



Original research article

The impacts of short-term temporal factors on the magnitude and direction of marine protected area effects detected in reef fish monitoring



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ABSTRACT

Marine protected areas (MPA) and in particular no-take marine reserves have been identified as important tools for the conservation of reef fish and habitats. A significant challenge of reef fish monitoring is to determine the influence of temporal factors on fish counts. Fish assemblages are dynamic and changes in activity patterns throughout the day can influence the results of surveys. While many monitoring programs account for the impacts of spatial heterogeneity on fish assemblages the effects of short-term temporal variation are less well known. In the present study, we analysed data from 197 video drops inside and outside New Caledonian MPAs and examined temporal variations in various metrics commonly used to monitor marine reserves. In addition to describing short-term temporal patterns related to time of day, tide height and state, and lunar cycle; we also examined the influence of these temporal factors on the size and direction of any MPA effects detected. Fewer Serranidae were observed at full moon than the rest of the lunar cycle and there were negative correlations between Chaetodontidae and Acanthuridae abundance and tide height. We did not find any consistent effects of time of day. Generally, variation in short term temporal factors did not affect the direction MPA effects detected but did affect the size of the effects for some metrics. For both small fish abundance and species richness, bigger differences between protected and unprotected sites were detected at high tide than low tide. These results highlight how survey results can vary with timing of sampling and have implications for developing optimal monitoring programs.

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1. Introduction

Coral reefs are highly biodiverse ecosystems that provide numerous ecosystem services such as coastal protection, food for coastal communities and income from tourism (Moberg and Folke, 1999). However, many reefs are threatened by over-exploitation, disease, increased sedimentation and nutrient levels, and the impacts of climate change (McCook, 1999; Fabricius, 2005; Aeby et al., 2011; Hoegh-Guldberg, 2011; Kennedy et al., 2013). Overfishing has been identified as one of the most widespread threats to reefs with direct effects through the removal of species but also indirect effects through the removal of top predators (Burke et al., 2011). Marine protected areas (MPA) and in particular no-take marine reserves (NTMR) have been identified as important tools for the conservation of reef fish and habitats (Bellwood et al., 2004; Pandolfi

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et al., 2005; Allen, 2008) with reported effects including increases in density and biomass especially for commercial species and increases in body size (McClanahan and Arthur, 2001; Friedlander et al., 2003; Unsworth et al., 2007; Russ and Alcala, 1996). However, without effective management MPAs are likely to fail to meet conservation goals (Fox et al., 2014).

An important component of effective management is precise and accurate monitoring data. Good monitoring programs provide information on changes that are occurring within MPAs and also on how well the MPAs are meeting management objectives (Pelletier et al., 2005). One of the challenges of MPA monitoring is that the effects of protection on fish assemblages can be obscured by natural variation (Kulbicki et al., 2007). The strong relationship between the abundance of coral reef fish and habitat is well known (Friedlander and Parrish, 1998) and the need to account for habitat heterogeneity in MPA studies is well established (Garcia Charton et al., 2000). Many MPA studies currently employ methods to partition reserve and habitat effects (Miller and Russ, 2014). In contrast, it is less often acknowledged that short-term temporal variation in fish assemblages due to factors such as time of day, tidal state or lunar phase also has the potential to affect the outcome of monitoring studies (Bijoux et al., 2013).

The primary aim of monitoring programs is to measure real changes in fish abundance and assemblage composition over time so that the effects of protection can be assessed. However, short-term changes in fish behaviour can affect the outcome of monitoring fish counts. Diurnal variability can be caused by changes in the local abundance of species as a result of daily movement patterns (e.g. between different feeding habitats) or by fish being more or less visible to observers as a result of behavioural changes (e.g. water column feeding vs predator avoidance) (Thompson and Mapstone, 2002). A number of studies have found distinct diurnal patterns in local fish abundance (Colton and Alevizon, 1981; Galzin, 1987). This short-term temporal variation has the potential to affect fish monitoring counts in a number of ways. For example, logistical constraints sometimes mean that fish counts from a particular survey site are carried out on the same day or time of day. As a result, differences in time of day when surveys are carried out could confound among location comparisons (e.g. MPA and control sites). In addition, this temporal variation could increase within treatment variability, reducing statistical power to detect protection effects. Alternatively, if counts are always carried out at the same time, variation in fish counts due to temporal variation may be reduced, increasing the accuracy of monitoring counts. However, results could still be biased if there is systematic temporal variation in fish abundances or assemblage composition. For example, if the local abundance of a species decreases during the day and surveys are carried out in the afternoon, monitoring counts are likely to underestimate the abundance of this species.

In addition to time of day, there are a number of other factors that operate over relatively short times scales (hours to months), such as the phases of the lunar cycle and tidal state, that have been associated with changes in fish behaviour and could potentially influence fish counts (Curtis-Quick et al., 2012; Zeller, 1998; Starr et al., 2007). Changes in the lunar cycle have been associated with the timing of spawning of a number of fish species (Samoilys, 1997; Hoque et al., 1999). Migrations of individuals to spawning sites could affect local fish abundance and consequently monitoring fish counts. Another temporal factor associated with short term changes in fish behaviour is tidal state. For instance, daytime spawning peaks of fishes at Johnson Atoll in the Central Pacific were shown to be correlated with local changes in current direction (Sancho et al., 2000). Tidal state can also potentially influence fish feeding behaviour as individuals take advantage of differences in the resources available to them (Curtis-Quick et al., 2012). Differences in fish abundance observed at particular tidal states could be related to changes in activities making them more or less visible to observers. For instance, depending on which monitoring method is being used, a fish feeding on plankton in the water column on a flood tide might be more visible than an individual foraging near the substrate.

Although many studies have highlighted the potential of temporal variability in fish assemblages to influence the outcome of monitoring surveys (Colton and Alevizon, 1981; Thompson and Mapstone, 2002; Willis et al., 2006), in practice, quantifying and accounting for these effects presents a number of difficulties. Characterizing short term variability in fish assemblages requires the collection of high-frequency data across relevant time scales, which can be expensive, time consuming and potentially beyond the scope of most monitoring programs. However, potential benefits include more effective monitoring with increased power to detect protection effects.

Underwater video methods have been used for marine ecological studies since the 1950s, and more recently for monitoring marine biodiversity (see Mallet and Pelletier, 2014 for a review). Video methods have a number of advantages over conventional underwater visual census and fishing based methods for monitoring fish populations including their non-destructive nature, the fact that they cause minimal disturbance to marine life and their potential for high spatial and temporal replication. A rotating, unbaited camera system, STAVIRO (STATION Video ROTative, in French), has been used since 2007 to survey a number of reefs in close proximity to Nouméa, New Caledonia (Pelletier et al., 2012). The resulting dataset includes fish count data for a wide range of species collected across a range of short-term temporal factors (tide height, time of day, tidal state, lunar cycle) and provides an opportunity to investigate the potential effects of temporal variables on monitoring fish counts. Our primary aim was to use this monitoring data to investigate the influence of temporal factors on metrics commonly used to monitor MPAs. We also investigate whether any MPA effects detected (size and direction) vary with temporal factors. Finally, we discuss the implications of these findings for the design of effective monitoring programs and the reporting of MPA effects.

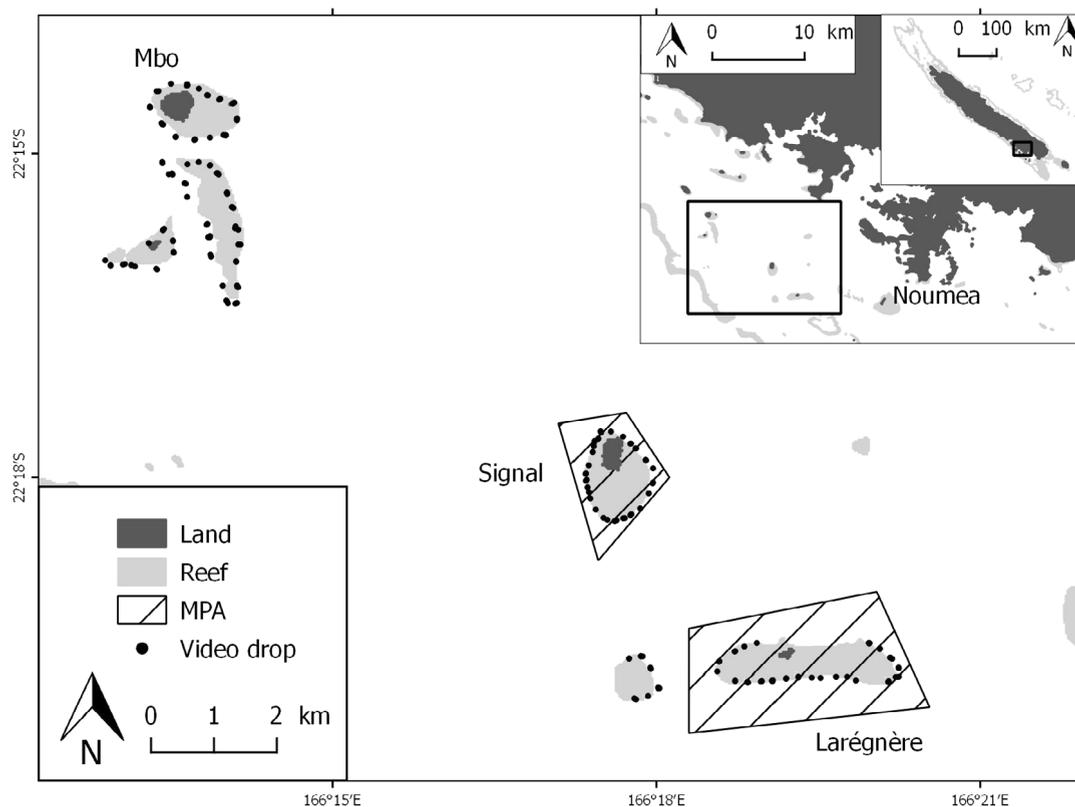


Fig. 1. Locations of the two marine protected areas and the camera drops included in the analysis (camera drops on sand/soft bottom substrates not shown). The inset shows the location of the study sites in the southwest of the New Caledonian lagoon.

2. Methods

2.1. Study site descriptions

Surveys were carried out in 2008, 2009 and 2010 on fringing and submerged reefs in the New Caledonian lagoon (see Fig. 1). Sampling was carried out on the fringing reefs surrounding three islets (Signal, Larégnère and Mbo) and on two submerged reefs (Larégnère and MbeKouen). Fishing effort on coastal fisheries stocks is generally lower in New Caledonia than in many Micronesian or Polynesian countries where fish are typically a more important component of many people's diets (Dalzell et al., 1996). Reef fisheries in New Caledonia are carried out by a relatively small commercial fleet, subsistence fishers, and recreational fishers. Total reef fish catches are dominated by Lethrinidae (31%), Serranidae (18%), Scombridae (13%) and Mugilidae (11%) (Dalzell et al., 1996). The main gear types used in the commercial fishery are gill nets and handlines. Landings are dominated by emperors and particularly, *Lethrinus nebulosus*. New Caledonia has a large number of recreational fishers who mostly use vessels berthed in the capital city Noumea. Previous research has shown there is a positive correlation between catch per unit effort of lagoon species and distance from Noumea. This relationship is evident up to a 50 km radius, which is the limit of most recreational fishing vessels (Kulbicki and Grandperrin, 1998). As a result, a large proportion of the total catches at our non-MPA study sites (Mbo, Récif Larégnère and MbeKouen), which are located relatively near the capital, is likely to be taken by recreational fishers.

Two of the islets in our study, Signal and Larégnère are two of five islands that were designated as no-take MPAs in 1989. Active enforcement of MPA regulations began in 1990 and fish assemblages at both of these sites were surveyed in 1990 and 1994 (Wantiez et al., 1997). A number of changes were observed in the fish assemblages at these sites after four years of protection from fishing. At Larégnère, species richness, density and biomass all increased significantly. Small increases in species richness and density were also observed at Signal but only biomass increased significantly. Species assemblages at protected sites were characterized by the presence of Serranidae, Lutjanidae, Lethrinidae, Chatodontidae, Labridae, Scaridae and Acanthuridae. Prior to MPA establishment assemblages were characterized by schooling species including, *Lutjanus gibbus*, *Gnathodentex aurolineatus*, *Lethrinus* spp., *Kyphosus vaigiensis* and *Signaus corallinus* (Wantiez et al., 1997). All of these sites are very popular with visitors and typical activities include swimming, snorkeling, boating and fishing (outside the protected areas).

2.2. Underwater video sampling and image analysis

Information on the fish and habitats in the study areas were obtained using a remote, unbaited, rotating video system the STAVIRO (**ST**ation**V**ideo**R**otative). A brief description of the method is given here but for more details see [Pelletier et al. \(2012\)](#). The STAVIRO consists of an HD video camera enclosed in a waterproof housing attached to a motor programmed to rotate the camera housing by 60° every 30 s (1 rotation takes ~3 min). It is relatively lightweight (~6 kg) and designed so that it can be easily lowered onto the seabed from a small boat (~6 m) in depths of approximately 1–40 m. The data used in this analysis were collected over a number of outings between February and August in 2008, 2009 and 2010. In total, 442 video drops were carried out but only 197 were used in the final analysis as drops on soft bottom habitats (silt/seagrass beds) were excluded (see details of habitat analysis below). Video drops were carried out at the three islets (Signal, Larégnère and Mbo) and the two submerged reefs (Récif Larégnère and MbeKouen). Camera drop locations were regularly spaced within the study area using ArcGIS. Substrate types sampled included live coral, coral rubble, seagrass, silt and sand. The distance between sample points was roughly 200 m on hard substrates and 400 m on soft bottom substrates (seagrass beds and sandy areas). Once a sampling station was reached, the STAVIRO was set on the seabed and the time and exact location of the camera drop recorded. The camera was then left to film for a minimum of 12 min (to allow time for three complete undisturbed rotations) after which it was picked up and deployed at the next sampling point. At the end of each day the camera sequences were downloaded and previewed to check that they were of suitable quality for analysis (at least three full rotations and 5 m horizontal visibility). Any stations that were rejected were resampled the following day. The images were analysed to obtain information on the fish at each station following the protocol described in [Pelletier et al. \(2012\)](#). As certain species cannot be consistently observed in videos (i.e. cryptic or nocturnal fish) a standardized species list was used to ensure consistency throughout analyses (see supplementary materials S1). Individuals identified were also assigned to a size class “small”, “medium” and “large” based on the maximum known length for each species. The habitat at each video drop site was characterized from the video footage using the medium-scale approach ([Clua et al., 2006](#)). In total, 442 video drops were deployed between 2008 and 2010.

2.3. Habitat stratification

As the aims of this study were to determine the effects of temporal rather than spatial factors, the stations were classified according to substrate type prior to the analysis. Habitat stratification was carried out in R using the FactoMineR package ([Le et al., 2008](#)) in two stages. A Principal Component Analysis (PCA) was performed on the 442 stations described by 7 substrate variables (%cover: “sand”, “rubble”, “rock”, “boulder”; “slab”, “live coral”, “dead coral”) followed by an ascending hierarchical clustering procedure based on Ward’s criterion to determine the optimal number of clusters. The results of this analysis were used to select video drops that were on hard substrates for the analysis (see supplementary materials S2). This resulted in 197 video drops that were used in the analysis. The number of samples from 2008, 2009 and 2010 was 56, 66 and 72 respectively. A breakdown of the number of samples inside and outside reserves for each year is shown in supplementary material S3.

3. Data analysis

3.1. Description of the temporal predictor variables and biological response variables (monitoring metrics) investigated

The temporal factors investigated included time of day, the lunar cycle, tidal height and tidal state. The lunar cycle was divided into four based on the percent illumination of the moon’s surface on the day of each video drop (0%–25%, 25%–50%, 50%–75%, 75%–100%). The tidal cycle was divided into four tidal states: ‘low tide’, ‘flood tide’, ‘high tide’ and ‘ebb tide’. Tide height and time of day were treated as continuous variables. The tide height in millimetres at the time each video station was sampled was obtained from the SHOM website (Service Hydrographique et Océanographique de la Marine). The time of each video drop corresponds to the number of minutes from sunrise on the sampling day as this was considered to be more biologically relevant than time of day. The biological response variables studied were total fish abundance, species richness, small fish abundance which included all individuals of any species that were classed as small for their species (<33% of the known maximum size for that species), large fish abundance (>66% of the known maximum size for that species) included all individuals of any species that were classed as large for their species) and the abundance of the following families: Serranidae, Acanthuridae and Chaetodontidae.

3.2. Assessing the relative importance of the temporal variables for each biological response (monitoring metric)

Model selection approaches can be used to identify environmental factors that are associated with variation in a biological response of interest. They are particularly useful when there are a number of different potential ‘predictor’ variables (e.g. ‘time of day’, ‘tide height’, ‘lunar cycle’) that could be related to a biological variable (e.g. ‘Serranidae abundance’). In model selection approaches a number of different models are generated and then ranked in order to identify which best approximates the biological response of interest ([Symonds and Moussalli, 2011](#)). Model selection approaches have a number of advantages over the more traditional null hypothesis testing approaches used in ecology. They are not restricted to

evaluating a single model where significance is measured by comparison to an arbitrary probability threshold. Models can be ranked and weighted providing a measure of relative support for each model. Finally, when models have similar support from the data model averaging can be used to make robust parameter estimates and predictions (Johnson and Omland, 2004).

In the current study a model selection approach was used to determine how much of the variation in each biological response could be attributed to temporal factors. The analysis was carried out separately for each of the biological response variables (total fish abundance, species richness, small fish abundance, large fish abundance, Serranidae, Acanthuridae, Chaetodontidae). A suite of Generalized Linear Models (GLM) representing all possible combinations of predictors was generated for the biological response variable being examined. The predictor variables included all of the temporal variables described above (time of day, the lunar cycle, tidal height and tidal state) but as we were also interested in whether the size and direction of any MPA effects detected were affected by the temporal factors, we also included the interaction terms of 'protection status' with the temporal factors in the models. Therefore the following potential predictors were investigated: 'protection status', 'year', 'lunar phase', 'time of day', 'tide height', 'tidal state' and interaction effects of 'protection status:year', 'protection status:lunar cycle', 'protection status:time of day', 'protection status:tide height' and 'protection status:tidal state'. This resulted in a list of 512 models that were evaluated for each biological response variable (see Supplementary Material S4 for a list of all the models). Draftsman's plots were used to check for skewness and multicollinearity in the predictors (Clarke and Gorley, 2006). None of the factors were found to be highly correlated with the other variables however, as tidal height and state were related they were not included in any models together (see supplementary material S5). Akaike's Information Criterion (AIC) was used to identify the best model for the biological response variable under investigation. AIC values indicate the goodness of fit of a model to the data, penalized for increasing number of variables (Symonds and Moussalli, 2011), and models with the lowest AIC are considered the most parsimonious.

In addition, to identifying the 'best' model with the lowest AIC, the Akaike weights of all models were quantified in order to account for uncertainty in model selection. The Akaike weights of a given model can be interpreted as the probability of that model being the best model for the observed data and can therefore be used to assess the uncertainty associated with model selection (Johnson and Omland, 2004). The Akaike weights were also used to estimate the relative importance of each predictor (Symonds and Moussalli, 2011). For each predictor, the Akaike weights of all the models that contained that predictor were summed which can be interpreted as the relative importance of that predictor. Those predictors that consistently occur in the most likely models have an Akaike weight close to 1 whereas variables that are absent from all models or are only present in poorly fitting models have an Akaike weight close to 0 (Symonds and Moussalli, 2011).

The relationships between temporal factors and the biological metrics that were identified in the multi-model procedure were investigated further by using multivariate methods to explore which species might be responsible for the associations that we detected. Constrained analysis of principal coordinates (CAP) was used to visualize the differences in the fish assemblages and to identify species that were characteristic of different sampling times (e.g. tide hide vs low tide) (Anderson and Willis, 2003).

3.3. Investigating the influence of temporal factors on the size and direction of MPA effects

When the results of the model selection procedure indicated that there was an interaction between protection status and any of the temporal factors, an additional procedure was carried out to examine how estimates of MPA effects varied with temporal factors. We examined both the size of MPA effects (e.g. the difference in fish abundance at protected vs. non-protected sites) and the direction of effects (e.g. were fish more abundant inside or outside MPAs). The aim of the procedure was to evaluate the metric of interest (e.g. species richness) between protected and unprotected areas for different levels of the temporal variable (e.g. among phases of the lunar cycle). Prior to this analysis, the two continuous predictors, 'time of day' and 'tide height', were converted into factors. Time of day was divided up into four bins roughly equivalent to two-hour time slots. Tide height was divided up into four bins equivalent to approximately 400 mm. Data was subset according to the levels of the temporal predictor and the metric of interest was then evaluated between protected and unprotected areas using a one factor generalized linear model (log link) with 'protection status' as a factor. To ensure a minimum number of replicates for the comparisons the GLM was not performed if there were fewer than six camera drops either inside or outside the MPAs for any of the bins. Alternate distributions were trialed (Poisson and negative binomial) and the results presented for the distribution that resulted in the lowest AIC statistic. The GLM results were plotted with the 95% CI.

Data analyses were performed in R version 3.0.1 (R Core Team, 2015) and the PRIMER-E v6 environment (Plymouth Routines in Multivariate Research) with the PERMANOVA add-on (Anderson et al., 2008).

4. Results

The results of the best model (lowest AIC value) for each individual metric are summarized in Table 1. The percentage variability explained was highest for our model of small fish abundance (31%) and lowest for Acanthuridae abundance (2%). The summed Akaike weights of the models for each predictor variable are also included in Table 2 as a measure of the relative importance of each of the predictor variables that takes into account the results of the full suite of models. For each of the biological metrics, we found that at least one of the temporal factors we studied was included in the best model for that metric. In addition, results indicate that the biological metrics were influenced by different temporal variables, as detailed below.

Table 1
Summary of the results for the model with the lowest AIC value for each metric.

Metric	AIC	% Total variability explained	Predictors included in best model
Total fish abundance	1556.4	16	Tidal State
Small fish abundance	1075.2	31	Protection Status: Time of Day Time of Day
Large fish Abundance	964.5	8	Protection Status: Lunar cycle Protection Status: Tidal State Protection Status Year Time of Day
Species Richness	1277.1	15	Protection Status: Time of Day Lunar Cycle Time of day Protection Status: Tide Height
Serranidae	290.6	10	Year Lunar Cycle
Acanthuridae	983.9	2	Tide Height
Chaetodontidae	551.56	4	Tide Height

Table 2
Table showing the summed Akaike weights for each parameter for each of the metric.

Predictors	Summed parameter weights for each response variable						
	Total fish abundance	Small fish abundance	Large fish abundance	Species richness	Serranidae	Acanthuridae	Chaetodontidae
Protection status	0.46	0.54	0.54	0.43	0.45	0.41	0.48
Year	0.42	0.21	0.70	0.25	0.62	0.25	0.34
Lunar cycle	0.36	0.49	0.25	0.60	0.80	0.22	0.36
Tide Height	NA	NA	NA	0.60	NA	0.65	0.69
Tidal State	0.41	0.56	0.12	NA	0.07	NA	NA
Time of Day	0.60	0.53	0.53	0.56	0.33	0.41	0.34
Year: Status	0.51	0.09	0.32	0.54	0.36	0.20	0.32
Status: Lunar cycle	0.27	0.56	0.24	0.5	0.25	0.32	0.40
Status: Time of day	0.77	0.33	0.84	0.33	0.21	0.38	0.26
Status: Tide	0.15	0.85	0.02	0.68	0.021	0.39	0.60

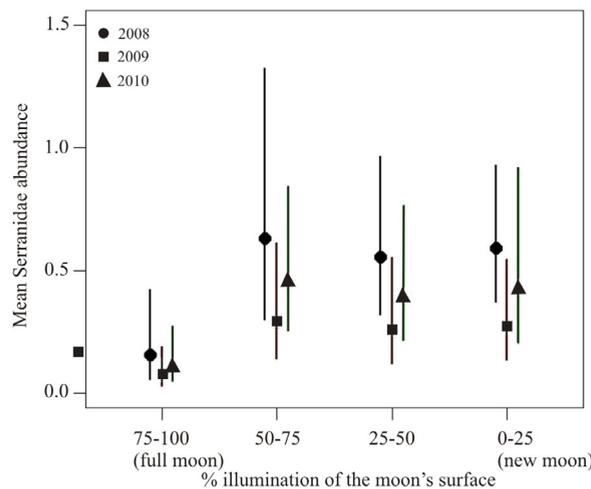


Fig. 2. Mean Serranidae abundance throughout the lunar cycle. Error bars represent 95% confidence intervals of the model estimates.

4.1. Lunar cycle

Lunar cycle was one of the predictors included in the best models for ‘Serranidae abundance’ and ‘species richness’ (Table 1). The summed Akaike weight for lunar cycle across the full set of models for Serranidae abundance was 0.8 indicating that it was included in the vast majority of most likely models (Table 2). Serranidae abundance was significantly lower in surveys carried out around the full moon (mean abundance at full moon in 2010 = 0.11, 95% CI = 0.048, 0.27) than the rest of the lunar cycle (mean abundance at new moon in 2010 = 0.43, 95% CI = 0.20, 0.92) (Fig. 2). The summed Akaike

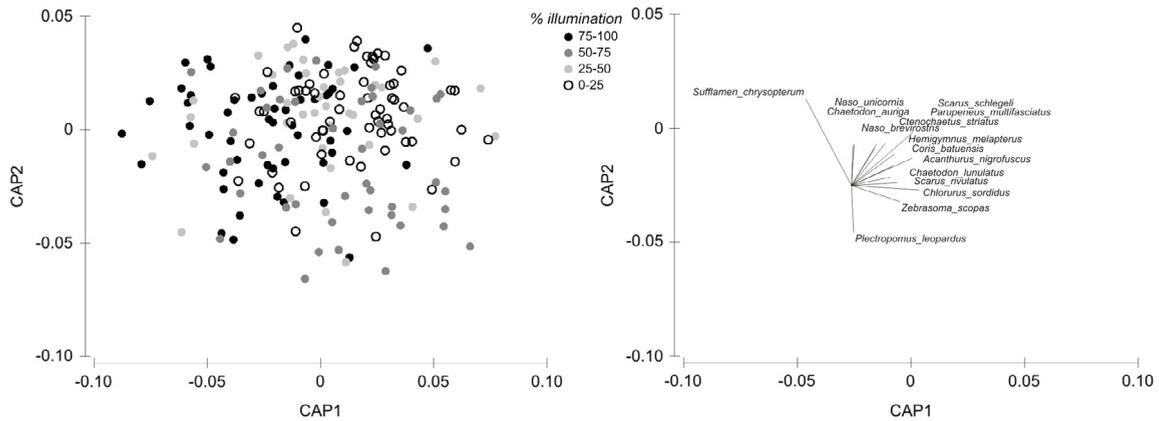


Fig. 3. CAP plot of the species assemblage throughout the lunar cycle. The vectors represent correlations of individual species abundances with the CAP axes.

weight for lunar cycle across the models for species richness was lower (0.6) indicating that there is only moderate support for the hypothesis that this metric is influenced by the lunar cycle. In contrast, overall species richness was lower around the new moon than the full moon. In addition, the CAP analysis showed that the multivariate fish assemblage was significantly different throughout the lunar cycle (Fig. 3). The allocation success scores of a ‘leave one out’ cross validation procedure were 53% correct for full moon, 36% correct for the 50%–75% illumination group, 26% correct for the 25%–50% illumination group and 44% correct for the new moon observations. These results indicate that the species assemblages were more distinct at full moon and new moon than in the middle of the lunar cycle. For all the other metrics the summed Akaike weights for lunar cycle were less than 0.5 indicating that these metrics are unlikely to be strongly influenced by the lunar cycle.

In addition to lunar cycle as a main effect, there was also evidence of an interaction between lunar cycle and protection status for the metric ‘small fish abundance’. This indicates that comparisons of the number of small fish inside and outside protected areas may vary depending on when the sampling takes place in the lunar cycle. The summed Akaike weight of 0.56 indicates moderate support for the hypothesis that variation in small fish abundance is related to changes in the lunar cycle. Small fish abundance was generally higher outside protected than inside protected areas and that this difference was greater around the new moon than at full moon (Fig. 4). The mean abundance of small fish at new moon was 2.55 (95% CI = 1.59, 4.29) inside reserves and 8.12 (95% CI = 5.13, 13.75) outside reserves. At full moon the mean abundance of small fish inside reserves was 3.87 (95% CI = 2.70, 5.65) and 7.68 (95% CI = 5.95, 10.07) at unprotected sites.

4.2. Tidal state and height

Tidal state was included in the best model for ‘total fish abundance’ but its summed Akaike weight was only 0.41, indicating that tidal state was not strongly related to total fish abundance. The interaction between tidal state and protection status was included in the best model of ‘small fish abundance’ (refers to all fish classified as “small” for their species—see method section) and had a summed Akaike weight of 0.85. The abundance of small sized individuals was consistently higher at non-protected sites than at protected sites across all tidal states, but this difference was greater at high tide than at low tide (Fig. 5). Mean abundance of small fish inside reserves at high tide was 1.87 (95% CI = 1.19, 2.84) compared with 6.13 (95% CI = 4.05, 9.30) outside reserves. At low tide mean small fish abundance was 4.37 inside reserves (95% CI = 3.04, 6.43) and 8.18 (95% CI = 6.38, 10.65) outside reserves.

Tide height was included in the best models for mean Acanthuridae and Chaetodontidae abundance and had a summed Akaike weight of 0.65 for Acanthuridae and 0.69 for Chaetodontidae, indicating that the abundance of these two families is associated with tide height. Chaetodontidae, abundance was weakly negatively correlated with tide height (Fig. 6). For species richness, tidal height was not included in the best model but it had a summed Akaike weight of 0.60 indicating that there is some support for the hypothesis that species richness varies with tide height. In addition, the best model of species richness included the interaction of tide height and protection status which also had a summed Akaike weight of 0.68. This indicates that the tide height during sampling could affect the results of comparisons of protected and non-protected sites. Generally, species richness was lower inside the reserve than outside the reserve but this difference was greatest at high tide heights (Fig. 5). At high tide mean species richness was 11.50 (95% CI = 8.79, 14.82) inside protected areas and 21.33 (95% CI = 18.00, 25.18). At low tide mean species richness was 14.64 (12.20, 17.64) inside reserves and 16.97 (95% CI = 14.50, 19.94).

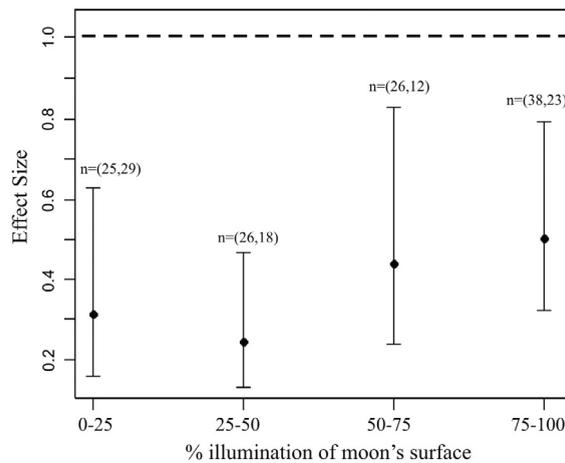


Fig. 4. Differences in mean small fish abundance for video drops inside and outside no-take areas (as given by the glms) for the different stages of the lunar cycle. Effect size is presented as a multiplicative term equal to the estimated small fish abundance for camera drops inside no-take areas divided by the estimated small fish abundance outside of reserves, such that values > 1 indicate higher small fish abundance inside reserves, relative to outside and values < 1 indicate lower small fish abundance inside reserves, relative to outside. Sample sizes (n) refer to the number of camera drops outside and inside MPA boundaries respectively. The error bars represent the 95% confidence intervals.

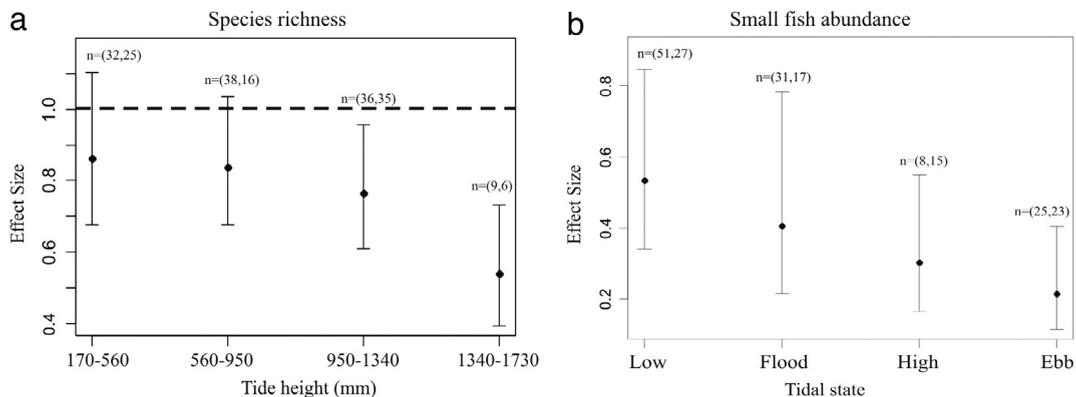


Fig. 5. (a) Difference in the mean species richness for video drops inside and outside no-take areas (as given by the glms) for the different tide heights. (b) Difference in the mean small fish abundance for video drops inside and outside no-take areas (as given by the glms) for the different tidal states. Effect size values > 1 indicate higher species richness/small fish abundance inside reserves, relative to outside and values < 1 indicate lower species richness/small fish abundance inside reserves, relative to outside. Sample sizes refer to camera drops outside and inside MPA boundaries respectively. The error bars represent the 95% confidence intervals.

4.3. Time of day

Time of day was included in the best models of mean 'small fish abundance,' 'large fish abundance,' and species richness. However, the summed Akaike weights for time of day were less than 0.5 for all these metrics indicating that there is only weak evidence that these metrics were influenced by time of day. Time of day was not included in the best model of 'total fish abundance' however this predictor had a summed Akaike weight of 0.6 providing moderate support for the hypothesis that total fish abundance is influenced by time of day. The interaction between time of day and protection status was included in the best models of 'total fish abundance' and 'large fish abundance'. The summed Akaike weights for this predictor were 0.77 for 'total fish abundance' and 0.84 for 'large fish abundance'. When total fish abundance was compared inside and outside protected areas at different times of day we found significantly fewer fish inside the reserves (mean fish abundance = 14.66, 95% CI = 11.58, 22.02) than outside (mean fish abundance = 31.93, 95% CI = 22.77, 46.59) in the morning (8am to midday) but no significant difference in the afternoon midday to 4pm) (Fig. 7). However, it should be noted that there were relatively few camera drops made after 14:00 ($n = 13$) so the estimate for the protection effect size was highly variable for the 14:00–16:00 time slot. For large fish abundance, we did not observe any consistent temporal patterns in the protection effects detected at different times of day (Fig. 7).

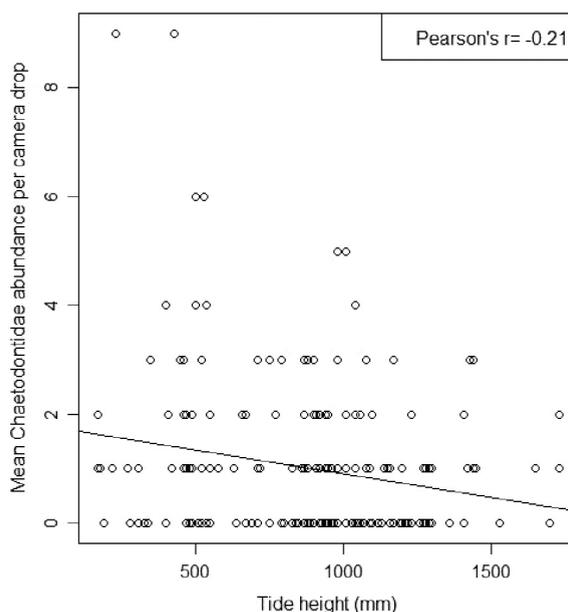


Fig. 6. Scatterplot showing mean Chaetodontidae abundance with water level.

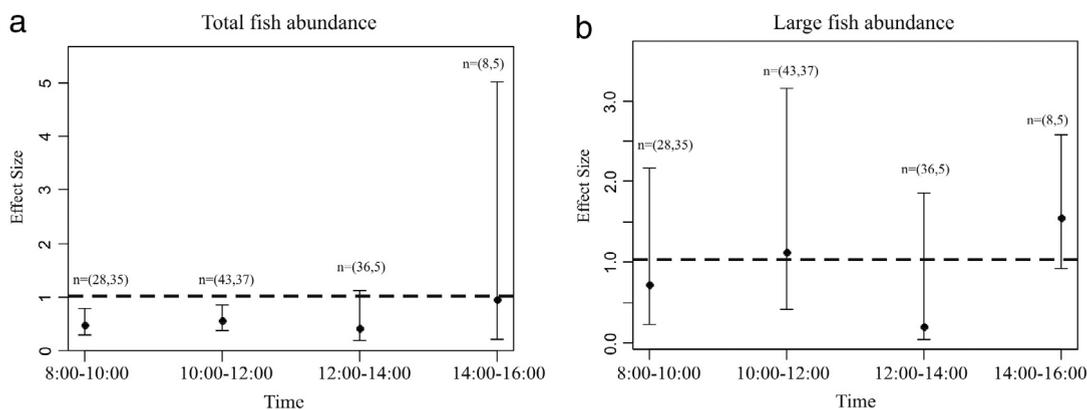


Fig. 7. (a) Difference in the mean total fish abundance for video drops inside and outside no-take areas (as given by the glms) for the different times of day. (b) Difference in the mean large fish abundance for video drops inside and outside no-take areas (as given by the glms) for the different times of day. Effect size values > 1 indicate higher total fish abundance/large fish abundance inside reserves, relative to outside and values < 1 indicate lower total fish abundance/large fish abundance inside reserves, relative to outside. Sample sizes refer to camera drops outside and inside MPA boundaries respectively. The error bars represent the 95% confidence intervals.

4.4. Protection status

When we examined the effects of protection status on the biological response variables without accounting for any of temporal variables (Fig. 8) we found that total fish abundance, small fish abundance and species richness were lower inside protected areas than outside. Serranidae abundance was variable but generally higher inside reserves than outside. There was no clear difference in mean Acanthuridae abundance, Chaetodontidae abundance or large fish abundance inside and outside protected areas.

5. Discussion and conclusions

The primary aim of our research was to uncover the effect of short-term temporal variability on a number of biological metrics used to monitor MPAs. In addition, we wanted to investigate whether the outcome of comparisons of non-protected and protected areas could be affected by this short-term variation. With regard to the first aim, we found that at least one of the temporal factors was associated with each of the biological metrics. Tide height explained some of the observed

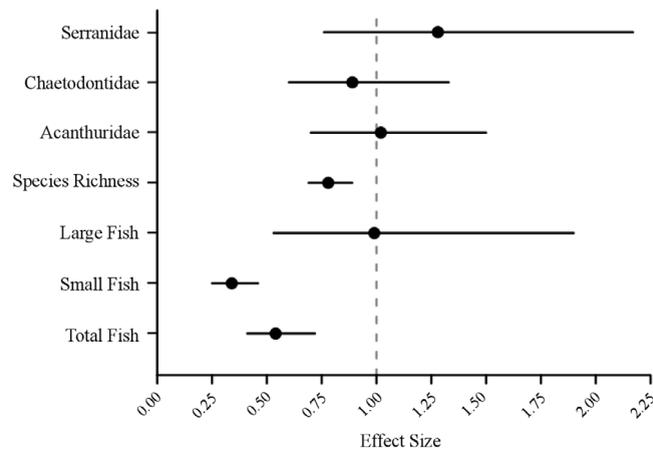


Fig. 8. Differences in the biological response metrics for video drops inside and outside no-take areas (as given by the glms). Effect size is presented as a multiplicative term equal to the estimated abundance for camera drops inside no-take areas divided by the estimated abundance outside of reserves, such that values > 1 indicate higher abundance inside reserves, relative to outside and values < 1 indicate lower abundance inside reserves, relative to outside. The error bars represent the 95% confidence intervals.

variability in the abundance of two fish families (Acanthuridae and Chaetodontidae), while tidal state was associated with variation in total fish abundance. Serranidae abundance and species richness were associated with changes in the lunar cycle. Time of day was included in the best models for a number of the metrics. With regard to the second aim, our results suggest that the outcome of MPA monitoring could be affected by short-term changes related to the tide and time of day for a number of metrics. In the following sections for each temporal factor, we discuss the main effects found, raise hypotheses to explain them, and potential implications for monitoring.

5.1. Lunar cycle

The lunar cycle significantly influenced the number of Serranidae recorded, with lower abundances observed around the full moon than during the rest of the lunar cycle. A number of studies have found changes in fish abundance including serranids related to changes in the lunar cycle (Galzin, 1987; Letourneur, 1996; Samoilys, 1997). These have been primarily attributed to the migration of individuals to spawning aggregation sites at particular times during the lunar cycle. This behaviour has been documented for a number of grouper species including coral trout, *Plectropomus leopardus*, one of the most common serranids in our study area. However, we believe it is unlikely the pattern that we observed was due to movements to spawning sites as our data were not collected during the reproduction season. In addition, this species does not appear to migrate to other reefs to spawn at this location. Chateau and Wantiez (2009) studied the movement patterns of four species including two serranids (*P. leopardus* $n = 12$ and *Epinephelus maculatus* $n = 7$) at sites including two of our study zones (Laregnère islet and Laregnère reef) over 17 months. They found that only one individual of *P. leopardus* moved between reefs, and this occurred outside of the spawning season. Three *E. maculatus* moved between reefs, but movements appeared to be related to movements within individual home ranges or home range shifts rather than to migrations to spawning aggregations. There are a number of other possible explanations for the lower Serranidae counts observed in our video samples collected around the full moon. For instance, groupers are known to be opportunistic visual predators that are particularly active hunters at dawn and dusk. It is possible that the increased lunar intensity at full moon enables them to hunt more effectively at dusk/night over this period and as a result they could be less active during the daytime and less likely to be observed on our video samples over this period.

5.2. Tidal state and tide height

Our results suggest that there was an association between tide height and the abundance of two functionally important fish families: Chaetodontidae (butterflyfishes) and Acanthuridae (surgeonfishes). We found a negative correlation between abundance and tide height for both of these families. One possible explanation for this is that the foraging behaviour of butterflyfish and surgeonfish in our study areas is influenced by tide height and this affected how many individuals were observed. Some shallow reef habitats that are inaccessible at low tide heights may become accessible at higher tide heights (Klump and Polunin, 1990). The majority of our video drops were located on reef slopes adjacent to shallow reef flats, so movements of fishes to forage on the reef flat at high tide could potentially explain why our observations of these families were lower at high tide. Irrespective of the underlying cause, these findings have potential implications for monitoring as

both of these families play important functional roles in reef ecosystems and are frequently surveyed as part of reef fish monitoring programs. Chaetodontidae have been proposed as indicators of reef health as this family contains a number of species that feed primarily on hard corals and are thus likely to respond to declines in habitat (Reese, 1981 and many others). Many different studies have focused on the relationship between butterflyfish and hard coral cover but results have been variable with some authors finding strong positive correlations between local corallivorous butterflyfish abundance and coral cover (Bell and Galzin, 1984; Bozec et al., 2005) but others finding relatively weak effects for a number of corallivorous species (Lawton and Pratchett, 2012). Our results suggest that accounting for tide height could increase statistical power to detect changes in Chaetodontidae abundance related to changes in habitat. Failure to do so could be one of the reasons why published results on the efficacy of butterflyfishes as indicators of habitat quality are so variable. Acanthuridae are one of the most important groups of herbivores on coral reefs and they play a key role in reef dynamics, particularly by influencing spatial competition between hard corals and algae through their grazing activity (Ogden and Lobel, 1978; Paddock et al., 2006; Cheal et al., 2010). Herbivore declines have been identified as one of the causes of shifts in coral reef ecosystems from coral dominated to algae dominated states (Bellwood et al., 2004; McManus and Polsenberg, 2004). Consequently, the ability to detect changes in major herbivore groups such as surgeonfish is an important component of many reef monitoring programs. Among the short-term temporal factors studied, tide height has the most potential to influence surgeonfish counts. Controlling or accounting for tide height could reduce the natural short-term temporal variability in surgeonfish counts, and increase power to detect changes in abundance caused by anthropogenic impacts, e.g. fishing.

5.3. Time of day

Time of day was included in the best models of small fish abundance, large fish abundance, and species richness, but the low summed Akaike weights for this predictor indicate that time of day explained only a small part of variation in these metrics. Our results contrast with other studies that have documented diurnal patterns in fish counts in tropical and temperate ecosystems (Colton and Alevizon, 1981; Galzin, 1987; Chabanet et al., 2012; Mallet, 2014). However, our sampling did not include the crepuscular periods which are known to be characterized by large shifts in fish assemblages (Hobson, 1975; Galzin, 1987). Mallet et al. (2016) studied the short term temporal variation of diurnal fish assemblages on the barrier reef close to our study area. They recorded videos hourly from 1 h after the sunrise to 1 h before the sunset and found that species richness was higher in the early morning and in the late afternoon but remained relatively constant in the middle of the day (from 2 h after the sunrise to 2 h before the sunset). The majority of the samples in the present study were collected during this relatively stable period during the middle of the day. In terms of monitoring at this location, our results suggest that time of day is unlikely to have a large effect on the metrics included in this study for surveys conducted between 2 and 9 h after sunrise.

5.4. Influence of temporal factors on the detection of protection effects

We found evidence for interactions between protection status and temporal variables for a number of metrics, suggesting that the effects of temporal variables can potentially confound the outcomes of spatial comparisons between protected and unprotected sites. In particular, for small fish abundance we found evidence of interactions between two temporal variables (lunar cycle and tidal state) and protection status. These two temporal factors did not affect the direction of the protection effects as small fish abundance was consistently lower inside protected areas compared to outside, however, the magnitude of the effects did change. Differences between protected and unprotected sites were larger around new moon than around full moon, and at high tide than at low tide. Similarly, the interaction between tide height and protection status observed for species richness resulted in larger effects being detected at high tide heights than at low tide heights.

The ecological mechanisms by which these short term temporal factors interact with protection status are currently unclear but may be related to differences in reef fish assemblage structure that take place inside protected areas. Protection from fishing can have numerous effects on reef fish assemblages including increasing the diversity and abundance of individuals inside reserves (particularly of commercially targeted and large predatory species) relative to unprotected sites (Côté et al., 2001; Halpern and Warner, 2002; Pelletier et al., 2005; Unsworth et al., 2007). Previous studies have found species-specific responses to short-term temporal variations (Thompson and Mapstone, 2002; Willis et al., 2006; Ponton et al., 2012). The interactions detected may be due to differences in assemblage composition (e.g. in the proportion of species that respond to variation in tide height) inside and outside MPAs which have a subsequent effect on comparisons of protected and unprotected sites.

5.5. Protection status

The finding that total fish abundance was higher outside reserves was likely due to the increased abundance of small fish outside protected areas. One possible explanation for this is that smaller fish are less likely to be eaten by predators like Serranids when they are outside the MPAs. Serranidae are targeted by fishers in New Caledonia (Dalzell et al., 1996; Loubens, 1978) and we found their abundance was generally higher inside protected areas than outside. We found that there was very little difference in the abundance of Acanthuridae and Chaetodontidae at protected and non-protected sites. Chaetodontidae abundance was slightly lower outside reserves than inside but this was variable. Butterflyfishes are not targeted by fisheries

in New Caledonia so the lack of a protection effect is not unexpected. In contrast, some species of Acanthuridae, particularly *Naso unicornis* are highly sought after (Dalzell et al., 1996) so we would have expected protection from fishing to have a positive impact on surgeonfish abundance. It is possible that the reserves are having an effect on exploited species such as *N. unicornis* but that these effects were masked by high numbers of non-targeted surgeonfish species outside reserves. In the present study we found that tide height had a greater influence on our counts of Chaetodontidae and Acanthuridae than protection status. The fact that we did not find higher numbers of large individuals inside MPAs was surprising but likely due to the fact that our 'large' fish category included both exploited and non-exploited species. Of the metrics that we used in this study, Serranidae abundance and small fish abundance were the most sensitive to protection from fishing, however, Serranidae abundance was also strongly associated with changes in the lunar cycle.

5.6. Strengths and limitations of the approach

Different studies have shown that short-term temporal variability can influence reef fish distributions and abundance. Understanding how this variability can affect the outcomes of fish monitoring can help to improve monitoring survey design and subsequent assessment. However, undertaking studies to characterize the influence of temporal variation is not always feasible within the logistical and financial constraints of many monitoring programs. Our approach can be applied to existing survey data to identify potential systematic effects of short-term variability on the metrics used to monitor protection effects. However, it requires samples collected across the range of the short-term temporal variables. One of the advantages of using underwater video surveys is that it allows a large number of replicates to be collected. Although we were not able to analyse the effects of time of day over the full range of daylight hours, the present study at least enabled us to determine that during the sampling period there were no strong effects of time of day upon the metrics considered.

6. Conclusions

We found evidence that the short-term temporal factors considered here were associated with some of the variability in all of the metrics we examined. In addition, this short-term variability can potentially affect the outcome of comparisons between protected and unprotected areas. The implications of our findings for reef monitoring will depend on the monitoring program objectives. Our results suggest that accounting for the lunar cycle may be important if identifying trends in Serranidae abundance is a priority. However, accounting for variation in tide height may be more important if the aim is to detect changes in Chaetodontidae abundance. Our results concur with the findings of other studies that avoiding sunrise and sampling towards middle of the day is a good strategy to avoid potential biases related to variation in time of day.

The implications for monitoring also depend on the monitoring approach being used. Controlling for an influential factor at the time of data collection may be appropriate if data collection is expensive and the number of replicates limited. Alternatively, explicitly accounting for this factor during the analysis is preferable if a larger dataset is available, with replicates for combinations of conditions of that factor.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2016.09.006>.

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