
Diurnal temporal patterns of the diversity and the abundance of reef fishes in a branching coral patch in New Caledonia

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Abstract :

Small-scale spatial and temporal variability in animal abundance is an intrinsic characteristic of marine ecosystems but remains largely unknown for most animals, including coral reef fishes. In this study, we used a remote autonomous unbaited video system and recorded reef fish assemblages during daylight hours, 10 times a day for 34 consecutive days in a branching coral patch of the lagoon of New Caledonia. In total, 50 031 fish observations belonging to 114 taxa, 66 genera and 31 families were recorded in 256 recorded videos. Carnivores and herbivore-detritus feeders dominated the trophic structure. We found significant variations in the composition of fish assemblages between times of day. Taxa richness and fish abundance were greater in the early morning and in the late afternoon than during the day. Fourteen taxa displayed well-defined temporal patterns in abundance with one taxon influenced by time of day, six influenced by tidal state and seven influenced by both time of day and tidal state. None of these 14 taxa were piscivores, 10 were herbivore-detritus feeders, three were carnivores and one was plankton feeder. Our results suggest a diel migration from feeding grounds to shelter areas and highlight the importance of taking into account small-scale temporal variability in animal diversity and abundance when studying connectivity between habitats and monitoring communities.

Keywords : coral reef fish, high-frequency sampling, patterns, temporal variation, underwater video

INTRODUCTION

Coral reef ecosystems are characterized by high diversity and complex co-evolved relationships between organisms (Sale 1991). They are highly dynamic systems with variable natural and anthropogenic disturbances acting at various spatial and temporal scales (Moberg & Folke 1999; Bellwood *et al.* 2003; Helfman *et al.* 2009). These variations are affecting biological processes, such as recruitment, competition and predation (Ricklefs 2004; Helfman *et al.* 2009; Bonaldo *et al.* 2012). These ecosystems contain the most diverse fish assemblages to be found anywhere on the planet (Lieske & Myers 2001). For instance, the archipelago of New Caledonia in the South-Pacific has a total of 2328 recorded fish species belonging to 246 families (Fricke *et al.* 2011). Understanding the functioning of such complex communities and gathering information on the biology of such diverse fish assemblages is challenging. Yet, it is crucial for appropriate coral reef management, especially in the current context of reef degradation at a global scale (Hughes *et al.* 2003; Burke *et al.* 2011).

Despite the large number of studies on spatial and temporal variations of reef fish populations, limited information exists at small scales (Bijoux *et al.* 2013). Most existing studies on fish temporal variations have focused on annual, seasonal or monthly variations (Galzin 1987; Fisk & Harriott 1990; Winemiller 1990; Connell & Jones 1991; Kingsford 1992; Jenkins & Wheatley 1998; Condal *et al.* 2012). Others compared diurnal and nocturnal fish assemblages (Hobson 1965; Colton & Alevizon 1981; Galzin 1987; Rooker & Dennis 1991; Danilowicz & Sale 1999; Aguzzi *et al.* 2013; Toobaie *et al.* 2013) and generally reported minimal abundances at night and maximum around midday. Some changeovers in behaviour, distribution and abundance of reef fish at sunrise and sunset were also identified (Hobson 1972; Galzin 1987; Danilowicz & Sale 1999; Santos *et al.* 2002; Azzurro *et al.* 2013). Several periods in the temporal organization of reef fish assemblages were identified with for example a period at dusk when diurnal fishes seek cover followed by a mass emergence of nocturnal species after an interim period (Hobson

1972). Predation risk was also defined to be significantly higher at dusk and at night than during the day (Bosiger & McCormick 2014).

Very little information exists on within-day temporal variations in fish assemblage while some authors have clearly shown that the abundance of certain species significantly varied according to the time of day (Thompson & Mapstone 2002; McClanahan *et al.* 2007; Birt *et al.* 2012; Chabanet *et al.* 2012) or tidal state (Abou-Seedo *et al.* 1990; Unsworth *et al.* 2007; Castellanos-Galindo & Krumme 2015). For instance, Birt *et al.* (2012) detected significant differences in the fish assemblage within and among days. Thompson and Mapstone (2002) found that within-day variation in abundance was highest for the Lutjanidae, Serranidae and Siganidae. Chabanet *et al.* (2012) found that Acanthuridae were more abundant in the morning, whereas Scaridae abundance was higher at sunrise and sunset. Such results provide new insights on fish territories, home range and site fidelity, movement and activity patterns, habitat connectivity and species interactions. These processes are probably most effectively studied by acoustic telemetry (Lowe *et al.* 2003; Egli & Babcock 2004; Meyer *et al.* 2007). However, for practical reasons, it is not possible to tag all fish of a study area, and thus most acoustic studies are constrained to a few large species (e.g. Zeller 1997; Egli & Babcock 2004; Wetherbee *et al.* 2004; Eristhee & Oxenford 2005; Chateau & Wantiez 2007; Meyer *et al.* 2007). Because small-scale spatio-temporal variations in fish abundance may involve many species in the assemblages (Colton & Alevizon 1981; Spyker & Van Den Berghe 1995), the use of underwater video systems permanently deployed on the reef may provide useful complementary information to both underwater visual census (UVC) surveys and acoustic telemetry. Like UVC, video can record many individuals and species, and like acoustic telemetry, it can provide data with a high temporal frequency. Conversely to fishing techniques, video is non destructive and can therefore be used in protected areas (see review by Mallet & Pelletier 2014). Nowadays, time series videos on fish assessment can be obtained by cabled observatories (e.g. Aguzzi *et al.* 2011; Aguzzi *et al.* 2012; Doya

et al. 2014; Aguzzi *et al.* 2015) or by programmable autonomous video systems (e.g. Mallet 2014).

The purpose of this study was to characterize the patterns of reef fish diversity and abundance in a live branching coral patch reef in relation to time of day and tidal state. To achieve this, we used a remote, unbaited and programmable rotating video system (see description in Mallet 2014) and recorded videos during daylight every 1.25 h (10 times a day) for 34 consecutive days. These videos were used to investigate the following hypotheses: (1) time of day and tidal state affect reef fish diversity and abundance patterns in a patch reef; (2) the influence of these factors on reef fish depends on species functional traits such as diet, and (3) most reef fish species display a well-defined abundance pattern depending on the time of day and/or on tidal state.

METHODS

Study area

The study was conducted in the Marine Protected Area (MPA) of Aboré Reef located 20 km off Nouméa (22°26'S, 166°21'W) in the Southwest Lagoon of New Caledonia in the South Pacific (Fig. 1). This MPA has a total area of 80 km² and has been closed to fishing since 1996. The reserve is composed of a barrier reef bordered by a strip of sand and by submerged patch reefs (Kulbicki *et al.* 2007). For the study, one permanent video system was deployed on a patch reef of the inner barrier reef slope at 5 m depth on sand surrounded by branching corals (mostly *Acropora* spp.) (Fig. 2).

Sampling technique and design

Censuses were conducted from 27 September 2012 to 31 October 2012. The underwater video rotating system used is programmable, remote, unbaited and autonomous named "MICADO" (see full description in Mallet 2014). Like the STAVIRO system (Pelletier *et al.* 2012 and Mallet *et al.* 2014), the MICADO system rotates from 60° every 30 seconds. It consists of a single waterproof housing enclosing a high-definition camera; an engine which induces the rotation of the camera; and a timer to program the time periods for switching the system on and off. The housing and the camera result in a focal angle of 60° and the housing is fixed onto a weighted tripod (6 kg) to stabilize the system set on the sea floor (Fig. 2). For the present study, the system was programmed to record 2 full (360°) consecutive rotations. In order to have enough natural light for video analyses, all videos were recorded during daylight hours from 30 min after sunrise to 30 min before sunset. Videos were recorded every 1.25 h in order to have the same time period between each record homogeneously distributed throughout the light period of the day for the season. This resulted in 10 videos per day with each video lasting 7 minutes (2 rotations x 6 sectors x 30 s per sector lasted 6 minutes + 1 minute of rotations corresponding to the time required for the system to rotate from one sector to the next one during 2 rotations).

Video analyses

Videos were analyzed by a single observer using the procedure described in Pelletier *et al.* (2012). For each video sequence, all individuals were identified at the highest taxonomic level possible within a radius of 6 m around the camera (representing a sampling area of 113 m²). The radius of 6 m corresponded to the poorest water visibility observed at the sampling site during the experiment and was defined by *in situ* measurement of distances from the camera to several coral colonies in the field of view of

the camera. In coral reefs, many fish species are similar and difficult to distinguish on videos unless they are close enough to the camera. Species which were impossible to distinguish on videos were thus grouped in five following species complexes: (i) *Stegastes* gp for the group *Stegastes fasciolatus*, *S. nigricans*, *S. punctatus*; (ii) *Ctenochaetus* gp for *Acanthurus nigrofuscus*, *Ctenochaetus striatus*, *C. binotatus*, *C. cyanocheilus*; (iii) *Acanthurus* gp for *Acanthurus blochii*, *A. dussumierii*; (iv) *Chromis* gp for *Chromis viridis*, *C. atripectoralis*; (v) *Pomacentrus* gp for *Pomacentrus pavo*, *P. coelestis*. Each complex was addressed as a single taxon in the analysis and taxa richness represents the number of identified species and complexes. Taxa richness was calculated as the total number of species and complexes observed over 2 consecutive rotations. Individuals were counted per sector (sequence of 30 sec) and then summed over the six sectors of a rotation (360°). To minimize potential double counting from one sector to another, particular attention was given to the direction of fish movement with respect to camera rotation. Visual count per taxon at a given time was calculated as the maximum count taken over the two rotations. Visual counts were expressed in densities (number of individuals per 10 m²) computed from fish observed within a 6 m radius from the camera.

Trophic groups

All fishes (whatever their taxonomic level of identification) were assigned to the following trophic groups based on Kulbicki *et al.* (2011): “H” for herbivore-detritus feeders that feed predominantly on epilithic algal; “K” for plankton feeders that feed predominantly on invertebrate material in the water column; “C” for carnivores that feed predominantly on sessile and mobile benthic invertebrates and “P” for piscivores that feed predominantly on fishes. Taxa were also classified depending on their frequency of occurrence (noted “Freq.” here below) in all the videos recorded throughout the entire study as permanent (Freq. \geq 75%), frequent (30% \leq Freq. < 75%), infrequent (10% \leq Freq. < 30%) or rare taxa (Freq. < 10%).

Data analyses

The effect of the time of day and tidal state on taxa richness and density were analysed separately using one-way repeated measures MANOVAs (with Wilks' lambda multivariate tests). One-way repeated measures MANOVAs were run for each metric on all observations together and then for each trophic group. Time of day (06:00, 07:15, 08:30, 09:45, 11:00, 12:15, 13:30, 14:45, 16:00, 17:15) and tidal state (low tide, rising tide, high tide, ebb tide) were treated as fixed factors and day as a repeated factor in all analyses. When MANOVAs showed significant differences depending on time of day or tidal state, pairwise comparison tests were performed at 5% confidence level to evidence differences between distinct times of day or tidal states.

At taxon level, patterns of variations between times of day or tidal states were identified using cluster analysis. Mean densities per time of day or tidal state were calculated for each taxon. Data were then standardized to account for differences in densities among taxa, and thus avoid that the most abundant taxa drive the patterns. Standardized data were clustered using the Hierarchical Ascending Classification method (HAC; Legendre & Legendre 1998) and the Ward aggregation procedure (Lebart *et al.* 1997). In order to formally test the differences between clusters, a between-class analysis (BCA, Chessel *et al.* 2004; Dray & Dufour 2007) including a Monte-Carlo test with 9999 random permutations was conducted using time of day or tidal state as factors. This was followed by repeated measures MANOVAs and pairwise comparison tests to best characterize the temporal patterns of taxa within each cluster as previously. Because both cluster and between-class analysis can be sensitive to rare occurrences, rare taxa were removed from the dataset prior to cluster analysis (Hair *et al.* 2010). All analyses were performed using R software.

RESULTS

During the field experiment, some technical issues with the video system resulted in 256 videos recorded instead of 340 covered by the sampling design. This reduced the statistical analysis to 17 days of data for the factor “time of day” (where one video each 1.25 h per day was needed) and 22 days for the factor “tidal state” (one video each tidal state per day).

Reef fish diversity

A total of 50032 fish observations belonging to 114 taxa (110 species and 4 complexes), 66 genera and 31 families were observed in the 256 videos analysed (Table 1, Supplementary material 1). 80% of fish observations were identified with 27576 observations identified at the species level and 12311 at the complex level (96% of complexes were Pomacentridae). 20% (10145) of fish observations could not be identified at species or complex levels. Most of them were Scaridae (8690) and Caesionidae (612) (Table 1).

The most frequent families were Acanthuridae (Freq. = 100% with six species and two complexes), Pomacentridae (Freq. = 100% with four species and two complexes), Scaridae (Freq. = 100% with 13 species), Labridae (Freq. = 99.6% with 19 species), Chaetodontidae (Freq. = 98.4% with 14 species), Lethrinidae (Freq. = 75% with five species) and Serranidae (Freq. = 67.2% with six species). The most frequent taxa were carnivores and herbivore-detritus feeders (Table 2). 54% of taxa (61 species and one complex) were rare and observed in less than 10% of the videos; and for some families, only one species was seen in a single video (Belonidae, Hemiramphidae, Monacanthidae and Myliobatidae) or in two videos (Ginglymostomatidae and Stegostomidae). These rare families were mostly carnivores and piscivores (Table 2) and composed of large mobile

species (e.g. sharks or rays) passing within the field of view of the camera, or small cryptic species (e.g. filefishes) (see Supplementary material 2 for details on observed fish).

Effect of time of day

Taxa richness and density significantly varied with time of day (one-way repeated measures MANOVA, $p < 0.01$ for both variables) (Fig. 3A and 3C). More taxa were observed in the early morning (06:00, mean \pm SE: 29.1 ± 1.3 taxa) and in the late afternoon (17:15, 29.6 ± 1.0 taxa) than during the rest of the day (07:15 to 16:00, 23.6 ± 1.0 taxa in average, Fig. 3A). Density also displayed a U-shaped curve (Fig. 3C). It was maximal in the early morning (06:00: 14.1 ± 0.6 ind/10m²) and late afternoon (17:15: 14.0 ± 0.8 ind/10m²), gradually decreased between 06:00 and 11:00, remained at a minimum between 11:00 and 14:45 (9.4 ± 0.4 ind/10m² in average) and increased between 14:45 and 17:15 (Fig. 3C). MANOVAs performed for each trophic group showed that taxa richness of herbivore-detritus, carnivores and plankton feeders significantly varied with time of day ($p < 0.05$) but not for piscivores; whereas density only changed significantly for herbivore-detritus feeders ($p < 0.01$) (Fig. 3B,D). Pairwise comparisons indicated that taxa richness of herbivore-detritus feeders was significantly higher at 06:00 (12.8 ± 0.4 taxa) and 17:15 (11.7 ± 0.5 taxa) than at any other times (9.1 ± 0.5 taxa in average) ($p < 0.01$, Fig. 3B). Similar results were observed for densities with significantly higher values at 06:00 (6.0 ± 0.4 ind/10m²) and 17:15 (5.1 ± 0.6 ind/10m²) than at any other times (2.0 ± 0.2 ind/10m² in average) ($p < 0.01$, Fig. 3D). Taxa richness of plankton feeders was significantly higher in late afternoon (16:00 = 6.2 ± 0.2 and 17:15 = 6.1 ± 0.2 taxa) ($p < 0.05$) compared to the rest of the day (5.3 ± 0.3 taxa in average). Taxa richness of carnivores was substantially higher at 17:15 (12.8 ± 0.7 taxa) ($p < 0.05$) than during the afternoon (12:15-16:00: 10.6 ± 0.7 taxa in average) (Fig. 3C).

Hierarchical Ascending Classification (HAC) of fish density grouped taxa into three main clusters (Fig. 4 and Supplementary Material 3 for examples of species specific

patterns of each group). The between-class analysis (BCA) revealed a highly significant difference between these three clusters (Monte-Carlo test with 9999 random permutations, $p < 0.01$). Cluster 3 displayed a flat pattern with no significant differences between times of day (pairwise comparison, $p > 0.05$). It was composed of 46 taxa including 41 species, three complexes, and unidentified Pomacentridae and Labridae from all trophic groups. The other two clusters displayed significant temporal patterns. Cluster 1 was composed of four species of herbivore-detritus feeders (*Acanthurus xanthopterus*, *Naso tonganus*, *Scarus ghobban* and *Zebrasoma scopas*) and one species and one taxon of plankton feeders (*Pterocaesio tile* and unidentified Caesionidae). These taxa were proportionally more abundant in the late afternoon (16:00: 20.2 ± 2.9 % and 17:15: 24.5 ± 4.3 % of total density) than in the morning (06:00 - 09:45: 5.9 ± 2.1 % of total density in average) and in the afternoon (13:30: 6.5 ± 1.5 % and 14:45: 5.5 ± 1.6 % of total density) (pairwise comparison, $p < 0.05$). Cluster 2 comprised three species of parrotfish (*Scarus chameleon*, *Scarus rivulatus* and *Scarus schlegeli*) and other unidentified Scaridae (juveniles and adults). These were proportionally more abundant in the early morning (25.1 ± 1.9 % of total density) compared to the rest of the day (10.2 ± 1.5 % of total density in average) (pairwise comparison, $p < 0.05$).

Effect of tidal state

Overall taxa richness significantly varied with tidal state (one-way repeated measures MANOVA, $p < 0.05$) whereas density was not significantly different ($p > 0.05$) (Fig. 5A and 5C). More taxa were observed at low tide (mean \pm SE: 26.2 ± 0.8 taxa) than at rising tide (23.3 ± 0.8 taxa) and ebb tide (23.2 ± 0.8 taxa) (pairwise comparisons, $p < 0.05$) (Fig. 5A). MANOVAs performed for each trophic group showed that taxa richness and density significantly varied according to tidal state only for herbivore-detritus feeders (one-way repeated measures MANOVA, $p < 0.05$) and remained constant for piscivores, plankton feeders and carnivores ($p > 0.05$) (Fig. 5B and 5D). More taxa of herbivore-detritus

feeders were recorded at low tide (10.5 ± 0.5 taxa) than at rising and ebb tides (rising tide: 8.9 ± 0.3 taxa and ebb tide: 9.1 ± 0.5 taxa) (pairwise comparisons $p < 0.05$) (Fig. 5B). The density of herbivore-detritus feeders was significantly higher at high tide (2.9 ± 0.4 ind/10m²) than at ebb tide (1.7 ± 0.2 ind/10m²) ($p < 0.05$) (Fig. 5D).

Three main clusters were identified for tidal state effect (HAC, Fig. 6 and Supplementary Material 4 for examples of species specific patterns of each group), and these clusters were significantly distinct (BCA, Monte-Carlo test with 9999 random permutations, $p < 0.01$). The first cluster included 40 taxa from all trophic groups, and corresponded to a flat pattern according to tidal state (pairwise comparison, $p > 0.05$) (Fig. 6, cluster 1). The second cluster was composed of two species of herbivore-detritus feeders (*Scarus rivulatus* and *Scarus schlegeli*) and one plankton feeder (*Pterocaesio tile*) and unidentified Caesionidae and adults Scaridae. These taxa occurred in higher densities at low tide (38.1 ± 4.0 % of total density) than at rising tide (19.2 ± 3.4 % of total density) and ebb tide (14.7 ± 1.2 % of total density) ($p < 0.05$) (Fig. 6, cluster 2). The last cluster included three carnivorous species (*Chaetodon bennetti*, *Gomphosus varius* and *Hologymnosus annulatus*) and eight taxa of herbivore-detritus feeders (*Chlorurus sordidus*, *Naso tonganus*, *Scarus chameleon*, *Scarus ghobban*, *Siganus doliatus*, *Siganus puellus*, *Zebrasoma scopas* and unidentified Scaridae juveniles). The density of these taxa in the assemblage was significantly higher at high tide (34.7 ± 1.6 % of total density) than at other tidal states (21.8 ± 0.8 % of total density in average) ($p < 0.05$) (Fig. 6, cluster 3).

DISCUSSION

Temporal variations of reef fish assemblages at an annual, seasonal or monthly scale have been described in many studies and linked to various biological events such as breeding and spawning (Ogden & Quinn 1984; Gladstone 2007; Meyer *et al.* 2007),

recruitment and settlement (Sale *et al.* 1984; Valles *et al.* 2006; Grorud-Colvert & Sponaugle 2009; Salinas-de-Le n *et al.* 2012), competition, predation or feeding activities (Hobson 1973; Letourneur *et al.* 1997; Danilowicz & Sale 1999; Chateau & Wantiez 2007; Fischer *et al.* 2007; Chateau & Wantiez 2008; Chateau & Wantiez 2009; Lefèvre & Bellwood 2011). At a smaller scale however, temporal variations have rarely been considered (Bijoux *et al.* 2013). Our 256 videos recorded over 34 consecutive days on a branching coral patch reef of New-Caledonia provide one of the first and most comprehensive example of small-scale high-frequency temporal variability in a coral reef fish assemblage.

Our study revealed a relatively stable fish assemblage in the patch reef with 11 taxa observed permanently (Freq. $\geq 75\%$), 21 frequently (Freq. $\geq 30\%$), 20 infrequently (Freq. $\geq 10\%$) and 62 rarely (Freq. $< 10\%$). The dominance of rare species even in one of the most diversified coral reef fish assemblage is consistent with other reports (Jones *et al.* 2002) and illustrates the functional vulnerability of coral reef ecosystems (Parravicini *et al.* 2014). Furthermore, carnivores and herbivore-detritus feeders dominated our trophic structure as described for other coral reefs in New Caledonia (Kulbicki *et al.* 2007; Chabanet *et al.* 2010; Guillemot *et al.* 2011).

Although relatively stable on a daily basis, we found significant variations in the composition of the fish assemblage between times of day. Taxa richness and density were greater in the early morning and in the late afternoon than during the day, with an average of 20 % difference for taxa richness and 35% for density between daily minima and maxima. Even if carnivores and plankton feeders presented significant variation of taxa richness depending on times of day, the overall patterns were mostly driven by herbivore-detritus feeding species which presented similar U-shaped curves for both metrics. These patterns contrast with previous studies from both temperate and tropical environments (Rooker & Dennis 1991; Spyker & Van Den Berghe 1995; Thompson & Mapstone 2002; Willis *et al.* 2006) which found no difference in fish assemblages within days. However, they are consistent with Birt *et al.* (2012) and Chabanet *et al.* (2012) who

reported an effect of time of day upon fish assemblages. However, patterns observed by Birt *et al.* (2012) differ to ours as they found that morning and mid-day assemblages were different from afternoon assemblages. Our results are more consistent with those of Chabanet *et al.* (2012) who found that Acanthuridae were more numerous during the morning whereas Scaridae were more abundant at sunrise and sunset. These findings corroborate our results in a sense, as Acanthuridae and Scaridae are herbivorous-detritus feeders. However, in the present study we highlighted that all the species from these families did not present the same diurnal temporal patterns depending on time of day.

In the patch reef studied, we found that tidal states only influenced the herbivorous-detritus feeders assemblage. Although significant, the tidal effect was actually small with only two taxa and 1 ind/10m² differences between tidal states for mean taxa richness and fish density respectively. The absence of tidal influence on taxa richness was also observed by Connell and Kingsford (1998) and Irigoyen *et al.* (2013), while the variability of density with tidal states was shown by Unsworth *et al.* (2007). These authors found that seagrass fish assemblages were more abundant at high tide in both coral reef and seagrass habitats. Even if small, the tide effect observed in the present study may be explained by the location of the video station in a branching coral microhabitat. Indeed, tides may create periodic feeding opportunities such as access to shallow areas of the reef flat during high tide (Bray 1981). Our study was not performed on the reef flat but species movements between the observation site and the reef flat could have occurred for some species during high tide, suggesting the existence of a daily feeding migration. The reef flat was located only 800 m from our study site, which is compatible with distances traveled by many species, from at least several kilometers to just a few meters (Mumby 2006; Apperloo *et al.* 2009; Chateau & Wantiez 2009).

14 of the 52 taxa observed in more than 10% of videos displayed a significant temporal pattern of abundance depending on times of day and/or tidal states. We believe that the observed patterns may be related to fish behaviour and habitat selection. For instance, the larger fish assemblages observed early in the morning and late in the afternoon may

be related to the known diel feeding migration from feeding areas to sheltered places to seek refuges for the night (e.g. Meyer & Holland 2005; Chateau & Wantiez 2007). Furthermore, afternoon feeding activity of herbivore-detritus feeders may be linked to a diurnal variation in the nutritional value and/or palatability of algal food (Letourneur *et al.* 1997; Polunin & Klumpp 1989). It could also reflect an increase in food availability and quality early in the morning (Klumpp & Polunin 1990).

The consistency of the temporal patterns observed in this study suggests the existence of small-scale reef fish movements linked to their daily activities such as daily migrations between feeding and resting habitats. As such, our results illustrate the importance of taking into account small-scale high-frequency temporal variation in reef fish assemblages when studying the connectivity between habitats and monitoring reef fish communities particularly in studies involving large species. However, in this study, we could only get highly-replicated temporal data from a single patch reef. As coral assemblage diversity and structural complexity are known to influence taxonomic and functional fish community structure (Messmer *et al.* 2011; Graham & Nash 2013; Komyakova *et al.* 2013), our results cannot be generalized to all coral reefs of New Caledonia. However, the development of improved video systems such as the MICADO system we used, allows us to study short-term temporal variations in reef fish assemblages at multiple sites. These improvements should provide a wealth of information about the ecology of these animals at a relevant scale for their daily activities.

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Tables

Table 1. Frequency of occurrence (%), number of genera, taxa as species and complexes and fish observations recorded per family. Complexes represent a group of resembling species (see methods) and information corresponding to these special groups are represented in parenthesis in the table. Families are sorted in decreasing order of frequency of occurrence in the 256 videos.

Family	Freq.	Number of genera	Number of taxa	Number of fish observations	
				Identified at species or complex level	Identified at genus or family level
Acanthuridae	100	4	6 (2)	3104 (511)	51
Pomacentridae	100	5	5 (2)	16795 (11800)	269
Scaridae	100	6	13	3178	8690
Labridae	99.6	12	19	1437	407
Chaetodontidae	98.4	2	14	1140	3
Lethrinidae	75	2	5	277	31
Serranidae	67.2	3	6	278	38
Nemipteridae	47.7	1	1	175	0
Pomacanthidae	44.9	2	3	151	0
Balistidae	43.4	2	2	126	0
Mullidae	42.6	1	6	182	4
Siganidae	32.4	1	4	152	0
Caesionidae	30.1	1	1	371	612
Aulostomidae	18.4	1	1	53	0
Pinguipedidae	13.3	1	1	34	0
Carcharhinidae	9.8	2	2	25	2
Carangidae	8.2	4	6	29	18
Echeneidae	6.2	1	1	21	0
Lutjanidae	5.1	3	3	14	0
Apogonidae	4.7	1	0	0	16
Tetraodontidae	4.7	1	1	11	1
Dasyatidae	3.1	2	2	8	0
Ostraciidae	1.6	1	1	4	0
Diodontidae	1.2	1	1	3	0
Gobiidae	1.2	1	1	1	2
Ginglymostomatidae	0.8	1	1	2	0
Stegostomatidae	0.8	1	1	2	0
Belonidae	0.4	1	1	1	0
Hemiramphidae	0.4	0	0	0	1
Monacanthidae	0.4	1	1	1	0
Myliobatidae	0.4	1	1	1	0
Total		66	110 (4)	27576 (12311)	10145

Table 2. Number of taxa (species (complex)), genera (ge.), families (fa.), observations (N), and number of taxa per trophic group for permanent permanent (Freq. \geq 75%), frequent (30% \leq Freq. < 75%), infrequent (10% \leq Freq. < 30%) or rare taxa (Freq. < 10%). H: herbivore-detritus, K: plankton feeders, C: carnivores and P: piscivores. Data corresponding to complexes (group of species) are represented in brackets in the table.

Freq.	taxa	ge.	fa.	N	Trophic group
Permanent	8 (3)	11	4	29577 (12286)	3(1) H, 3(2) K, 2 C
Frequent	21	14	10	5313	8 H, 1 K, 11 C, 1 P
Infrequent	20	15	11	2165	4 H, 2 K, 12 C, 2 P
Rare	61 (1)	47	27	666 (25)	9(1) H, 2 K 38 C, 12 P
Overall	110 (4)	66	31	37721 (12311)	24(2) H, 8(2) K 63 C, 15 P

Figures

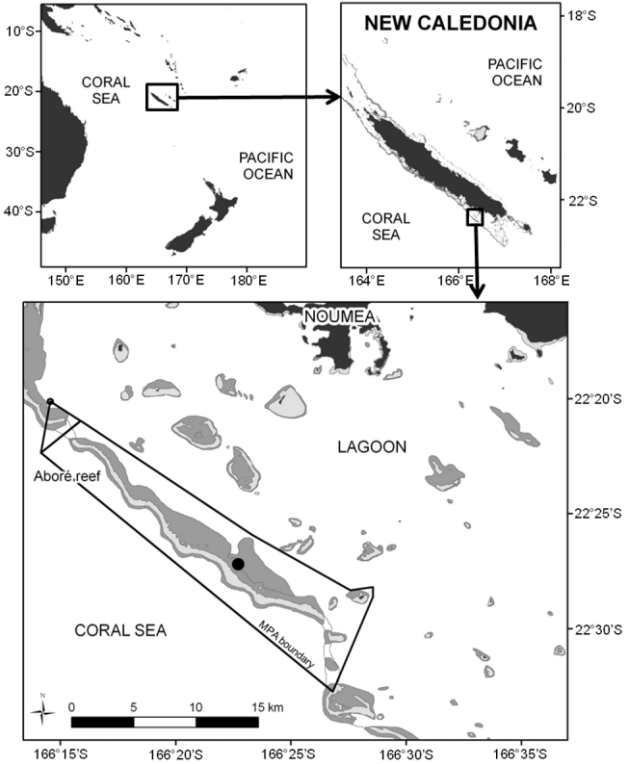


Figure 1. Study area. The polygon indicates the boundaries of Aboré Reef MPA. The MICADO video station is represented by a black dot.

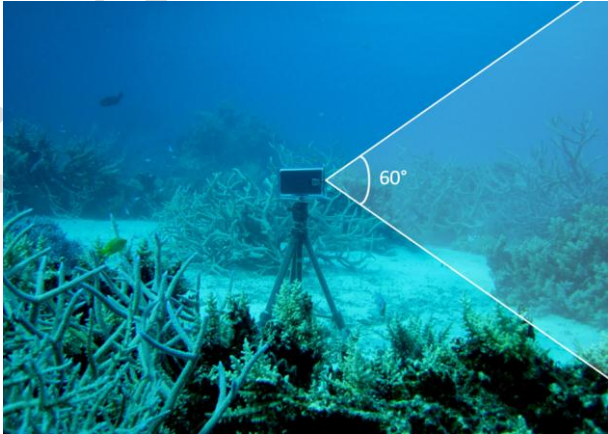


Figure 2. Setting of the MICADO system and representation of its field of view in the study area.

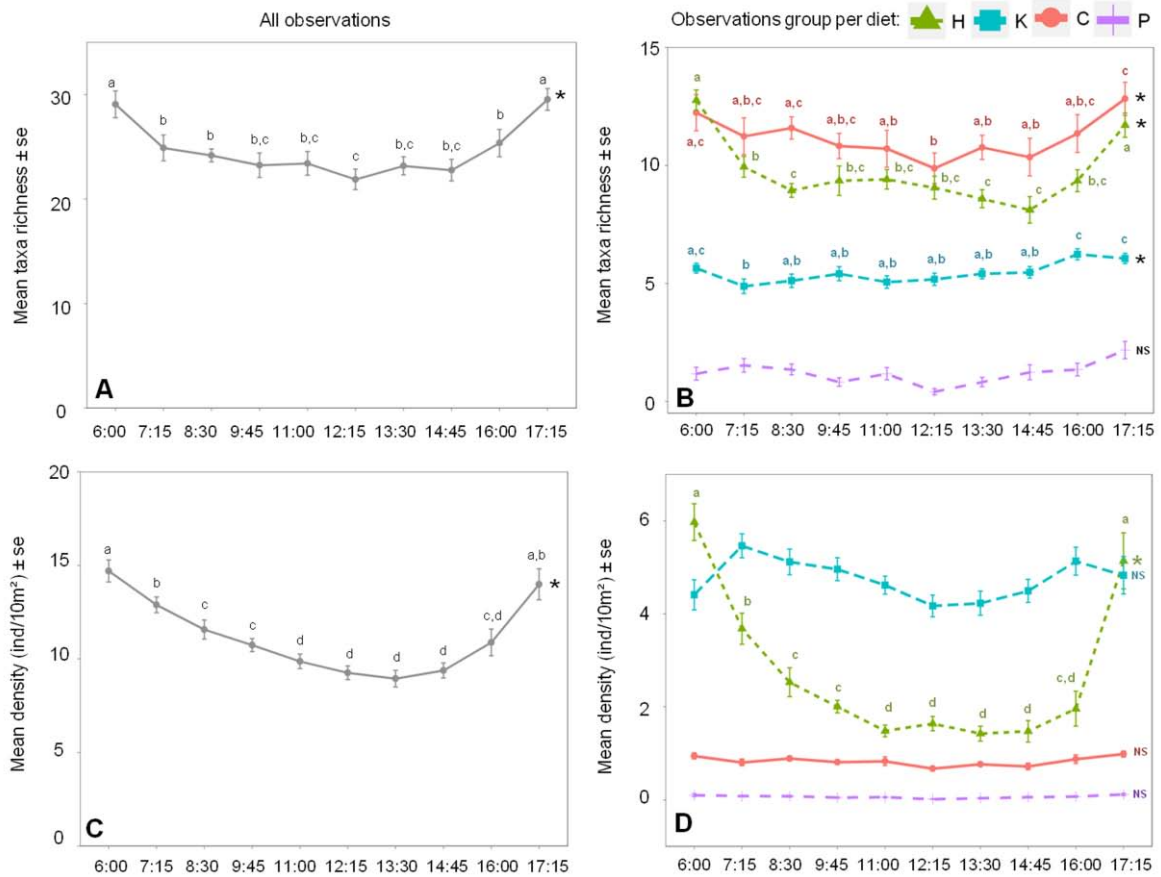


Figure 3. Average taxa richness and density (ind/10m²) per time of day for all observations and for each trophic group. Mean taxa richness and density recorded for all observations are represented on the left (A, C) and observations per trophic group are represented on the right (B, D). The significance of the time of day effect for each pattern is reported as “*”: $p < 0.05$ and “NS”: $p > 0.05$. Results from pairwise comparisons are represented by letters on patterns when time of day effect was found significant from repeated measures MANOVA: the same letter corresponds to $p \geq 0.05$ and different letters to $p < 0.05$.

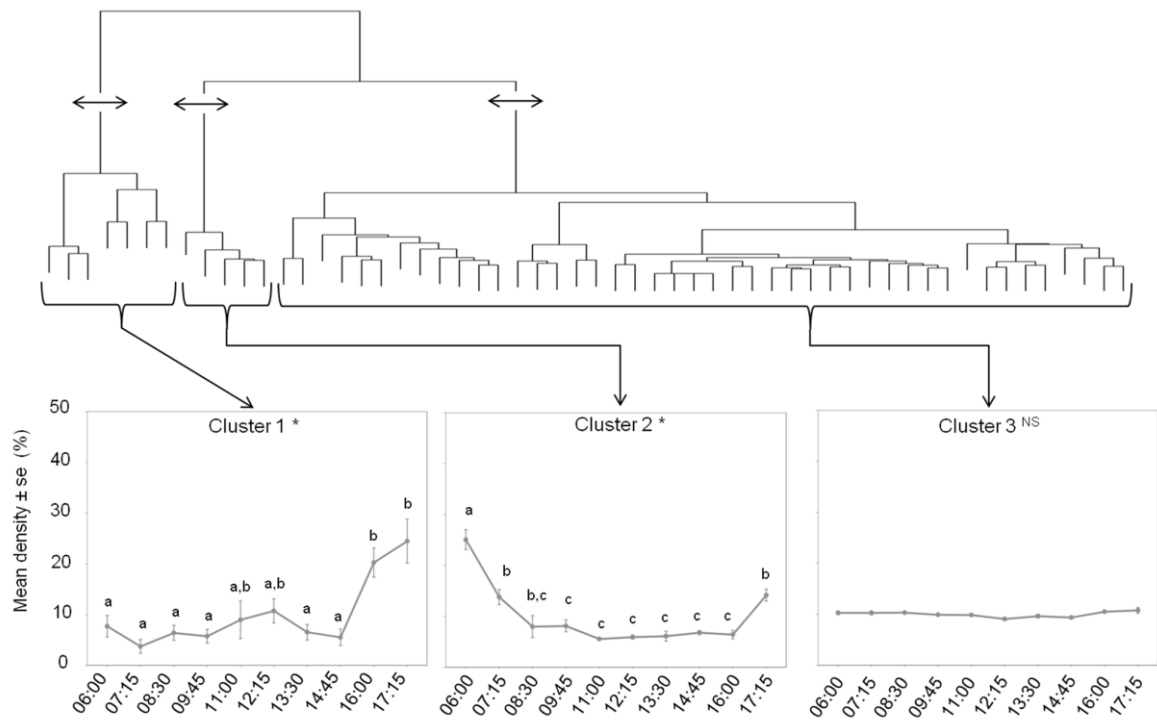


Figure 4. Clustering of taxa based on average density per time of day (rare species excluded). Top: Classification tree from HAC. Bottom: average patterns within each cluster. Differences between times of day from pairwise comparisons are represented by letters on patterns: the same letter corresponds to $p \geq 0.05$ and different letters to $p < 0.05$.

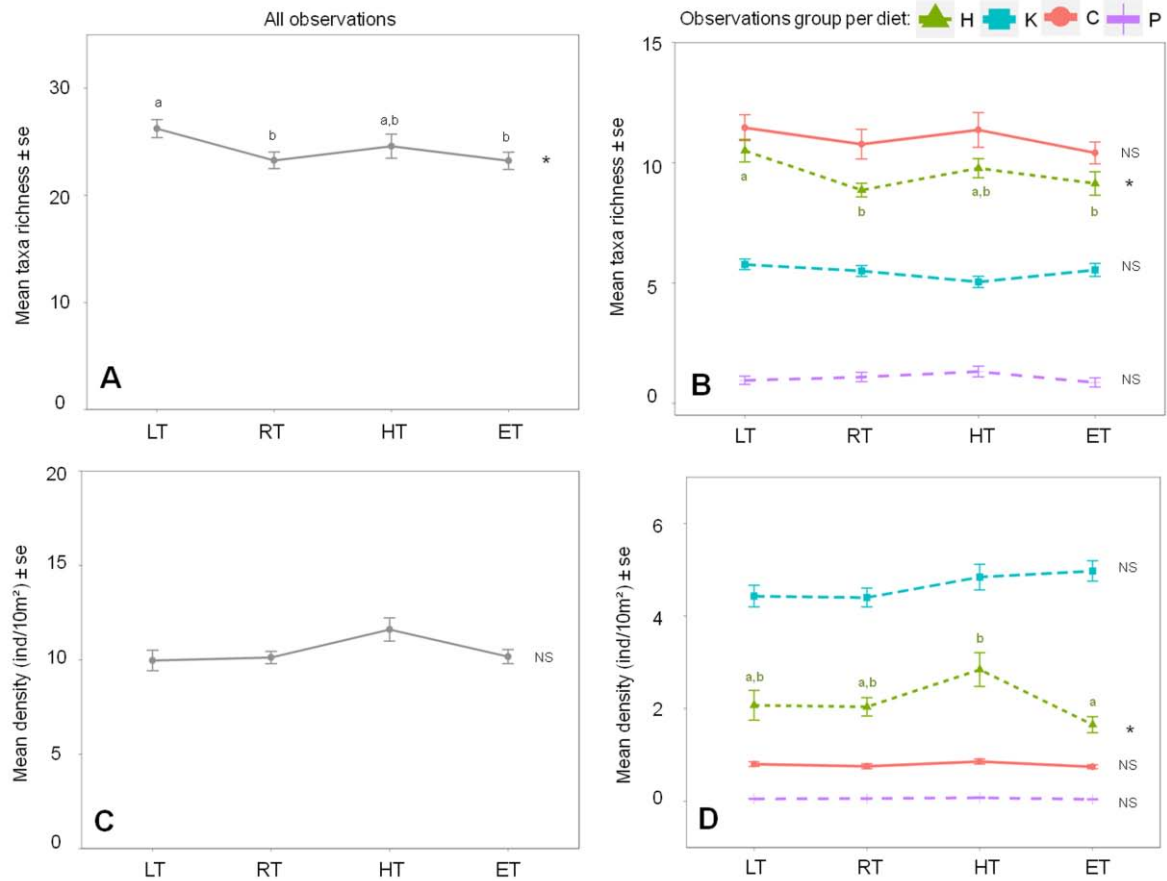


Figure 5. Average taxa richness and density (ind/10m²) per tidal state (LT: Low Tide; RT: Rising Tide; HT: High Tide and ET: Ebb Tide) for all observations and for each trophic group. Mean taxa richness and density recorded for all observations are represented on the left (A, C) and observations per trophic group are represented on the right (B, D). The significance of the tidal state effect for each pattern plotted is reported as “*”: p < 0.05 and “NS”: p > 0.05. Results from pairwise comparisons are represented by letters on patterns when time of day effect was found significant from repeated measures MANOVA: the same letter corresponds to p ≥ 0.05 and different letters to p < 0.05.

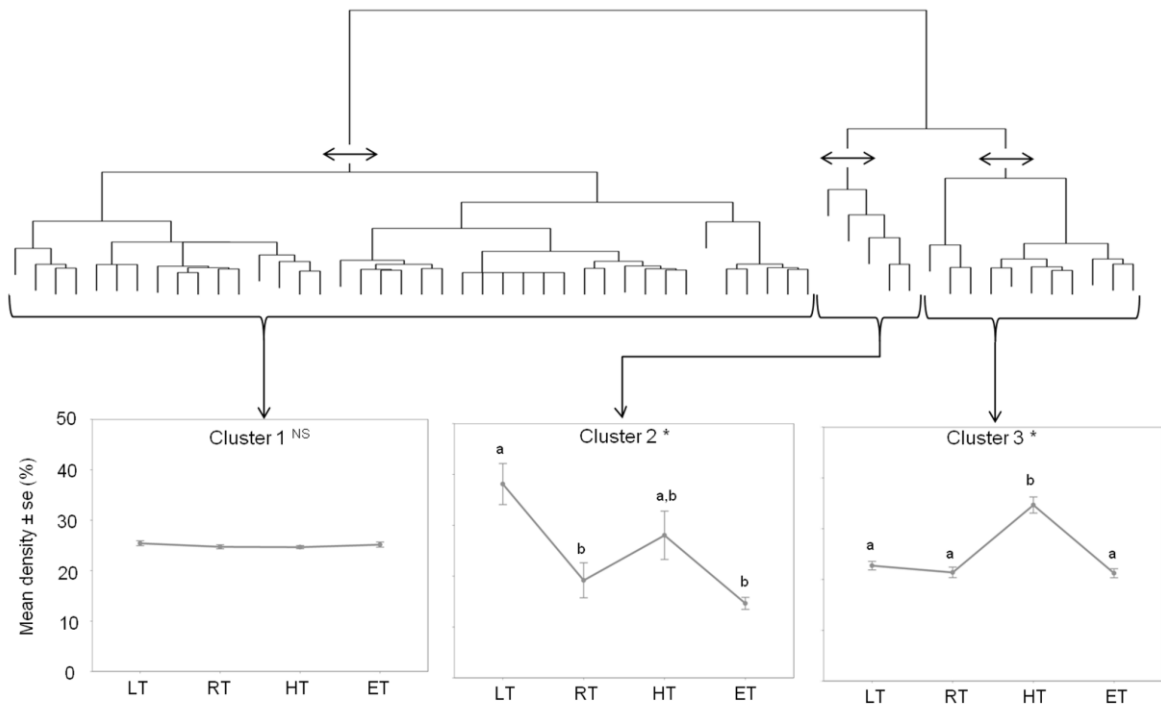


Figure 6. Clustering of taxa based on average density per tidal state (LT: Low Tide; RT: Rising Tide; HT: High Tide and ET: Ebb Tide) (rare species excluded). Top: Classification tree from HAC. Bottom: average patterns within each cluster. Differences between tidal state from pairwise comparisons are represented by letters on patterns: the same letter corresponds to $p \geq 0.05$ and different letters to $p < 0.05$.