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Environmental drivers of sheltering behaviour in large reef fishes

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ABSTRACT

Studies of shelter use can provide key insights into the ecology, and structural needs of mobile organisms. Using videos, we examined the usage of tabular corals by large reef fishes, over a 10 week period, compared to multiple environmental drivers: visibility, tide (and depth), irradiance, wind speed (as a proxy for wave energy) and water temperature. We found that two of these predictor variables (*visibility* and *wind speed*) had a significant effect and together accounted for almost half of the variation in tabular coral usage by fishes. Increases in both variables correlated with increased shelter use. To date use of shelters by fishes has primarily been attributed to UV avoidance. Our results support this notion as more turbid conditions (reduced visibility) have an attenuating effect on UV irradiance. Additionally, tabular corals may reduce the energetic costs of increased wave energy by reducing incidental water velocity beneath the structure.

1. Introduction

Sheltering behaviour is a key facet in the ecology of species throughout the animal kingdom. Shelter can provide multiple benefits to individuals, and may serve distinct functions for different species (Hinsley and Bellamy, 2000; McMaster and Downs, 2006; Webb and Shine, 1998). Studies of shelter usage reveal important details about species' ecology and can aid in conservation planning and effective habitat restoration for threatened populations (Dover et al., 1997; Manning et al., 2006; Pratchett et al., 2008; Webb and Shine, 1998).

For many species, shelter can be a critical resource and its availability has direct implications for their survival, enabling them to avoid predation (e.g. Almany, 2004; Eggleston and Lipcius, 1992; Heinsohn et al., 2003; Olsen, 1973) or lethal stress from environmental extremes (e.g. Langkilde et al., 2003; Schwarzkopf and Alford, 1996). Shelter sites may also provide individuals with more routine functions, allowing them to conserve energy and maximise fitness on a daily basis. For terrestrial animals, these functions include, proximity to food sources (Hinsley and Bellamy, 2000), enhanced predation success (Webb and Shine, 1998), avoidance of sub-lethal environmental stresses (Merckx et al., 2010), provision of long-term habitat (McMaster and Downs, 2006), thermoregulation (Walsberg, 1986), and simply, locations in which to rest (Lucherini et al., 1995). Many of these shelter functions are also relevant for fishes on coral reefs.

As the principle architects of coral reefs, hermatypic corals are largely responsible for structural complexity on coral reefs (Done et al., 1996), and provide a key source of shelter for reef-associated fishes (Jones et al., 2004; Kerry and Bellwood, 2015a; Khan et al., 2017; Wilson et al., 2006). Aside from being relatively permanent shelter locations, corals have been shown to improve access to food (Clarke, 1992), both enhance and diminish predation rates (Almany, 2004), and to mitigate environmental stresses such as wave energy (Fulton and Bellwood, 2002).

A recent study suggested that sheltering behaviour of large reef fishes beneath tabular corals was primarily to avoid high levels of ultraviolet (UV) irradiance in shallow reef environments (Kerry and Bellwood, 2015b). This behaviour is thought to reduce energetic expenditure for fishes, which would otherwise secrete costly protective substances to block UV radiation or have to invest in repairing epidermal damage (Kerry and Bellwood, 2015b). However, it remains unclear whether there are other environmental factors that might influence the sheltering behaviour of large reef fishes.

In addition to wave energy and UV radiation outlined above, other potentially important environmental factors include temperature, tides and turbidity. Assessing shifts in the usage of tabular corals by large reef fishes due to changes in each of these environmental factors may reveal their relevance to large reef fishes in shallow coral environments. The response of large reef fishes in terms of sheltering behaviour may also highlight mechanisms by which large reef fishes cope with changing or altered environmental parameters. Of particular importance are environmental drivers which may be altered by anthropogenic activities, such as levels of turbidity around coral reefs which may be exacerbated by increased inputs of sediments from terrestrial run off and dredging (Brodie and Pearson, 2016; Fabricius et al., 2014; Hughes

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et al., 2015; McCulloch et al., 2003).

This study, therefore, investigated changes in the sheltering behaviour of a diverse assemblage of large coral reef fishes to changes in tides (and depth), irradiance, wind speed (as a proxy for wave energy), water temperature and visibility over a 10 week period. Video and statistical analyses were used to identify the most relevant environmental factors driving sheltering behaviour and to generate a best-fit model for predicting large reef fish usage of tabular corals.

2. Materials and methods

This study was conducted between October 2013 and January 2014 at Lizard Island, a mid-shelf reef in the northern section of the GBR (14°40′S 145°28′E). Over 10 weeks, the sheltering behaviour of large reef fishes (total length (TL) > 20 cm) beneath four tabular corals (*Acropora hyacinthus*) was quantified using underwater video observations at two sites within the lagoon (Electronic supplementary material (ESM): Fig. S1). The four tabular corals provided a shaded canopy > 20 cm in height above the substratum, and had a similar planar surface area (mean = 2.78 m^2 ± 0.41 SE).

2.1. Video analysis

At each site the two large tabular corals were filmed from 1000 h to 1400 h using GoPro Hero 3 Silver video cameras (Battery BacPac; 16GB microSD Card; 720p; 25fps; Indicator Light < off >) in underwater housings attached with cable ties to a small dive weight. Cameras were placed in the same position each week, being close enough to fully capture the structure and identify any resident fishes even during low visibility. The tabular corals were no further than 50 m apart at both sites. The two sites were filmed on separate days of the week over the 10 week period, with the same site being filmed on the same day each week (leading to a total of 10 days of filming per site). Video footage was analysed from 1100 h to 1400 h, after 1 h of 'soak' time to allow fishes to recover from diver disturbance (cf. Dickens et al., 2011) and to acclimate to the presence of the camera. For each tabular coral, video analysis was carried out by watching the full 3 h of video footage and recording any large reef fishes that stopped to shelter beneath the corals. Over the 10 week period, 22 species of large reef fishes from nine families were observed sheltering beneath the four tabular corals: Acanthuridae, Balistidae, Ephippidae, Haemulidae, Labridae, Lethrinidae, Lutjanidae, Pomacanthidae and Serranidae (species listed in ESM Table S1).

Abundances of fishes using both tabular corals at a site were pooled so that the level of replication is a single day i.e. one data point represents the usage of two corals based on prevailing environmental conditions for that day. Care was taken not to record the same individual more than once, especially as it is possible that an individual fish might use both structures during the 3 h filming window. This was possible given the low numbers of any given species of large reef fish observed in this study, and because individuals could be clearly identified based on their size and distinctive markings (such as scarring or fin damage). Additionally, synchronous video footage from the two tabular structures could be cross-referenced to check if an individual might feasibly have moved from one structure to another.

2.2. Environmental data

Data were collected for five environmental variables over the same 10 week period: visibility, depth, temperature, wind speed and photosynthetically active radiation (PAR; recorded above the water). Visibility (m) was determined in situ at each site prior to deployment of the video cameras. Two divers moved apart along a transect tape, as soon as the diver moving along the transect lost sight of the diver at the beginning, the distance between the two divers was recorded to the nearest metre to give a relative measure of visibility. The same diver always performed the same role and the orientation, equipment and clothing of the both divers was the same in each instance.

Depth (every 5 min; m) and seawater temperature (every 5 min; °C) data were obtained from Sensor Float 2 (Blue Lagoon South; ESM Fig. S1), which is located within the lagoon at Lizard Island and is part of the Integrated Marine Observing System (IMOS; source: Australia Institute of Marine Science). For the purpose of analyses, the following data were calculated for each period of video analysis: mean depth (average depth over the 3 h filming window, n = 37), tide change (the relative change in depth over the 3 h filming window), and mean temperature (average temperature over the 3 h filming window, n = 37).

Wind speed (scalar average every 10 min; km h^{-1}) and PAR (every 10 min; μmol photons m^{-2} s^{-1}) data were obtained from Relay Pole 2 (Seabird Islet; ESM Fig. S1), which is also located within the study zone at Lizard Island (IMOS; source: Australian Institute of Marine Science). During the study period, wind direction was predominantly south-easterly (137° ± 11 SE). For the purpose of analyses, the following data were calculated for each period of video analysis: mean wind speed (average wind speed over the 3 h filming window, n = 19) and mean PAR (average PAR over the 3 h filming window, n = 19). The following six predictor variables were, therefore, available for each window of observation (3 h video analysis): mean depth, tide change, mean PAR, mean wind speed, mean water temp and visibility.

2.3. Data analyses

Variation in the assemblages of large reef fishes sheltering under tabular structures over the 10 week period were visualised using non-metric multi-dimensional scaling (nMDS) based on a Bray-Curtis similarity matrix. The rank-correlation Bio-Env + Stepwise routine (BEST analysis) was then run (999 permutations) to assess which combination of the predictor variables best correlated with variation in assemblages of large reef fishes sheltering beneath tabular structures. Prior to analyses, all six variables were normalised to put them on the same scale.

The BEST routine computes rank-correlations for all possible combinations of predictor variables, and converges on the combination with the strongest relationship to the dependent fish assemblage dataset (Clarke and Gorley, 2015). However, the BEST routine does not demonstrate which variables take high or low values for which samples. Therefore, for each environmental predictor variable identified by the BEST routine, a linear regression was performed based on their relationship to fish abundance and MDS primary axis scores.

Finally, distance-based redundancy analysis (dbRDA) was performed on the fish assemblage dataset using both the best and second-best combination of predictor variables. dbRDA performs a multivariate multiple regression of principle component axes on predictor variables and is, therefore, able to determine the percent variation in the dataset that is explained by the selected variables (Anderson et al., 2008). Examination of the optimal and sub-optimal combinations of predictor variables in this manner indicates the level of confidence that can be placed in the optimal model as the best predictor of variance in the fish assemblages throughout the 10 week study. All analyses were conducted using the software *Primer 7* & *Permanova* + (Clarke and Gorley, 2015).

3. Results

Over the 10 week period, 343 fishes were recorded sheltering under the four tabular structures (174 on site 1 and 169 on site 2). The BEST analysis revealed that most variation in fish assemblage could be attributed to the predictor variables with *visibility* and *wind speed* as the best combination (rho = 0.485, $P < 0.01$), although *visibility* by itself was also a strong predictor of fish assemblage (ESM Table S1).

Exploration of the data using nMDS also suggested that environmental variables played an important role in influencing sheltering

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