro-habitats (e.g. Tebbett et al. 2020) and reef habitats (Fox and Bellwood 2008;
68 Rasher et al. 2013) did not explicitly assess values of the temporal variability. Hence, the magnitude of
69 variations of fish feeding behavior within and across days is still largely unknown for coral reef fishes.
70 Yet, higher rates of herbivory in the afternoon relative to the morning have been reported for over 20
71 coral reef fish species from the Great Barrier Reef (Zemke-White et al. 2002). This finding supports the
72 diel feeding hypothesis which posits a higher feeding activity in the afternoon due to the increased
73 nutritive quality of algae during that time (Taborsky and Limberger 1980). The herbivory activity in
74 temperate ecosystems has also been documented to mostly occur in brief large pulses within each day,
75 highlighting the significance of considering within-day variation when analyzing feeding activity of fishes
76 (Magneville et al. 2023). Temporal variation of trophic activities for other key guilds such as corallivores
77 and invertivores has received limited attention in literature.

78

79 Using remote underwater cameras deployed on two fringing reefs around Mayotte Island
80 (Western Indian Ocean), we assessed the temporal variations of fish feeding activities within and
81 between two days and examined whether there were any shifts in the dominant species engaged in
82 these activities. Specifically, we addressed the following questions: (i) What is the magnitude of
83 temporal variability in the three main feeding activities of reef fishes? (ii) Does the identity of species
84 responsible for these activities vary through time and across sites? We first expect an increase in
85 herbivory activity during the afternoon, as suggested by the diel feeding hypothesis (Taborsky and
86 Limberger 1980; Zemke-White et al. 2002). We expect corallivory and invertivory and the identity of
87 species responsible for the feeding activities to also exhibit high temporal variability within and between
88 days due to fluctuations in species abundance and activity at such scales (Colton and Alevizon 1981;
89 Rooker and Dennis 1991; Birt et al. 2012; Myers et al. 2016; Bacheler et al. 2021).

90
91

92 **Material and Methods**

93

94 **Remote Underwater Video recording**

95

96 This study was carried out on two fringing reefs around Mayotte Island (Western Indian Ocean).

97 The two fringing reefs were similar with an average depth of three meters and habitat made by a mix of

98 branching, massive and encrusting living corals, turf on dead corals and sandy sediment (see Supp.

99 Fig. 1 for filmed quadrat). The first reef, Bouéni (-12.9162° lat; 45.0807° long) is within a Poorly

100 Protected marine Area (PPA) ("Parc Naturel Marin de Mayotte" <https://parc-marin-mayotte.fr/>)

101 encompassing all the lagoon. The second reef, N'Gouja (-12.9639° lat; 45.0870° long), is within a Fully

102 Protected marine Area (FPA) where fishing is prohibited and is 5.3 km away from the poorly protected

103 site.

104 Surveys were carried out on four days spanning from 03/11/2020 to 06/11/2020, monitoring

105 each site every other day. Rainfall events occurred on the second surveyed day in N'Gouja. Five GoPro

106 Hero 5 (GoPro Inc, United States) mounted on a 35 cm high tripod were set to record high-definition

107 videos (1920 by 1080 pixels at 25 frames per second) with a 90° field-of-view ("Linear" mode on GoPro

108 settings). Cameras were set up from 18 to 140 meters apart with no substrate obstructing the camera's

109 field-of-view up to 3m. After the start of the recording, a 2m² quadrat was briefly placed in front of each

110 camera to eventually measure fish diversity over this standardized area (Longo et al. 2014). A reference

111 watch was also displayed in front of each camera soon after the start of recording so that all videos

112 were eventually synchronized with a one second precision.

113 Cameras recorded continuously on three time spans: 07:00-09:00, 11:15-13:15 and 15:30-

114 17:30. To minimize the effects of diver presence on fish behavior, we limited our feeding annotations

115 with buffer periods after camera placement and before retrieval. For each video, annotations

116 commenced 30 minutes after divers left the survey area following camera placement and ended 30 min

117 before divers returned within 250m of the camera. This allowed three discontinued hours of video for

118 each day (from 07:30:00 to 08:30:00, from 11:30 to 12:30 and from 15:30 to 16:30).

119

120

121

122

123 **Measuring feeding activities**

124

125 As annotating all individuals and their feeding activity is demanding (up to 10 minutes of

126 annotation for each minute of video), we assessed the feeding activity on a subset of the video recorded.

127 More precisely, annotations of feeding activities were done on four evenly spaced sequences of five

128 minutes (i.e. every 15 minutes) yielding 12 annotated sequences per day and per camera (equivalent

129 to 60 minutes of annotations per day and per camera).

130 An individual was considered to be feeding when its mouth was in contact with the substrate
131 within the 2m² quadrat. The diet of each species was first retrieved from Parravicini et al. (2020). Three
132 main feeding activities were then assessed: corallivory (i.e. bites by corallivorous species on live coral
133 colonies), herbivory (i.e. bites by detritivorous, microbivorous and/or herbivorous fishes on the epilithic
134 algal matrix) and invertivory (i.e. bites on soft sediment by fishes feeding mostly on benthic mobile,
135 micro and macro invertebrates and large crustacea). We verified that the main diet associated with each
136 species had a high likelihood ratio exceeding 70% (Supplementary Table 3 - Parravicini et al. 2020).
137 This criterion was not met for three corallivorous species (*Chaetodon auriga*, *Henochius acuminatus*
138 and *Labrichtys unilineatus* which could also feed on invertebrates). We thus identified the substrate
139 type upon which each bite was taken (these three species only fed on corals in our videos). Similarly,
140 as parrotfishes can feed on endolithic algae in dead corals or on live corals (Bonaldo et al. 2014), we
141 identified the substrate type upon which each bite was taken and categorized their activity as either
142 corallivory or herbivory. Four scarine labrid species (*Chlorurus sordidus*, *Scarus ferrugineus*, *Scarus*
143 *frenatus* and *Scarus niger*) were observed feeding on both turf and on living corals with most of their
144 feeding activity performed on turf.

145

146 **Statistical analysis**

147

148 The feeding activity of each species was assessed for each of the five-minute sequences as
149 the total number of bites in the five quadrats (hence measured in number of bites per five minutes per
150 10m²).

151

152 To test the effect of the time of the day (three time slots: 07:00-09:00, 11:15-13:15, 15:30-17:30)
153 and site on the intensity of corallivory, herbivory and invertivory, we applied Generalised Linear Mixed
154 Models (GLMMs) with a negative binomial distribution. Five-minute sequences were used as replicates
155 and the surveyed day was counted as a random effect:

156

$$\text{Number of bites} \sim \text{time slot} + \text{site} + (1|\text{day})$$

157

158 To test the effect of the time of the day (three time slots: 07:00-09:00, 11:15-13:15 or 15:30-17:30) on
159 the intensity of the three feeding activities in each site separately we applied likewise Generalised Linear
160 Mixed Models (GLMMs) with a negative binomial distribution. Five-minute sequences were used as
161 replicates and the surveyed day was counted as a random effect:

162

$$\text{Number of bites} \sim \text{time slot} + (1|\text{day})$$

163

164 GLMMs were performed using the *glmer.nb()* function of the *lme4* (vers. 1.1-31) package. Model validity
165 was checked using the *DHARMA* package (vers. 0.4.6).

166

167 To test for a turnover in species composition across the three time slots and the two sites, we
168 computed Jaccard dissimilarity between all pairs of five-minute sequences based on the presence or

169 absence of each species. Subsequently, we performed a Permutational Multivariate Analysis of
170 Variance (PERMANOVA) on this dissimilarity matrix with time slots and sites as groups.

171

172 To test for a turnover in species dominance in feeding intensity across the three time slots and
173 the two sites, we calculated Bray Curtis distances between five-minutes sequences based on species
174 bites number. We then performed a PERMANOVA with time slots and sites as groups. PERMANOVAs
175 analyses were applied using the *adonis2* function of the *vegan* package (vers. 2.6-4).

176

177 **Results**

178

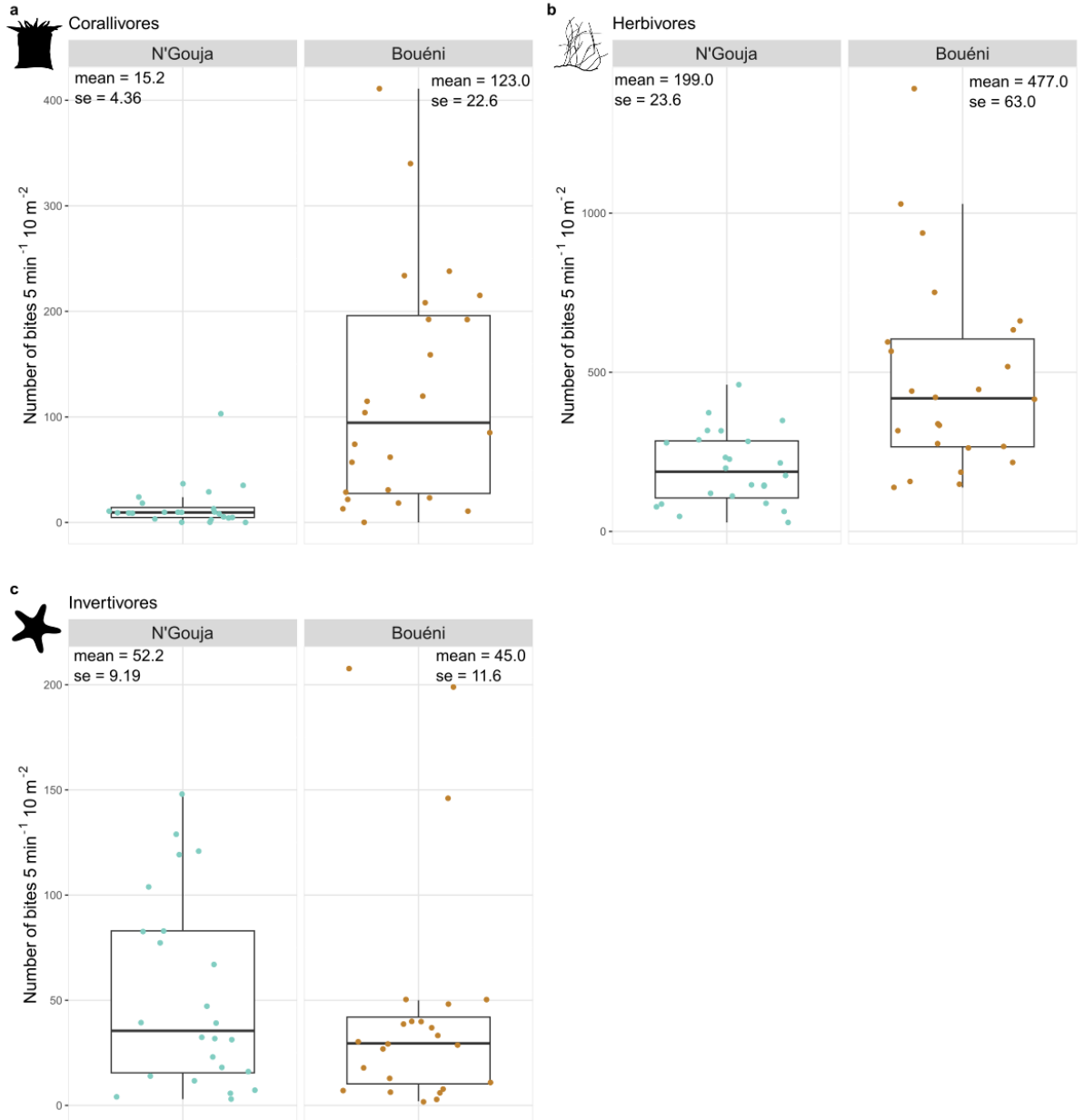
179 Fifty-one species were seen interacting with the substrate with 14 species feeding on corals,
180 13 species feeding on primary producers, and 28 invertivorous species.

181

182 *Within and between day variability of feeding activities*

183

184 Corallivory, herbivory and invertivory varied by up to two orders of magnitude across 5-minutes
185 sequences (Figure 1). Corallivory and herbivory were significantly more frequent in Bouéni than in
186 N’Gouja (Supp Table 1) with on average 8.1 and 2.4 times higher bite rates of corallivory and herbivory,
187 respectively (Figure 1). The bite rate of invertivory was similar in both sites (Supp Table 1).



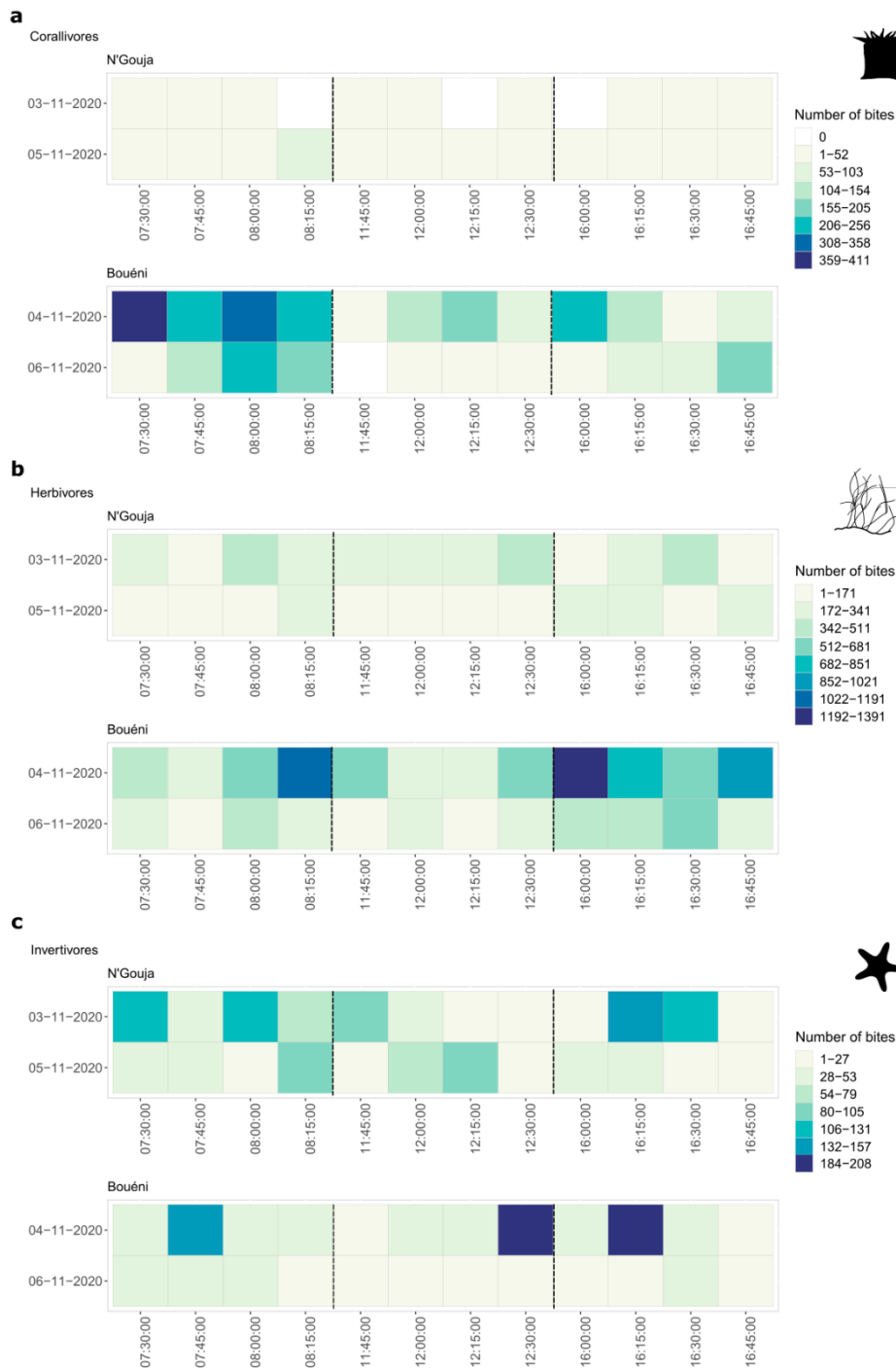
188

189

190 Figure 1: Variation in the number of bites across trophic groups and sites. The number of bites by all
 191 fish from a trophic group were counted for 5-minute sequences over 10m² (5 quadrats of 2m² surveyed
 192 each by a camera).

193

194 Feeding activities differed between the two surveying days. More than 60% of each feeding
 195 activity performed in N'Gouja and in Bouéni were occurring in one surveyed day. Corallivory varied
 196 significantly between time slots in Bouéni (Supp Table 2) with three-fifths of the activity realized between
 197 7:30 - 8:30 and one quarter of the activity performed between 16:00 - 17:00 (Figure 2 - a). The herbivory
 198 intensity was significantly different between time slots in Bouéni (Supp Table 2) with nearly half of the
 199 activity recorded between 16:00 - 17:00 (Figure 2 - b). The invertivory intensity was not significantly
 200 different between time slots in both sites (Figure 2 - c) (Supp Table 2).



201
202

203 Figure 2: Heatmaps of corallivores (a), herbivores (b) and invertivores (c) feeding activities. Colors
 204 reflect the number of bites recorded on 10m² for five minutes. Classes were defined to represent one
 205 eighth of the span of the feeding activity recorded across the two sites. The top row of each feeding
 206 activity is the heatmap of N'Gouja while the bottom row reflects the heatmap of Bouéni. Dark vertical
 207 bars represent the delimitations of the time slots (07:30-08:30, 11:45-12:45, 16:00-17:00).
 208

209 For the three feeding activities there was no significant difference in species composition
 210 between time slots (PERMANOVA on Jaccard dissimilarity p-value > 0.05 ; Supp Table 3 and 4) and

211 no significant difference in the contribution of species to feeding activities (PERMANOVA on Bray-Curtis
212 dissimilarity p-value > 0.05 ; Supp Table 5 and 6).

213

214 Feeding activities were primarily concentrated within a few short bursts, either by few
215 individuals feeding intensely, or by many individuals with lower intensity. In N'Gouja the five sequences
216 with the highest feeding activity contributed to 62.47%, 38.08% and 48.28% of the corallivory, herbivory
217 and invertivory realized on the 24 sequences, respectively. In Bouéni, the five sequences with the
218 highest feeding activity contributed to 48.70 %, 41.68% and 60.52% of the corallivory, herbivory and
219 invertivory realized on the 24 sequences, respectively. The three types of feeding activities were not
220 significantly correlated between each other across time (Supp Table 7).

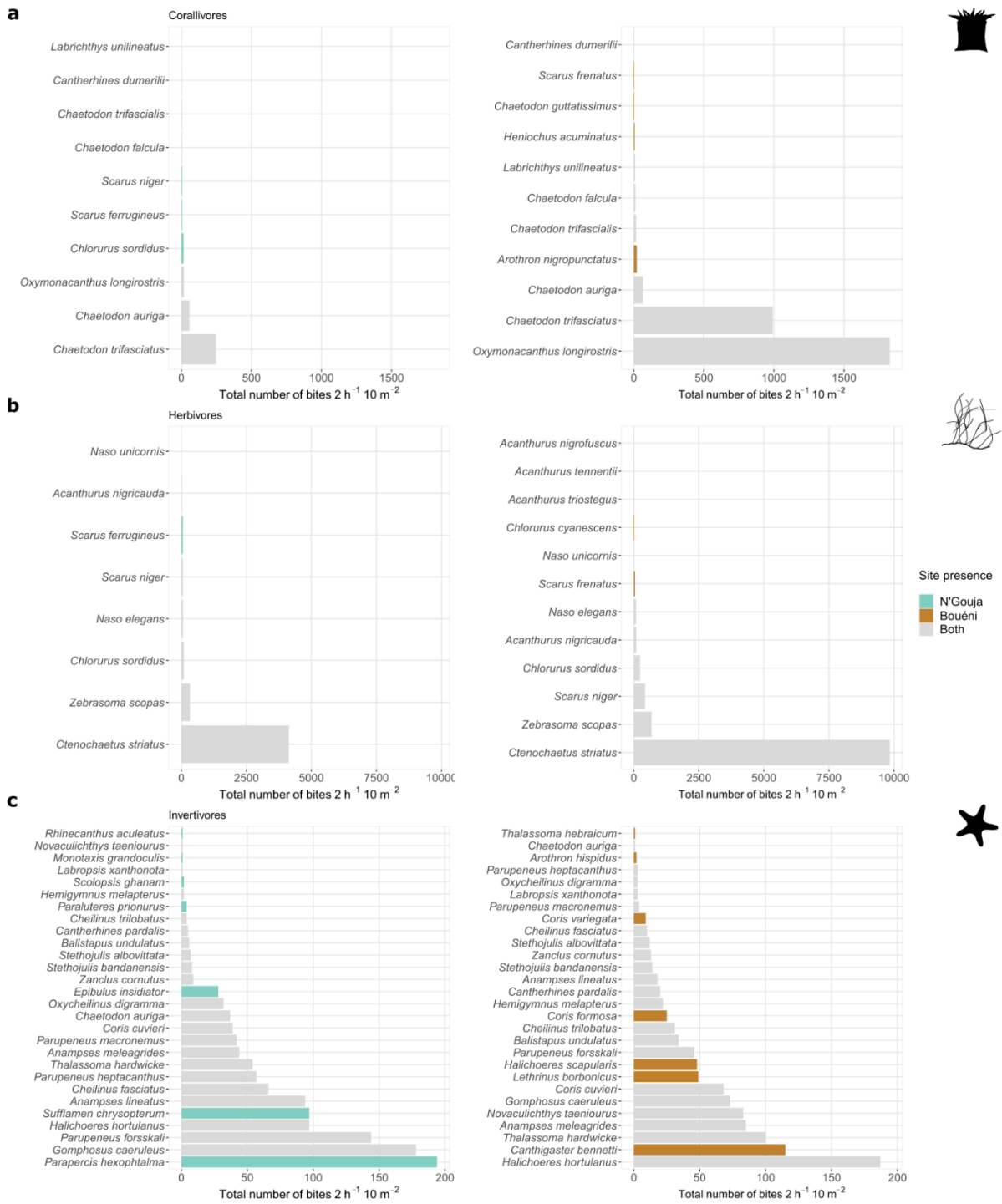
221

222 *Species dominance on feeding activities*

223

224 Corallivory and herbivory were dominated by the few same species in the two sites (Figure 3).
225 In fact, three species contributed to 90.40% of the corallivory in N'Gouja and 97.68% in Bouéni
226 (*Chaetodon auriga*, *Chaetodon trifasciatus* and *Oxymonacanthus longirostris*) while a single species
227 (*Ctenochaetus striatus*) contributed to 86.92% of the herbivory in N'Gouja and 84.32% in Bouéni. 15
228 species contributed to 95.93% and 91.38% of the invertivory in N'Gouja and Bouéni, respectively.

229



230

231

232 Figure 3: Total bite number per species for each feeding activity and site. Corallivory (a), herbivory (b),

233 and invertivory (c) are expressed per species (y axis) as the overall number of bites across all 24

234 sequences of 5 minutes over 10m² (x axis). For each of the three feeding activities, the left plot

235 represents data for N'Gouja and the right plot represents data for Bouéni. Bars are coloured if the

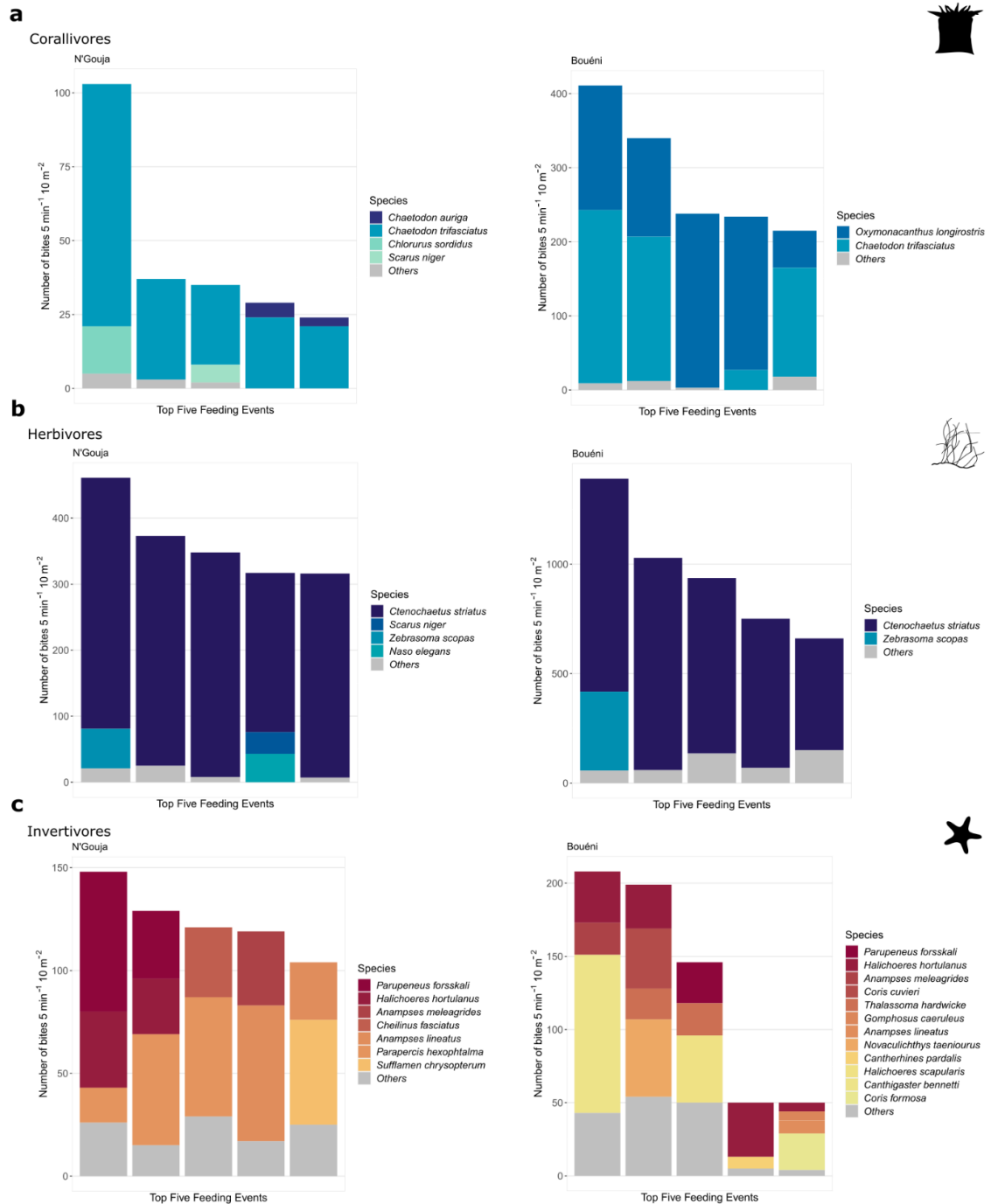
236 species is only seen in the N'Gouja (green) or in Bouéni (brown) and are grey if present on both sites.

237

238 In both sites, the five highest peaks of corallivory were due to *Chaetodon trifasciatus* which did

239 82.46% and 41.93% of the observed bites on corals in N'Gouja and Bouéni, respectively (Figure 4). In

240 Bouéni, *Oxymonacanthus longirostris* contributed to 55.14% of the corallivory in these five events. The
 241 five highest herbivory events were characterized by *Ctenochaetus striatus* which contributed to 89.15%
 242 and 82.57% of the activity realized on these five events in N’Gouja and in Bouéni respectively. The five
 243 highest events in terms of invertivory intensity were performed by five species in N’Gouja and three
 244 species in Bouéni with all species contributing equally to the activity.
 245



246
 247
 248
 249
 250

Figure 4: Species contribution to the five sequences showing the highest feeding activities. Corallivory (a), herbivory (b), and invertivory (c) are expressed as the number of bites per five minutes per 10m² (y axis). Colors represent species contributions in decreasing numbers of bites per unit of time. Species

251 gathered as “Others” are species whose activity represented less than 10% of the total activity of the
252 feeding event. For each of the three feeding activities, the left graph represents data for N’Gouja reef
253 and the right one represents data for Bouéni reef.

254

255 **Discussion**

256

257 Using remote underwater cameras recording throughout the day, we found on both reef sites that
258 corallivory, herbivory and invertivory activities were highly variable both within and between
259 days. Corallivory and herbivory activities varied significantly within a day. For instance, more than half
260 of the corallivory activity was measured in the morning (07:30-08:30) in Bouéni and nearly half of it was
261 realised in this same time slot in N’Gouja. Inversely, nearly half of the herbivory activity was realised in
262 the afternoon time slot (16:00-17:00) in Bouéni and more than one third of it was realised in this same
263 time slot in N’Gouja. This higher intensity of the herbivory activity in the afternoon has already been
264 reported in coral reef fishes (Fouda and El-Sayed 1996; Zemke-White et al. 2002) and in temperate
265 fishes (Magneville et al. 2023). Our results further supports the diel feeding hypothesis (Taborsky and
266 Limberger 1980) which proposes that a higher feeding activity in the afternoon is due to a higher algal
267 nutritional value at this moment of the day (Zemke-White et al. 2002). Yet, as *C. striatus* was the most
268 active feeder, and this species actually feeds on detrital organic matter, this result suggests that the
269 nutritional quality of these detrital resources may also increase at the end of the day. Further
270 investigations on the diel temporal variability of nutrient content in fish food sources are needed
271 especially for coral tissues. It has already been shown that uptakes of nutrients by corals vary with light
272 intensity and temperature but it is still unclear how it translates in nutritional quality for their consumers
273 (Palardy *et al.* 2005, 2006; Treignier et al. 2008; Houlbreque and Pagès 2009). The invertivory was not
274 significantly different within the day. However, the overall stability of invertivory may mask temporal
275 variability in different prey types, particularly due to their varying mobility. Thus, it would be relevant to
276 analyze invertivores gut content sampled throughout the day to get a more detailed assessment of their
277 diet (proportion of Mollusca, Echinoidea, small and large Crustacea, Annelids). In this study we did not
278 assess the activity of planktivores, as standardizing the surveyed area would require stereovideo. As
279 planktivores are a key trophic group on coral reefs (Siqueira et al. 2021) the variability of their feeding
280 activity should be investigated beside the existing binary categorization into diurnal vs nocturnal
281 strategies.

282

283 For a given reef surface, feeding activities were performed in pulses with nearly half of the total
284 corallivory and invertivory activities and more than one third of the herbivory activity occurring in less
285 than one fifth of the time. Such pulses have already been depicted in terrestrial and subtidal
286 environments (Armitage et al. 2013; Gibson et al. 2021) on time periods larger than a day and in
287 temperate marine ecosystems at short temporal scales (Magneville et al. 2022). These pulses of
288 feeding are likely to drive later (i.e. after digestion) pulses of nutrient excretion and egestion. For
289 herbivorous fish feeding before night, it could eventually impact biogeochemical fluxes in resting places
290 (Escalas et al. 2022). The three feeding activities were not correlated through time as it has already

291 been shown for species abundance (Magurran & Henderson 2010). This result highlights the
292 importance of including within-day temporal variation when studying ecological processes. In fact, if
293 trophic-based processes are censused at a single time of the day, it could bias the perception of their
294 respective magnitude. Specifically this variation of feeding activities could be driven by a mix of
295 environmental and behavioral conditions which drive species mobility and thus foraging activity. For
296 instance, solar radiations can influence species mobility as they seek shelter beneath tabular structures
297 to avoid UV radiation (Kerry and Bellwood 2015). Additionally, tides present a range of feeding
298 opportunities (Thompson and Mapstone 2002).

299

300 Two-thirds of each activity occurred in only one of the two surveyed days. This inter-day
301 variability can be due to the weather difference between the surveyed days. This variation could be
302 attributed to differences in solar exposure on the surveyed days for both sites: a greater proportion of
303 herbivory, invertivory, and corallivory was observed on sunny days, whereas cloudy and rainy days
304 exhibited lower levels of feeding activity. This result highlights the importance of surveying fish feeding
305 activities for several days and among different.

306

307 We found that corallivory and herbivory differed between the two surveyed sites, with a lower
308 intensity in the site with the highest level of protection (N’Gouja). This surprising result could be
309 explained by a higher level of predation in this site where piscivorous species are protected from fishing.
310 While no piscivory event was seen, there was a higher number of piscivorous species in N’Gouja than
311 in Bouéni (diversity accumulation through time retrieved for another manuscript (Magneville pers obs)
312 on other remote underwater videos recorded in the same sites). Four piscivorous species only recorded
313 in N’Gouja belonged to the groupers (*Plectropomus laevis*, *Cephalopholis nigripinnis*) and jacks
314 (*Carangoides ferdau*, *Scomberoides lysan*) while two carnivorous species were only recorded in Bouéni
315 (*Lethrinus nebulosus*, *Fistularia commersonii*) with one feeding on small fishes (*Fistularia commersonii*)
316 (Froese & Pauly 2023). The higher predation presence in N’Gouja could lead to a higher predation level
317 and therefore decrease the intensity of foraging activities. It has indeed been shown that herbivorous
318 fishes can decrease their foraging activities when sensing visual or chemical cues of predation (Catano
319 et al. 2017; Shapiro Goldberg et al. 2021). It would therefore be valuable to assess the abundance and
320 feeding activity of predators to confirm this hypothesis. Moreover, we studied feeding activities as bite
321 rates. However, being able to quantify individuals’ size using stereo-cameras is of utmost importance
322 as protection usually favors bigger individuals. It would allow translating bite rates into biomass removal
323 which could thus differ between both sites while taking fish size into account.

324 Corallivory and herbivory were dominated by the same few species in both reefs. This limited
325 functional redundancy has already been depicted with single species dominating the herbivory process
326 (Fox & Bellwood 2008; Hoey & Bellwood 2009). Here, *Ctenochaetus* was the most active feeder on
327 epilithic algal matrices which demonstrates the importance of such detritivorous species in reef food
328 webs (Tebbett et al 2017). The most active grazer, *Zebrasoma scopas*, represented 88% of the bites
329 performed by grazers on both sites. Previous research conducted on other coral reefs (Fouda and El-

330 Sayed 1996; Luise Bach and Smith 2021) has also identified *C. striatus* as the most abundant species.
331 The dominance of ecological processes by a single species could make coral reefs vulnerable to
332 disturbances if this species undergoes an important decrease in abundance. At the same latitude in
333 tropical Atlantic region in unprotected sites, Longo et al. (2019) found that the herbivorous process was
334 dominated by few species with a bite rate nearly two-fold lower than the herbivory found in this study
335 (456 bites/5min/10m² (sd = 339.26) in our study versus *ca* 250 bites/5min/10m² in Longo et al. (2019)).
336 In addition, we found that the same set of species supported each trophic-based process throughout
337 the day.

338 Ecological processes are highly variable in space (Longo et al. 2019) even at very fine scales
339 (Semmler et al. 2021) and in time at seasons and month scales (Lehodey et al. 2006; Robinson et al.
340 2008; Bijoux et al. 2013). Yet, this study illustrates that trophic-based processes also vary at short
341 temporal scales and this within-day and between-day variations should be taken into account when
342 designing ecological studies. Patch-centric approaches used in this study, allowed us to understand the
343 impact of feeding behavior of mobile animals on the local benthic habitat. Forager-centric approaches
344 (e.g. (Pickholtz et al. 2018, 2022)) could help to unravel the drivers of the observed temporal variability
345 by allowing the tracking of individuals over space. Remote underwater videos have already helped to
346 unravel how trophic-based processes vary with latitude across the Western Atlantic reefs (Longo et al.
347 2019). One step further, we call for quantifying the temporal variability of trophic activities and the
348 contributions of species to those activities across various environmental conditions (such as
349 temperature, benthic complexity) and level of protection. In fact, the dissimilarity of the substrate types
350 and associated biodiversity can impact feeding activities differently (Price et al. 2021). This challenge
351 could be tackled by a collective effort taking advantage of the easy to use long duration remote
352 underwater cameras (Dunkley et al. 2023) to record videos over several days on reefs from all realms
353 as done with other survey methods (such as the World Passive Acoustic Monitoring Day or the Reef
354 Check program). We annotated five-minute sequences that were evenly distributed across the 60
355 surveyed hours to allow detecting change through time and days while keeping the time of annotation
356 of these 60 hours of videos at 200h of work. We acknowledge that this subsampling approach driven
357 by the annotation effort available may have prevented detection of extreme peaks of activity. The
358 advancement of deep-learning algorithms for the identification of fish individuals, species, and their
359 behavior (Ditria et al. 2020) has the potential to decrease annotation time and facilitate the utilization of
360 long-duration remote underwater videos in marine ecology.

361
362
363
364
365
366

367

References

- 368 Armitage AR, Ho C-K, Quigg A. 2013. The Interactive Effects of Pulsed Grazing Disturbance and
369 Patch Size Vary among Wetland Arthropod Guilds. *PLOS ONE* **8**:e76672. Public Library of Science.
- 370 Bacheler NM, Shertzer KW, Runde BJ, Rudershausen PJ, Buckel JA (2021) Environmental conditions,
371 diel period, and fish size influence the horizontal and vertical movements of red snapper. *Sci Rep*
372 **11**:9580
- 373 Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems:
374 resilience and ecosystem function on coral reefs. *Ecol Lett* **6**:281–285
- 375 Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature*
376 **429**:827–833
- 377 Bellwood DR, Hughes TP, Hoey AS (2006) Sleeping Functional Group Drives Coral-Reef Recovery.
378 *Curr Biol* **16**:2434–2439
- 379 Bennett S, Bellwood DR (2011) Latitudinal variation in macroalgal consumption by fishes on the Great
380 Barrier Reef. *Mar Ecol Prog Ser* **426**:241–252
- 381 Bijoux JP, Dagorn L, Berke G, Cowley PD, Soria M, Gaertner J-C, Robinson J. 2013. Temporal
382 dynamics, residency and site fidelity of spawning aggregations of a herbivorous tropical reef
383 fish *Siganus sutor*. *Marine Ecology Progress Series* **475**:233–247.
- 384 Birt MJ, Harvey ES, Langlois TJ (2012) Within and between day variability in temperate reef fish
385 assemblages: Learned response to baited video. *J Exp Mar Biol Ecol* **416–417**:92–100
- 386 Bonaldo RM, Hoey AS, Bellwood DR (2014) The Ecosystem Roles of Parrotfishes on Tropical Reefs.
387 *Oceanography and Marine Biology*. CRC Press,
- 388 Brandl SJ, Rasher DB, Côté IM, Casey JM, Darling ES, Lefcheck JS, Duffy JE (2019) Coral reef
389 ecosystem functioning: eight core processes and the role of biodiversity. *Front Ecol Environ*
390 **17**:445–454
- 391 Catano LB, Barton MB, Boswell KM, Burkepile DE. 2017. Predator identity and time of day interact to
392 shape the risk–reward trade-off for herbivorous coral reef fishes. *Oecologia* **183**:763–773.
- 393 Colton DE, Alevizon WS (1981) Diurnal variability in a fish assemblage of a Bahamian coral reef.
394 *Environ Biol Fishes* **6**:341–345
- 395 Cvitanovic C, Bellwood DR (2009) Local variation in herbivore feeding activity on an inshore reef of
396 the Great Barrier Reef. *Coral Reefs* **28**:127–133
- 397 Ditria EM, Lopez-Marcano S, Sievers M, Jinks EL, Brown CJ, Connolly RM (2020) Automating the
398 Analysis of Fish Abundance Using Object Detection: Optimizing Animal Ecology With Deep
399 Learning. *Front Mar Sci* **7**:
- 400 Dunkley K, Dunkley A, Drewnicki J, Keith I, Herbert-Read JE (2023) A low-cost, long-running, open-
401 source stereo camera for tracking aquatic species and their behaviours. *Methods Ecol Evol*
402 *n/a*:
- 403 Escalas A, Avouac A, Belmaker J, Bouvier T, Clédassou V, Ferraton F, Rieuvilleneuve F, Rilov G,
404 Roviroso Mulet A, Shapiro Goldberg D, Villéger S (2022) An invasive herbivorous fish
405 (*Siganus rivulatus*) influences both benthic and planktonic microbes through defecation and
406 nutrient excretion. *Sci Total Environ* **838**:156207

407 Fouda, El-Sayed (1996) Distribution and Feeding Habits of Two Surgeonfish, *Zebrafish* *xanthurum*
408 and *Ctenochaetus striatus* in the Gulf of Aqaba. *Red Sea. Mar Sci* 17:1–2

409 Fox R, Bellwood D (2008) Direct versus indirect methods of quantifying herbivore grazing impact on a
410 coral reef. *Mar Biol* 154:325–334

411 Froese, Pauly. 2023. FishBase. World Wide Web electronic publication. Available from
412 www.fishbase.org.

413 Gibson K, Olofsson J, Mooers AØ, Monroe MJ. 2021. Pulse grazing by reindeer (*Rangifer tarandus*)
414 can increase the phylogenetic diversity of vascular plant communities in the Fennoscandian
415 tundra. *Ecology and Evolution* 11:14598–14614.

416 Hoey AS, Bellwood DR (2009) Limited Functional Redundancy in a High Diversity System: Single
417 Species Dominates Key Ecological Process on Coral Reefs. *Ecosystems* 12:1316–1328

418 Houlbrèque F, Ferrier-Pagès C (2009) Heterotrophy in Tropical Scleractinian Corals. *Biological*
419 *Reviews* 84:1–17

420 Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, van de
421 Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017) Coral reefs in the
422 Anthropocene. *Nature* 546:82–90

423 Kerry JT, Bellwood DR (2015) The functional role of tabular structures for large reef fishes: avoiding
424 predators or solar irradiance? *Coral Reefs* 34:693–702

425 Knowlton N, Jackson JBC (2008) Shifting Baselines, Local Impacts, and Global Change on Coral
426 Reefs. *PLOS Biol* 6:e54

427 Lefèvre CD, Bellwood DR (2011) Temporal variation in coral reef ecosystem processes: herbivory of
428 macroalgae by fishes. *Mar Ecol Prog Ser* 422:239–251

429 Lehodey P, Alheit J, Barange M, Baumgartner T, Beaugrand G, Drinkwater K, Fromentin J-M, Hare
430 SR, Ottersen G, Perry RI, Roy C, Lingen CD van der, Werner F (2006) Climate Variability, Fish, and
431 Fisheries. *Journal of Climate* 19:5009–5030

432 Longo GO, Ferreira CEL, Floeter SR (2014) Herbivory drives large-scale spatial variation in reef fish
433 trophic interactions. *Ecol Evol* 4:4553–4566

434 Longo GO, Hay ME, Ferreira CEL, Floeter SR (2019) Trophic interactions across 61 degrees of
435 latitude in the Western Atlantic. *Global Ecology and Biogeography* 28:107–117

436 Luise Bach L, Smith B (2021) Within and between day variability in coral reef fish assemblages:
437 implications for fish community surveys. *J Appl Ichthyol* 37:847–856

438 Magneville C, Leréec Le Bricquie M-L, Dailianis T, Skouradakis G, Claverie T, Villéger S (2023) Long-
439 duration remote underwater videos reveal that grazing by fishes is highly variable through time and
440 dominated by non-indigenous species. *Remote Sensing in Ecology and Conservation* 9:311–322

441 Magurran AE, Henderson PA. 2010. Temporal turnover and the maintenance of diversity in ecological
442 assemblages. *Philosophical Transactions of the Royal Society B: Biological Sciences*
443 **365**:3611–3620. Royal Society. Available from
444 <https://royalsocietypublishing.org/doi/10.1098/rstb.2010.0285> (accessed February 8, 2023).

445 Myers EMV, Harvey ES, Saunders BJ, Travers MJ (2016) Fine-scale patterns in the day, night and
446 crepuscular composition of a temperate reef fish assemblage. *Mar Ecol* 37:668–678

447 Palardy JE, Grottoli AG, Matthews KA (2006) Effect of naturally changing zooplankton concentrations
448 on feeding rates of two coral species in the Eastern Pacific. *Journal of Experimental Marine Biology*
449 *and Ecology* 331:99–107

450 Palardy J, Grottoli A, Matthews K (2005) Effects of upwelling, depth, morphology and polyp size on
451 feeding in three species of Panamanian corals. *Mar Ecol Prog Ser* 300:79–89

452 Parravicini V, Casey JM, Schiettekatte NMD, Brandl SJ, Pozas-Schacre C, Carlot J, Edgar GJ,
453 Graham NAJ, Harmelin-Vivien M, Kulbicki M, Strona G, Stuart-Smith RD (2020) Delineating reef fish
454 trophic guilds with global gut content data synthesis and phylogeny. *PLOS Biol* 18:e3000702

455 Pickholtz R, Kiflawi M, Crossin GT, Pickholtz EY, Zamsky R, Kahan I, Gavriel T, Belmaker J (2022)
456 Highly repetitive space-use dynamics in parrotfishes. *Coral Reefs* 41:1059–1073

457 Pickholtz R, Kiflawi M, Friedlander A, Belmaker J (2018) Habitat utilization by an invasive herbivorous
458 fish (*Siganus rivulatus*) in its native and invaded range. *Biol Invasions* 20:1–14

459 Price NW, Chen K-S, Chen CA, Wen CK-C (2021) Scraping and grazing herbivorous/detritivorous fish
460 display opposite feeding behaviours under different protection regulations. *Mar Biol Res*
461 17:876–891

462 Rasher DB, Hoey AS, Hay ME (2013) Consumer diversity interacts with prey defenses to drive
463 ecosystem function. *Ecology* 94:1347–1358

464 Robinson J, Aumeeruddy R, Jörgensen TL, Öhman MC. 2008. Dynamics of Camouflage
465 (*Epinephelus Polyphekadion*) and Brown Marbled Grouper (*Epinephelus Fuscoguttatus*)
466 Spawning Aggregations at a Remote Reef Site, Seychelles. *Bulletin of Marine Science*
467 83:415–431.

468 Rooker JR, Dennis GD (1991) Diel, Lunar and Seasonal Changes in a Mangrove Fish Assemblage off
469 Southwestern Puerto Rico. *Bull Mar Sci* 49:684–698

470 Schiettekatte NMD, Brandl SJ, Casey JM, Graham NAJ, Barneche DR, Burkepile DE, Allgeier JE,
471 Arias-González JE, Edgar GJ, Ferreira CEL, Floeter SR, Friedlander AM, Green AL, Kulbicki
472 M, Letourneur Y, Luiz OJ, Mercière A, Morat F, Munsterman KS, Rezende EL, Rodríguez-
473 Zaragoza FA, Stuart-Smith RD, Vigliola L, Villéger S, Parravicini V (2022) Biological trade-offs
474 underpin coral reef ecosystem functioning. *Nat Ecol Evol* 6:701–708

475 Semmler RF, Brandl SJ, Keith SA, Bellwood DR. 2021. Fine-scale foraging behavior reveals
476 differences in the functional roles of herbivorous reef fishes. *Ecology and Evolution* 11:4898–
477 4908.

478 Shapiro Goldberg D, Rilov G, Villéger S, Belmaker J. 2021. Predation Cues Lead to Reduced
479 Foraging of Invasive *Siganus rivulatus* in the Mediterranean. *Frontiers In Marine Science* 8.
480 Frontiers Media SA.

481 Siqueira AC, Morais RA, Bellwood DR, Cowman PF (2021) Planktivores as trophic drivers of global
482 coral reef fish diversity patterns. *Proc Natl Acad Sci* 118:e2019404118

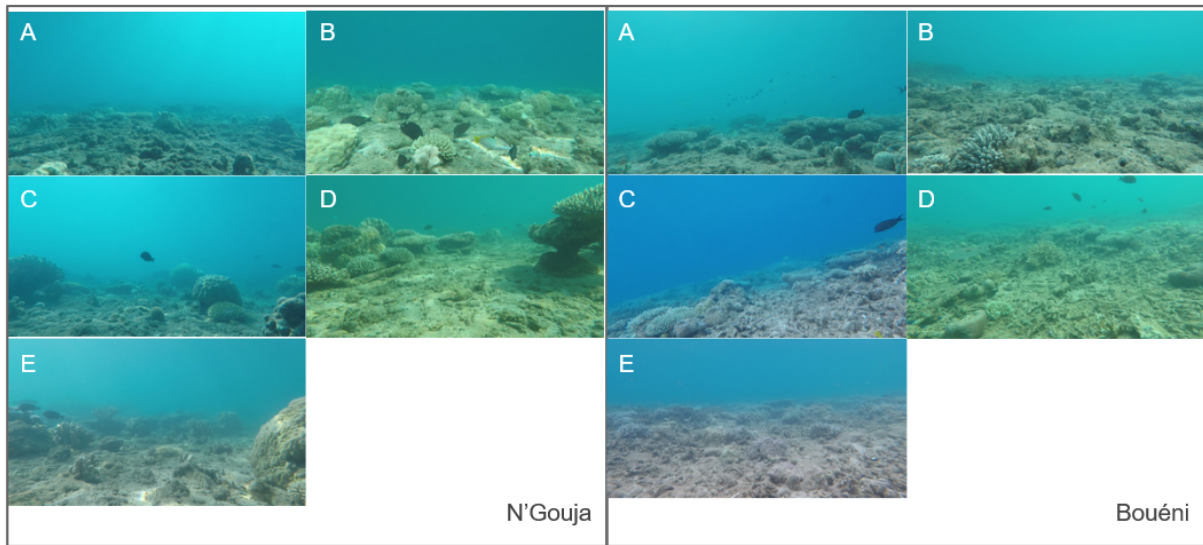
483 Taborsky M, Limberger D (1980) The Activity Rhythm of *Blennius sanguinolentus* Pallas*. *Mar Ecol*
484 1:143–153

485 Tebbett SB, Goatley CHR, Bellwood DR (2017) Clarifying functional roles: algal removal by the
486 surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus*. *Coral Reefs* 36:803-813

487 Tebbett SB, Hoey AS, Depczynski M, Wismer S, Bellwood DR (2020) Macroalgae removal on coral
488 reefs: realised ecosystem functions transcend biogeographic locations. *Coral Reefs* 39:203–214
489 Thompson A, Mapstone B (2002) Intra- versus inter-annual variation in counts of reef fishes and
490 interpretations of long-term monitoring studies. *Mar Ecol Prog Ser* 232:247–257
491 Treignier C, Grover R, Ferrier-Pagés C, Tolosa I (2008) Effect of light and feeding on the fatty acid
492 and sterol composition of zooxanthellae and host tissue isolated from the scleractinian coral
493 *Turbinaria reniformis*. *Limnology and Oceanography* 53:2702–2710
494 Vergés A, Bennett S, Bellwood DR (2012) Diversity among Macroalgae-Consuming Fishes on Coral
495 Reefs: A Transcontinental Comparison. *PLoS ONE* 7:e45543
496 Zemke-White WL, Choat J, Clements K (2002) A re-evaluation of the diel feeding hypothesis for
497 marine herbivorous fishes. *Mar Biol* 141:571–579
498
499

500
501

Supplementary Informations



502
503
504

Supplementary Figure 1: Captions of the field-of-view of the six cameras recording in the two studied sites.

505 Supplementary Table 1: Results of Analysis of Deviance Table based on the Generalised Linear Mixed
 506 Model testing the effect of site and time slots on feeding activities intensities with surveyed day being a
 507 random effect.
 508

Feeding activity	Effect studied	ChiSq	Pvalue
Corallivory	Site	22.79	< 0.01
Corallivory	Time of the day	9.14	< 0.01
Herbivory	Site	4.25	< 0.01
Herbivory	Time of the day	9.34	< 0.01
Invertivory	Site	0	0.998
Invertivory	Time of the day	2.117	0.346

509
 510
 511
 512
 513
 514
 515
 516
 517
 518
 519

520 Supplementary Table 2: Results of the Analysis of Deviance Table based on the Generalised Linear
 521 Mixed Model testing the effect of time slots on feeding activities intensities with surveyed day being a
 522 random effect.

523

Protection level	Feeding activity	ChiSq	Pvalue
N'Gouja	Corallivory	2.03	0.361
Bouéni	Corallivory	14.06	< 0.01
N'Gouja	Herbivory	1.249	0.536
Bouéni	Herbivory	22.149	< 0.01
N'Gouja	Invertivory	1.189	0.552
Bouéni	Invertivory	1.624	0.444

524

525

526 Supplementary Table 3: Results of the analysis of variance to test difference in variation in species
 527 composition over time slots or sites for each feeding activity (permdisp test)
 528

Feeding Activity	Variable	F	Pvalue
Corallivory	Time slots	0.036	0.965
Corallivory	Site	0.214	0.887
Herbivory	Time slots	0.462	0.644
Herbivory	Site	0.056	0.818
Invertivory	Time slots	0.620	0.560
Invertivory	Site	0.349	0.568

529

530 Supplementary Table 4: Results of the PERMANOVA testing for effect of site and time slots on species
 531 composition.
 532

Feeding Activity	Effect studied	F	Pvalue
Corallivory	Time slots	1.190	0.320
	Site	0.840	0.589
Herbivory	Time slots	1.600	0.124
	Site	1.567	0.155
Invertivory	Time slots	0.680	0.899
	Site	1.667	0.069

533

534 Supplementary Table 5: Results of the analysis of variance to test of difference in variation in the
 535 distribution of feeding activities over time slots or sites (permdisp test)
 536

Feeding Activity	Variable	F	Pvalue
Corallivory	Time slots	0.017	0.983
Corallivory	Site	0.110	0.747
Herbivory	Time slots	0.002	0.998
Herbivory	Site	0.023	0.882
Invertivory	Time slots	0.339	0.721
Invertivory	Site	0.412	0.535

537
 538

539 Supplementary Table 6: Results of the PERMANOVA testing for effect of site and time slots in the
 540 contribution of species to feeding activities.
 541

Feeding Activity	Effect studied	F	Pvalue
Corallivory	Time slots	0.610	0.747
	Site	5.910	< 0.01
Herbivory	Time slots	0.591	0.706
	Site	3.99	< 0.01
Invertivory	Time slots	0.889	0.616
	Site	1.730	0.061

542

543 Supplementary Table 7: Spearman's correlations test between feeding activities based on sequences
 544 bites number in N'Gouja and in Bouéni separately.

Protection level	Pair	Rho	S	Pvalue
N'Gouja	Corallivory/ Invertivory	0.382	789.61	0.065
N'Gouja	Corallivory/ Herbivory	-0.1636	2676.6	0.444
N'Gouja	Invertivory/ Herbivory	0.322	2139.3	0.124
Bouéni	Corallivory/ Invertivory	0.626	859.37	< 0.01
Bouéni	Corallivory/ Herbivory	0.344	1508.8	0.099
Bouéni	Invertivory/ Herbivory	0.402	1313.8	0.051

545

546

547