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

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Abstract :

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

Keywords : Feeding activities, Coral reef fishes, Temporal variability, Daily variability, Species dominance

Introduction

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

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

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

Material and Methods

Remote Underwater Video recording

This study was carried out on two fringing reefs around Mayotte Island (Western Indian Ocean). The two fringing reefs were similar with an average depth of three meters and habitat made by a mix of branching, massive and encrusting living corals, turf on dead corals and sandy sediment (see Supp. Fig. 1 for filmed quadrat). The first reef, Bouéni (-12.9162° lat; 45.0807° long) is within a Poorly Protected marine Area (PPA) ("Parc Naturel Marin de Mayotte" https://parc-marin-mayotte.fr/) encompassing all the lagoon. The second reef, N'Gouja (-12.9639° lat; 45.0870° long), is within a Fully Protected marine Area (FPA) where fishing is prohibited and is 5.3 km away from the poorly protected site.

Surveys were carried out on four days spanning from 03/11/2020 to 06/11/2020, monitoring each site every other day. Rainfall events occurred on the second surveyed day in N'Gouja. Five GoPro Hero 5 (GoPro Inc, United States) mounted on a 35 cm high tripod were set to record high-definition videos (1920 by 1080 pixels at 25 frames per second) with a 90° field-of-view ("Linear" mode on GoPro settings). Cameras were set up from 18 to 140 meters apart with no substrate obstructing the camera's field-of-view up to 3m. After the start of the recording, a 2m² quadrat was briefly placed in front of each camera to eventually measure fish diversity over this standardized area (Longo et al. 2014). A reference watch was also displayed in front of each camera soon after the start of recording so that all videos were eventually synchronized with a one second precision.

Cameras recorded continuously on three time spans: 07:00-09:00, 11:15-13:15 and 15:30-17:30. To minimize the effects of diver presence on fish behavior, we limited our feeding annotations with buffer periods after camera placement and before retrieval. For each video, annotations commenced 30 minutes after divers left the survey area following camera placement and ended 30 min before divers returned within 250m of the camera. This allowed three discontinued hours of video for each day (from 07:30:00 to 08:30:00, from 11:30 to 12:30 and from 15:30 to 16:30).

Measuring feeding activities

As annotating all individuals and their feeding activity is demanding (up to 10 minutes of annotation for each minute of video), we assessed the feeding activity on a subset of the video recorded. More precisely, annotations of feeding activities were done on four evenly spaced sequences of five minutes (i.e. every 15 minutes) yielding 12 annotated sequences per day and per camera (equivalent to 60 minutes of annotations per day and per camera).

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

Statistical analysis

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

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) and site on the intensity of corallivory, herbivory and invertivory, we applied Generalised Linear Mixed Models (GLMMs) with a negative binomial distribution. Five-minute sequences were used as replicates and the surveyed day was counted as a random effect:

Number of bites ~ time slot + site + (1|day)

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 the intensity of the three feeding activities in each site separately we applied likewise Generalised Linear Mixed Models (GLMMs) with a negative binomial distribution. Five-minute sequences were used as replicates and the surveyed day was counted as a random effect:

Number of bites ~ time slot + (1|day)

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

To test for a turnover in species composition across the three time slots and the two sites, we computed Jaccard dissimilarity between all pairs of five-minute sequences based on the presence or absence of each species. Subsequently, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) on this dissimilarity matrix with time slots and sites as groups.

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

Results

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

Within and between day variability of feeding activities

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

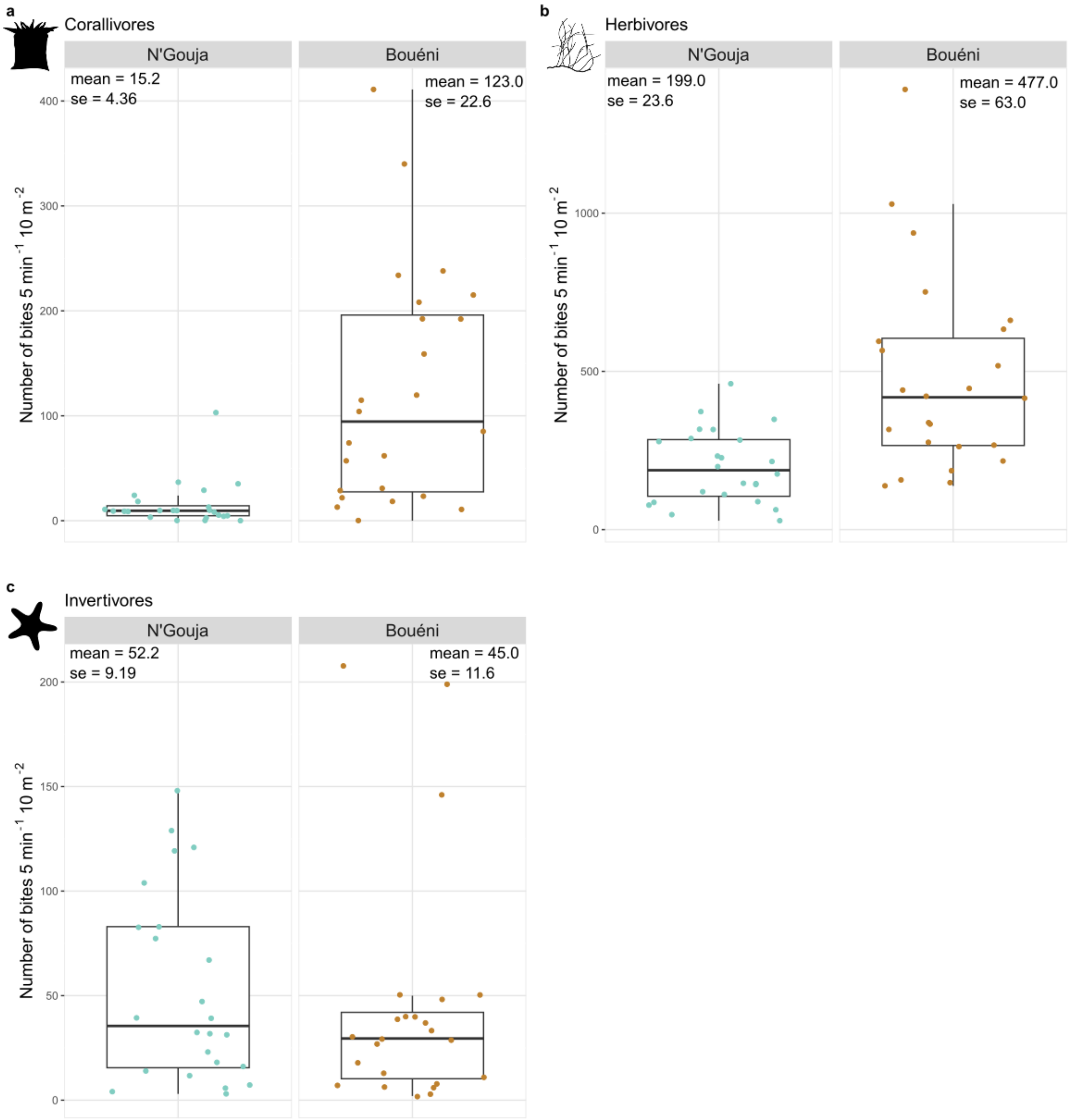

Figure 1: Variation in the number of bites across trophic groups and sites. The number of bites by all fish from a trophic group were counted for 5-minute sequences over 10m² (5 quadrats of 2m² surveyed each by a camera).

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

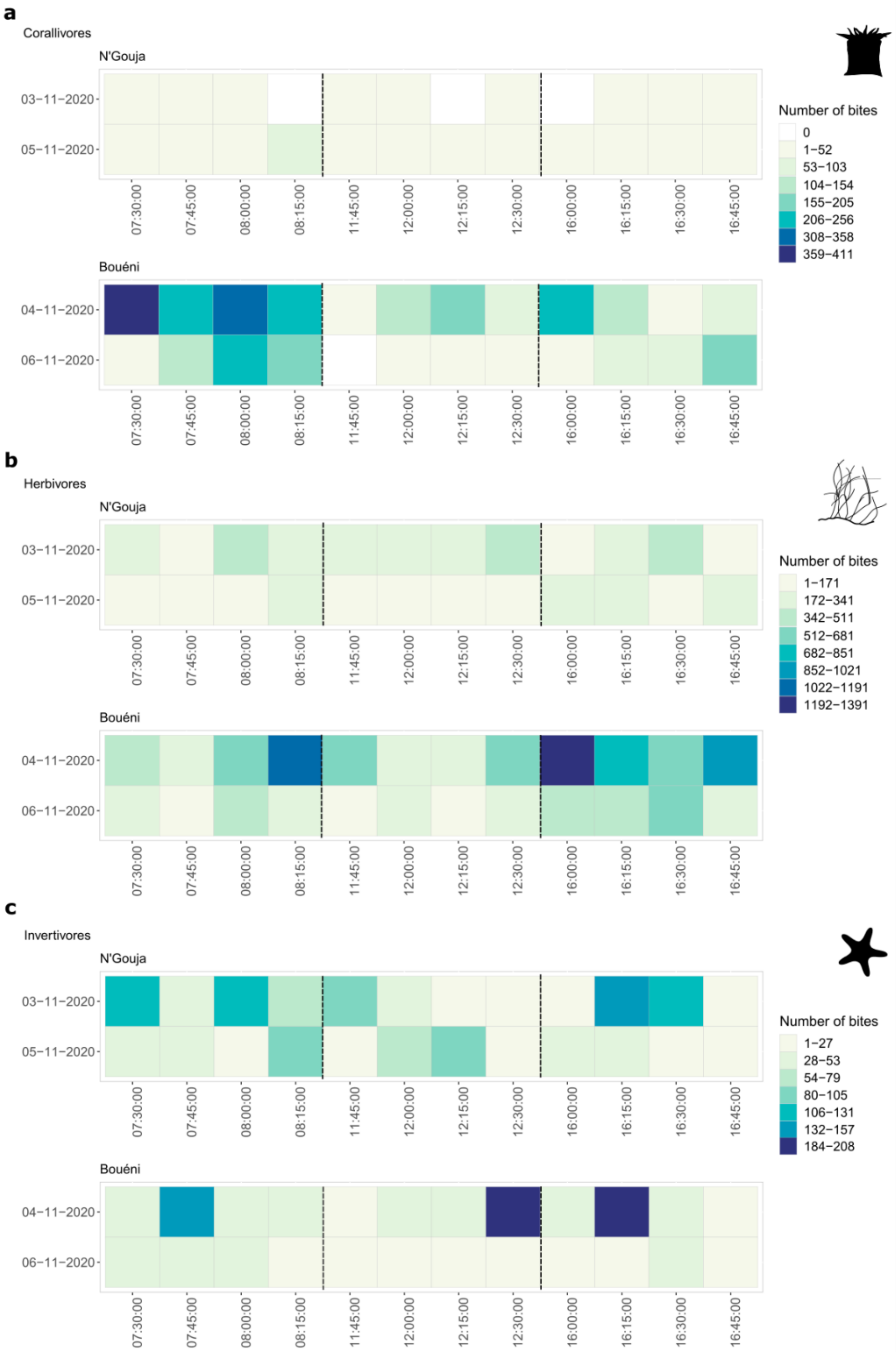

Figure 2: Heatmaps of corallivores (a), herbivores (b) and invertivores (c) feeding activities. Colors reflect the number of bites recorded on 10m² for five minutes. Classes were defined to represent one eighth of the span of the feeding activity recorded across the two sites. The top row of each feeding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

For the three feeding activities there was no significant difference in species composition between time slots (PERMANOVA on Jaccard dissimilarity p-value > 0.05 ; Supp Table 3 and 4) and no significant difference in the contribution of species to feeding activities (PERMANOVA on Bray-Curtis dissimilarity p-value > 0.05 ; Supp Table 5 and 6).

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

Species dominance on feeding activities

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

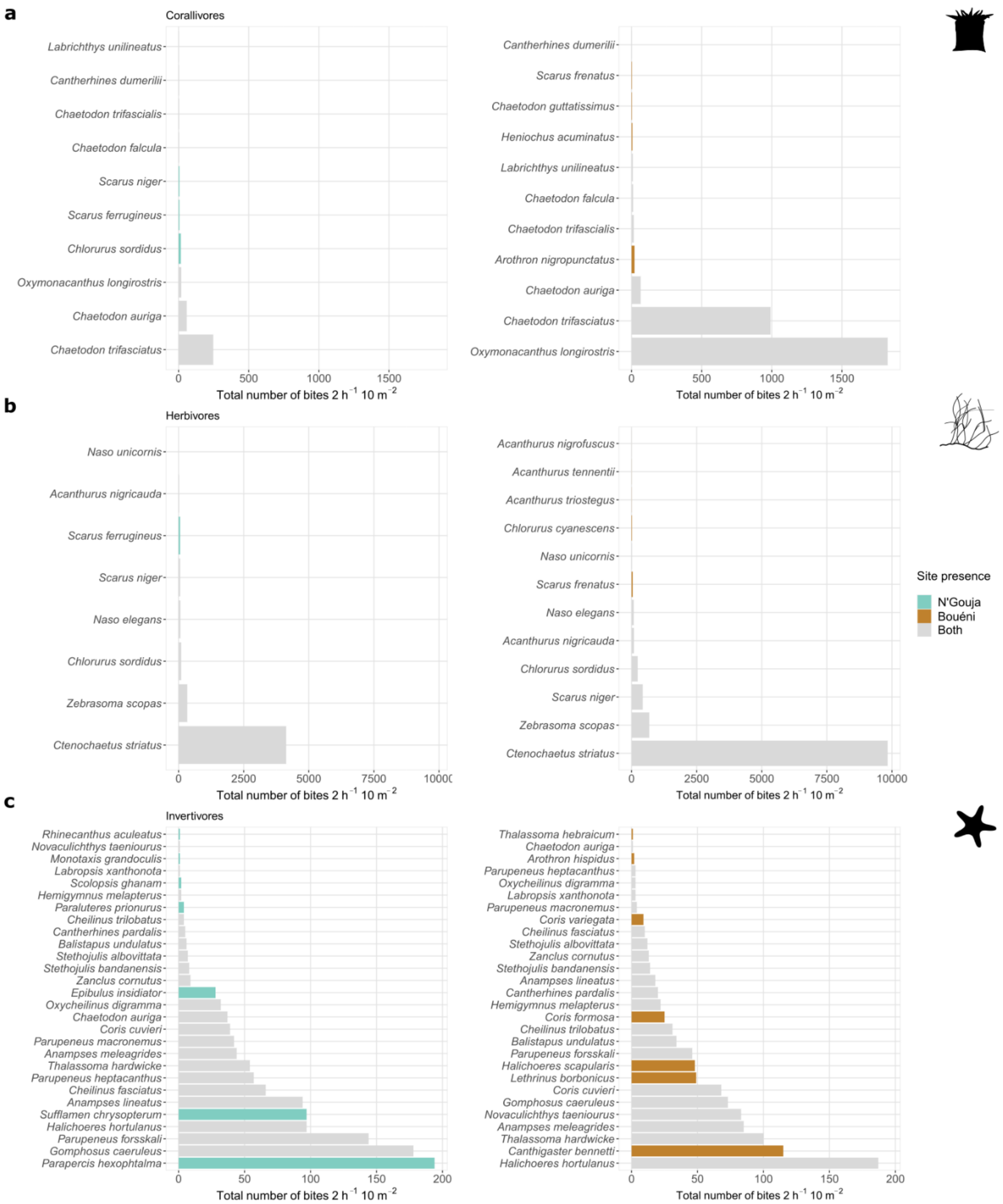

Figure 3: Total bite number per species for each feeding activity and site. Corallivory (a), herbivory (b), and invertivory (c) are expressed per species (y axis) as the overall number of bites across all 24 sequences of 5 minutes over 10m² (x axis). For each of the three feeding activities, the left plot represents data for N'Gouja and the right plot represents data for Bouéni. Bars are coloured if the species is only seen in the N'Gouja (green) or in Bouéni (brown) and are gray if present on both sites.

In both sites, the five highest peaks of corallivory were due to *Chaetodon trifasciatus* which did 82.46% and 41.93% of the observed bites on corals in N'Gouja and Bouéni, respectively (Figure 4). In

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

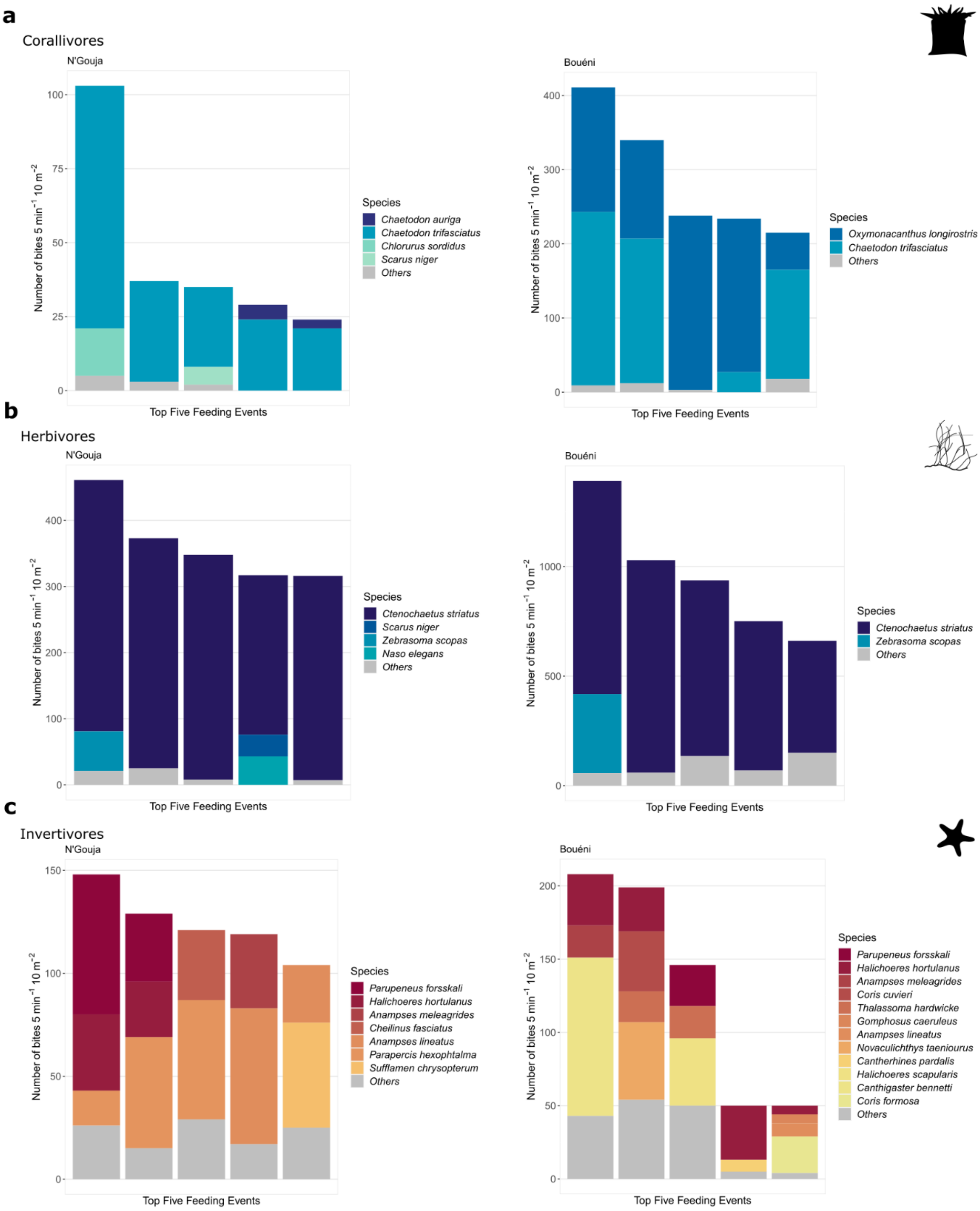

Figure 4: Species contribution to the five sequences showing the highest feeding activities. Corallivory (a), herbivory (b), and invertivory (c) are expressed as the number of bites per five minutes per 10m² (y axis). Colors represent species contributions in decreasing numbers of bites per unit of time.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

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

Discussion

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

For a given reef surface, feeding activities were performed in pulses with nearly half of the total corallivory and invertivory activities and more than one third of the herbivory activity occurring in less than one fifth of the time. Such pulses have already been depicted in terrestrial and subtidal environments (Armitage et al. 2013; Gibson et al. 2021) on time periods larger than a day and in temperate marine ecosystems at short temporal scales (Magneville et al. 2022). These pulses of feeding are likely to drive later (i.e. after digestion) pulses of nutrient excretion and egestion. For herbivorous fish feeding before night, it could eventually impact biogeochemical fluxes in resting places (Escalas et al. 2022). The three feeding activities were not correlated through time as it has already been shown for species abundance (Magurran & Henderson 2010). This result highlights the importance of including within-day temporal variation when studying ecological processes. In fact, if trophic-based processes are censused at a single time of the day, it could bias the perception of their respective magnitude. Specifically this variation of feeding activities could be driven by a mix of environmental and behavioral conditions which drive species mobility and thus foraging activity. For instance, solar radiations can influence species mobility as they seek shelter beneath tabular structures to avoid UV radiation (Kerry and Bellwood 2015). Additionally, tides present a range of feeding opportunities (Thompson and Mapstone 2002).

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

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

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

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

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

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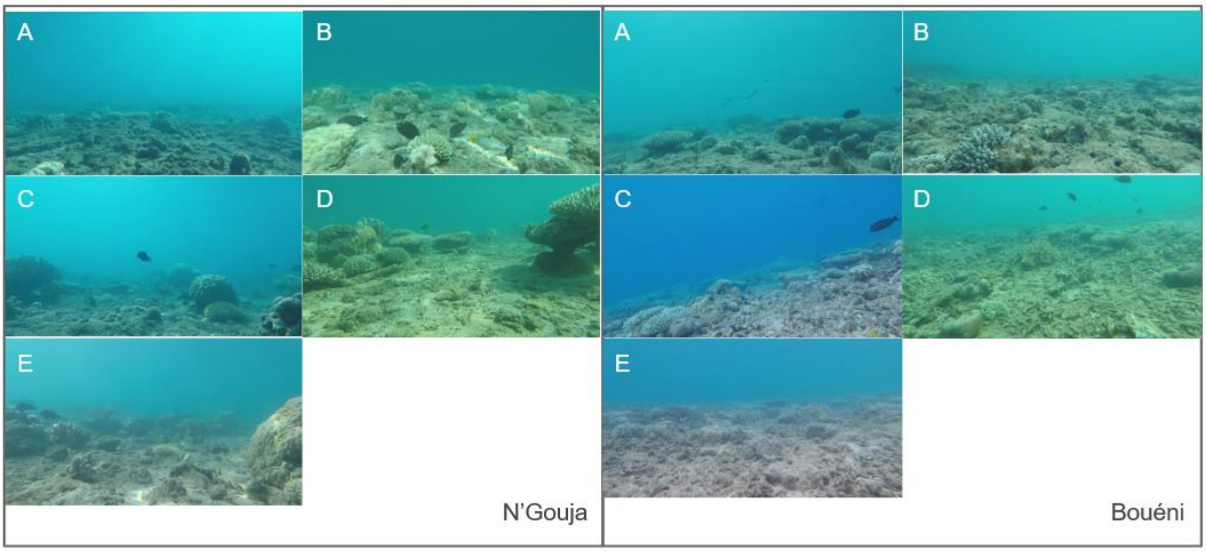
Supplementary Informations



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

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

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

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

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

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

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

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

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

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

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

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

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

Supplementary Table 7: Spearman's correlations test between feeding activities based on sequences 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