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Diurnal variation of fish and macrobenthic invertebrate community structure in an isolated oceanic island of the South Atlantic

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The trophic structure of Ascension Island's sub-tidal reef assemblages is poorly understood. Unlike other tropical reef systems, sub-tidal habitats have very low abundance of both coral and macrophyte species. Visually dominant is a diverse assemblage of fish species, with particularly high densities of Melichthys niger, *a voracious omnivore. In contrast, the nocturnal species assemblage is notably different, visually dominated by benthic invertebrates. To quantify the difference between day and night visible assemblages, we conducted day/night pairs of transect surveys of fish and invertebrates across three depths, and spanning 9 months, assigning all species to one of 10 functional groups. Multivariate analysis of surveys revealed significant turnover in species between day and night surveys and between survey periods, with concomitant changes in species rank-abundance distributions. Juveniles of a number of fish species were determinate in observed differences. Conversely, diversity of functional groups between day/night surveys and between seasons were not different, however there was significant species turnover within functional groups between day and night assemblages. The lack of proportional change in functional groups but a turn-over of species between day and night assemblages suggest that there may be a degree of functional redundancy in Ascension Island's marine trophic profile. Further investigation into the spatio-temporal variation in trophic profile and functional diversity around the island will benefit conservation and fisheries management in this isolated and poorly understood marine system.*

Keywords: trophic, tropical reef, nocturnal, species turn-over, functional redundancy

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INTRODUCTION

Describing the trophic dynamics of marine communities can provide better understanding of the organization and functioning of assemblages (Paine, 1966; Menge, 1992; Hamilton *et al.*, 2014), enable prediction of responses to disturbance or disease (Witman, 1985; Harley *et al.*, 2006; Rodríguez-Barreras *et al.*, 2014), and ultimately enhance their long-term management and conservation (Graham *et al.*, 2003; Pauly & Watson, 2005; Mumby *et al.*, 2007). In tropical reef systems, trophic dynamics tend to be 'top-down' (Carpenter & Edmunds, 2006; Hamilton *et al.*, 2014), where the trophic interactions of predatory fish and their herbivore prey have direct and significant impact on fluctuations between coral and algal abundance (Floeter *et al.*, 2005 for review). Consequently the relationships between predators, herbivores and primary producers have drawn a great deal of attention in shallow reef community studies due to their integrated role in structuring nutrient flow throughout the reef system (e.g. Barneche *et al.*, 2014; Vinueza *et al.*, 2014).

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In response to typically high densities of visual predators on tropical reefs (e.g. fish species), prey species have evolved predator avoidance strategies such as migration into cracks and crevasses or other habitats that offer refuge during the day, and emerging at night when there is a lower encounter rate with visual predators (Dill, 1987; Barnes & Crook, 2001; Clark *et al.*, 2003). In these cases, prey species must trade-off between optimal foraging opportunities and prey avoidance, because often foraging in predation refugia is sub-optimal (Holomuzki & Messier, 1993; Barnes & Crook, 2001 for review). For example, such daily retreat to predation refugia has been well documented for echinoids in tropical and temperate reefs (Nelson & Vance, 1979; Barnes & Crook, 2001), avoiding fish predators (see Tuya *et al.*, 2004 for review). Similarly, a lack of daily migration in echinoids has been observed elsewhere when there are low abundances of predatory fish (Glynn *et al.*, 1979). In these instances, echinoids are considered 'keystone' herbivores (e.g. *D. antillarum* in the tropical Atlantic: Hughes *et al.*, 1987; Carpenter & Edmunds, 2006; Rodríguez-Barreras *et al.*, 2014), where the reduced abundance of this species can result in dramatic increases in algal cover (Phinney *et al.*, 2001). Therefore, when relating the importance of echinoids in reef trophic dynamics and their nocturnal feeding behaviour, it can be assumed that nocturnal grazing is when this species exerts maximum grazing pressure. However, herbivorous fish also play a major 'top-down' role in structuring tropical reef assemblages (Hughes *et al.*, 1987; Hamilton *et al.*, 2014 and references therein). Given that herbivorous fish are generally active in the day (Hay *et al.*, 1988; Choat & Clements, 1993) when historically most reef surveys have been carried out (although see Azzurro *et al.*, 2007), then a key period of critical trophic activity has been unstudied in Ascension Island; both night and day surveys of the reef assemblage are necessary for fully understanding trophic dynamics in tropical reef systems.

The inshore benthic habitats in Ascension Island are characterized by bedrock, boulders, cobble, maerl and sand, and conspicuously low coral substrate. Non-geniculate coralline red algae formations widely dominate the rocky bottom, where fleshy seaweeds are relatively inconspicuous, reduced to thin epibenthic turf-like mats, including diminutive and repent forms of various green, brown and red macroalgae (such as *Wrangelia argus* and *Dictyota* sp.) (Tsiamis *et al.*, 2014). Visually dominating the daytime underwater seascape of Ascension Island is an abundant fish assemblage, with elements characteristic of both western and eastern Atlantic assemblages (Floeter *et al.*, 2008, reviewed in Wirtz *et al.*, 2014). Similar to other oceanic islands in the tropical Atlantic (Floeter *et al.*, 2008; Pinheiro *et al.*, 2011), richness is relatively low compared with coastal tropical Atlantic regions, with intermediate levels of endemism (Floeter *et al.*, 2008). Characteristic of Ascension Island are the disproportionally dominant black triggerfish *Melichthys niger* in terms of both numbers and biomass (Price & John, 1980; Kavanagh & Olney, 2006). *Melichthys niger* is a voracious omnivore common throughout the tropical Atlantic. Analysis of stomach contents has revealed a wide spectrum of diet including benthic algae, invertebrates spanning most phyla, planktonic organisms and fish (Kavanagh & Olney, 2006) similar to other balistid fish (McClanahan, 2000). As such they are likely to exert significant grazing pressure on algal turf as well as predation pressure on invertebrate fauna. In contrast, preliminary night surveys (personal observation) showed an underwater seascape visually dominated by benthic invertebrate fauna, with a distinct lack of active fish present. Conspicuous nocturnal invertebrates include *Diadema antillarum* and the holothurian *Euapta lappa*. Interestingly, in addition to invertebrates, also seen are numerous *M. niger* in a state of deep rest, lying motionless on the rocky seabed.

There is currently no published quantitative information on the nocturnal benthic assemblage of Ascension Island. We therefore ask the following questions: (1) what are the differences between the day and night fish and invertebrate assemblages in terms of composition and abundance and (2) how are these assemblages structured in terms of their functional groups? To elucidate these questions, we carried out a series of day *vs* night scuba surveys collecting visual census data for the first time, providing a quantitative baseline of species that may otherwise be missed during day surveys as well as allowing for the comparison of the difference in relative abundance and species composition of marine fauna present between day and night.

MATERIALS AND METHODS

A total of 12 transect surveys were conducted at Wigan Pier, Ascension Island (7.894°S 14.384°W) spanning 9 months. The site is a small embayment at the base of a cliff headland. The seabed consists of very large (>1 m diameter) irregularly shaped and highly rugose boulders on very rugged bedrock, with numerous large fissures and crevasses. The reef slopes down to a sand/cobble/boulder field at a depth of 15–20 m, over a horizontal distance of approximately 200 m. In each survey period (season), six transect surveys were carried out; three day transects and three night transects (4 September 2012; day: 1500 h; night: 2025 h and 4 June 2013; day: 1500 h; night: 2030 h). In 2012, the three transects were placed at mean depths of 5.5 m (D1/N1), 5.1 m (D2/N2) and 7.0 m (D3/N3). In 2013, transects were placed at mean depths of 7.0 m (D1/N1), 6.3 m (D2/N2) and 8.5 m (D3/N3).

Surveys were carried out using standard visual survey methods, counting all fish and invertebrates within a 2 m belt (1 m either side of the tape measure) along a 50 m transect (based on methods in http://www.reeflifesurvey.com; Edgar *et al.*, 2009). Transects were anchored on the seabed at three depths during the day surveys, suitably separated such that fish counts did not overlap between transects. The same transects were surveyed at night. Transects were marked with a single Cyalume-like glow stick at each end so they could be relocated by divers. Although the glow stick created a light field at night, it was deemed not significant enough to bias night survey results beyond the first metre of the transect. For the night survey, the survey diver wore a head-mounted torch. In all six night surveys, the head torch did not attract any fish species during the survey. All surveys in both seasons were carried out by the same diver surveyor, who was highly experienced in fish surveys in Ascension Island. Start and end depth and habitat type were noted for each transect.

All individuals were identified to species or closest practical taxonomic unit. Juvenile and adult forms of fish were recorded separately. All night observations of *M. niger* were of fish lying dormant on the seabed, and thus their presence was counted but classified separately from *M. niger* counted during the day. Categorizing these separately takes into account the different functional roles of *M. niger* in the day or night while at the same time, records their presence in the assemblage. Fish species were assigned to functional group codes based on Halpern & Floeter (2008), or from FishBase (http://www.fishbase.org. Last accessed 23 October 2014) if not recorded in that study. Invertebrates were classified using the same terminology as fish, on the basis of a wide range of peer-reviewed sources. If specific species information could not be found, then functional grouping was assumed from the genus or family. Classifications are: Macrocarnivores (MCAR) – consume mobile benthic organisms and fish; Strict piscivores (PISC) – consume fish only; Mobile benthic invertivores/cleaners (MINV) – consume primarily benthic mobile and parasitic invertebrates; Coral/colonial sessile invertivores (SINV) – consume sessile benthic invertebrates; Planktivore (PLA) – consume primarily macro- and micro-zooplankton; Turf grazing (TURF) – herbivores feeding on algae and epiphytic organisms; Scrapers (SCRP) – herbivores that leave shallow bite scars; General omnivores (OMNI) – consume a variety of animal and plant material in similar quantities; Detritivore (DETR) – consume sediments and decomposing material. The category DETR was needed for some species of invertebrates. The category INRT was used to classify *M. niger* at night.

All statistics were done in Rv3.1.0 (R Core Team, 2014). Multivariate analysis was conducted using the package 'vegan' v2.0–10. Principal component analysis (PCA) was

Table 1. Species presence/absence in all surveys. Trophic guilds adapted from Halpern & Floeter (2008)

	Code	Trophic guild	Day	Night
Fish species				
Triggerfish				
Melichthys niger (day)	MELNIG_d	OMNI	+	−
Melichthys niger (night)	MELNIG_n	INRT	−	+
Surgeonfish				
Acanthurus coeruleus	ACACOE	TURF	+	+
Acanthurus coeruleus (j)	ACACOE_j	TURF	+	−
Acanthurus bahianus	ACABAH	SCRP	+	+
Creolefish				
Paranthias furcifer	PARFUR	PLA	+	+
Paranthias furcifer (j)	PARFUR_j	PLA	+	+
Butterflyfish				
Chaetodon sanctaehelenae	CHASAN	SINV	+	−
Boxfish				
Canthigaster sanctaehelenae	CANSAN	SINV	+	−
Damselfish				
Chromis multilineata	CHRMUL	PLA	+	+
Stegastes lubbocki	STELUB	TURF	+	+
Stegastes lubbocki (j)	STELUB_j	TURF	+	+
Abudefduf saxatilis	ABUSAX	OMNI	+	−
Jacks				
Caranx lugubris	CARLUB	PISC	+	+
Hawkfish				
Amblycirrhitus earnshawi	AMBEAR	MINV	+	+
Amblycirrhitus earnshawi (j)	AMBEAR_j	MINV	+	−
Lizardfish				
Synodus synodus	SYNSYN	PISC	+	−
Trumpetfish				
Aulostomus strigosus	AULSTR	PISC	+	−
Tilefish				
Malacanthus plumieri (j)	MALPLU_j	MCAR	+	−
Wrasse				
Thalassoma ascensionis	THAASC	PLA	+	−
Thalassoma ascensionis (j)	THAASC_j	PLA	+	−
Thalassoma sanctaehelenae	THASAN	PLA	+	−
Bodianus insularis	BODINS	MINV	+	+
Bodianus insularis (j)	BODINS_j	MINV	+	−
Grouper				
Epinephelus adscensionis	EPIADS	MCAR	+	+
Epinephelus adscensionis (j)	EPIADS_j	MCAR	+	+
Soapfish				
Rypticus saponaceus	RYPSAP	MCAR	+	+
Squirrelfish				
Holocentrus adscensionis	HOLADS	MINV	+	+
Holocentrus adscensionis (j)	HOLADS_j	MINV	+	+
Soldierfish				
Myripristis jacobus	MYRJAC	MCAR	+	+
Myripristis jacobus (j)	MYRJAC_j	MCAR	+	+
Moray eels				
Channomuraena vittata	CHAVIT	MCAR	+	+
Enchelycore anatina	ENCANA	MCAR	+	+
Quassiremus ascensionis	QUAASC	MINV	+	+
Gymnothorax moringa	GYMMOR	MCAR	+	+
Gymnothorax moringa	GYMMIL	MCAR	+	+
Gymnothorax unicolor	GYMUNI	MCAR	−	+
Goby				
Priolepis ascensionis	PRIASC	MINV	+	−
Blenny				
Ophioblennius sp.	OPISP	TURF	+	+
Cardinalfish				
Apogon axillaris	APOAXI	PLA	+	+
Apogon pseudomaculatus	APOPSE	PLA	−	+
Scorpaenodes insularis	SCOINS	MINV	−	+
Invertebrate species				
Echinodermata				
Ophidiaster guildingi	OPHGUI	PLA	+	−
Eucidaris tribuloides	EUCTRI	TURF	+	+
Diadema antillarum	DIAANT	TURF	+	+
Holothuria (*Platyperona*) *sanctori*	HOLSAN	DETR	+	+
Holothuria (*Halodeima*) *grisea*	HOLGRI	DETR	−	+
Euapta lappa	EUALAP	DETR	−	+
Crustacea				
Percnon abbreviatum	PERABB	MINV	+	+
Panulirus echinatus	PANECH	MINV	+	+
Corallianassa longiventris	CORLON	PLA	+	+
Dardanus imperator	DARIMP	OMNI	−	+
Euryozius pagalu	EURPAG	OMNI	−	+
Enoplometopus antillen	ENOANT	MINV	−	+
Decorator crab	DECCRA	OMNI	−	+
Stenopus hispidus	STEHIS	MINV	−	+
Hippolysmata grabhami	HIPGRA	MINV	+	+
Brachycarpus biunguiculatus	BRABIU	MINV	−	+
Polychaeta				
Amphinomidae	FIRWOR	SINV	−	+
Mollusca				
Bursa (*Colubrellina*) *corrugata*	BURCOR	MINV	−	+
Platydoris angustipes	PLAANG	SINV	−	+
Charonia variegata	CHAVAR	MINV	−	+
Octopus vulgaris	OCTVUL	MINV	−	+
Cnidaria				
Telmatactis sp1	TELSP1	PLA	−	+
Telmatactis sp2	TELSP2	PLA	−	+
Telmatactis sp3	TELSP3	PLA	−	+
Isarachnanthus maderensis	ISAMAD	PLA	−	+

carried out on the species matrix of day and night transect observations after 4th root transformation, reducing the weight of large values while retaining relative abundance information (Legendre & Legendre, 1998). Significance of site groupings was done using ANOSIM (analysis of similarity). SIMPER (similarity percentage) was used to determine the species having the highest 90% of influence on site groupings. Functional group diversity of day and night assemblages was examined in terms of richness (S), Shannon diversity (H') and Pielou's evenness (J') (Maurer & McGill, 2011). Morisita–Horn index was used to examine the difference (dissimilarity) in species composition between day and night surveys, within each functional group (Maurer & McGill, 2011). This is an abundance-based index of species overlap between two groups (day *vs* night).

RESULTS

Species composition and abundance

A total of 57 taxa were identified among a total of 6547 individuals counted, including 32 species of fish, 10 of which included juvenile forms, and 25 invertebrate species (Table 1). Of the fish species, 29 species were found during

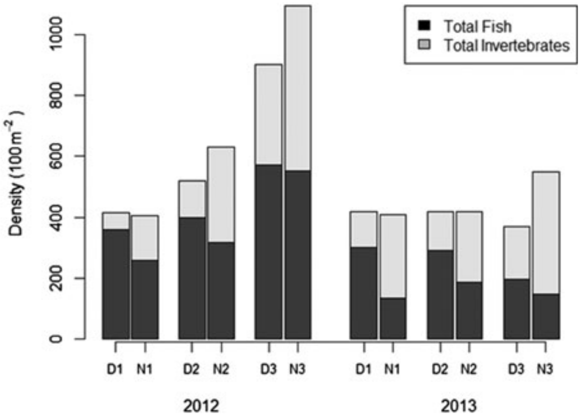

Fig. 1. Density of total fish and invertebrates between paired transects (D1, D2, D3, N1, N2, N3) between seasons (September 2012 and June 2013).

day transects with 13 found exclusively during the day. At night 23 species were found, with the brown moray eel (*Gymnothorax unicolor*), cardinal fish (*Apogon pseudomaculatus*) and scorpion fish (*Scorpaenodes insularis*) found exclusively at night. Of the invertebrates, eight species were found during the day transects, with the ophiuroid *Ophidiaster guildingi* found exclusively during the day. All other invertebrates were recorded at night, with 16 taxa occurring exclusively at night.

In all transect pairs, the density of all fish decreased between day and night surveys by an average of 27.9% (±15.6% SD) (Figure 1). Conversely, the density of invertebrates increased between day and night surveys by an average of 53.5% (±8.4% SD). In 2012, density of combined fish and invertebrates (using day and night transects as replicates) increased with depth (ANOVA, df = 2, $F = 22.645$, $P = 0.0155$). There was no similar increase or decrease detected in 2013. Rank abundance analysis of all species from all transects shows that *M. niger* and *D. antillarum* were ranked among the highest three species in all day and night transects in both seasons (Table 2). In addition to these two species, juvenile *Paranthias furcifer* ranked highly in 2012, but were not recorded in 2013. *Ophioblennius* sp. and juvenile *Epinephelus adscensionis* also ranked highly in

Table 2. Abundance (100 m^{-2}) of the top 10 ranked species in all transects. Ranks are coded dark grey (highest rank) to light grey (lowest rank) for ease of interpretation.

Species	**2012**						**2013**					
	D1	**N1**	**D2**	**N2**	**D3**	**N3**	**D1**	**N1**	**D2**	**N2**	**D3**	**N3**
Paranthias furcifer (j)	135	101	180	200	360	370						
Melichthys niger d/n	120	124	100	57	100	135	100	74	120	127	60	95
Diadema antillarum	55	132	121	301	329	510	107	237	119	208	166	337
Ophioblennius sp	24		24		19		18		15		9	
Epinephelus adscensionis (j)	20	5	28	15	33	6						
Stegastes lubbocki	16		16		31		23	4	30	6	29	4
Thalassoma ascensionis	13		7				4					
Malacanthus plumieri (j)	7				7							
Abudefduf saxatilis	7											
Holocentrus adscensionis	5	10	15	8	7	12	6				4	
Euapta lappa		6		7		13		16		8		15
Apogon axillaris		5				4		21		19	4	14
Brachycarpus biunguiculatus		3								5		12
Paranthias furcifer		3						10	7	4		10
Holothuria (*Platyperona*) *sanctori*		2		3								
Myripristis jacobus			1	11	16							
Malacanthus plumieri (j)			10									
Acanthurus bahianus				7	3							
Acanthurus coeruleus				5								
Telmatactis sp2						7						
Telmatactis sp1						6						
Gymnothorax moringa						10						
Thalassoma ascensionis (j)							100		60		30	
Stegastes lubbocki (j)							16		27		25	
Percnon abbreviatum							6		4			
Chaetodon sanctaehelenae							4					
Telmatactis sp3								4				24
Hippolysmata grabhami								4				
Scorpaenodes insularis								4				
Holocentrus adscensionis (j)								4		5		
Chromis multilineata									9			
Eucidaris tribuloides									4			
Myripristis jacobus (j)										4		5
Epinephelus adscensionis										4		
Corallianassa longiventris											4	
Priolepis ascensionis											4	
Channomuraena vittata												3

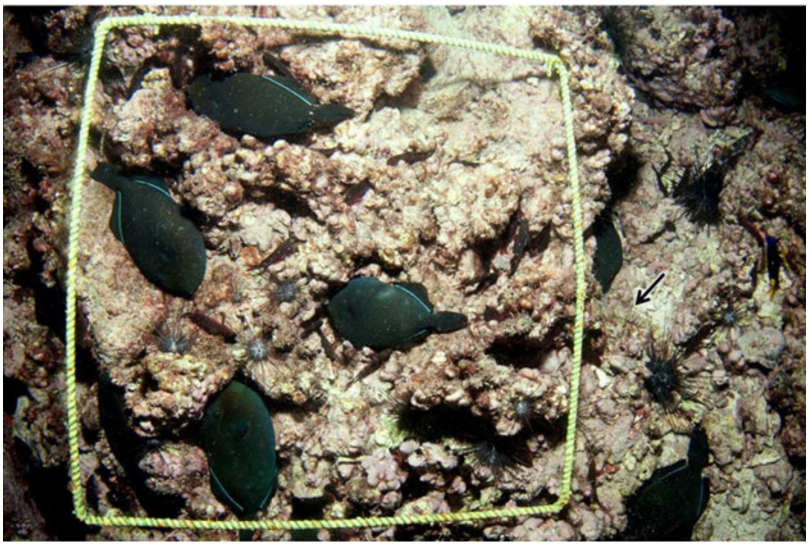

Fig. 2. Photo of resting *M. niger* at night (4 September 2014, N1Quadrat 5). Also seen are *D. antillarum*, and *Euapta lappa* (arrow). Quadrat is 0.5 × 0.5 m.

day surveys. In 2013 top ranked species also included juvenile *Thalassoma ascensionis* and juvenile and adult *Stegastes lubbocki* in day surveys, and *Apogon axillaris* and *Telmatactis* sp3 in night surveys. In total, there were 37 out of the total of 57 species ranked in the top 10 most abundant species among all transects.

Because *M. niger* and *D. antillarum* were found in large numbers consistently throughout all transects (*M. niger*; mean density = 101.0 individuals 100 m^{-2}, range = 57–135: *D. antillarum*; mean density = 218.5 individuals 100 m^{-2}, range = 55–510), these species are analysed separately. Two-sample Wilcoxon test (as data did not conform to parametric assumptions) was used to compare day and night densities among pairs of day/night transects in these species. There was no significant difference found between day and night densities of *M. niger* ($W = 16$, $P = 0.81$). However, all night observations of this species were of individuals in a state of deep rest (Figure 2). In contrast, pairs of day and night densities of *D. antillarum* were significantly different ($W = 5$, $P = 0.0411$). *Diadema antillarum* tended to hide during day transects, although many could be observed by the surveyor. At night however, urchins were observed out on open rock surfaces (Figure 2).

Principal component analysis of the day and night species matrix shows significant groupings of day and night surveys and surveys between seasons (ANOSIM, R-statistic = 0.8827, $P = 0.001$) (Figure 3). PC1 explains 39.5% of the variation in surveys, and represents the gradient between day (negative PC1) and night (positive PC1) surveys. This gradient seems to be strongly influenced by active or resting *M. niger*. As noted above, their day and night densities were not significantly different. Therefore in the PCA (Figure 3), the influence of *M. niger* effectively cancels each other out, and the abundance of other species can be interpreted with respect to their relative influence on survey groupings. Species driving this gradient are the echinoderms *Euapta lappa, Holothuria* (*Platyperona*) *sanctori, Holothuria* (*Halodeima*) *grisea, D. antillarum* at night, and the fish *Ophioblennius* sp., *Thalassoma ascensionis, Stegastes lubbocki* (adult) during the day. The gradient shown along the PC2 axis (explaining 29.5% of variation between surveys) represents the change in day and night assemblages between season (September 2012 and June 2013). These groupings are heavily influenced by the presence or absence of the juveniles of *Paranthias furcifer, Epinephelus adscensionis, Malacanthus plumieri, Myripristis jacobus* in 2012, and *Apogon axillaris, Stegastes lubbocki, Holocentrus adscensionis* and *Thalassoma ascensionis* in 2013. Analysis using SIMPER (per group identified in PCA) confirms these species are important for distinguishing groups; further detail of species driving the top 90% of these groupings are shown in Table 3.

Functional group diversity

Both day and night functional group profiles showed large proportions of herbivores (TURF) and planktivores (PLA) (Figure 4). The main difference in functional group profile was the presence (day) or absence (night) of omnivores (OMNI). These were composed almost entirely of *M. niger*, where active fish in the day were replaced by resting (INERT) *M. niger* at night. Other species of omnivore were present in the day and at night, although in low numbers (Table 1). Other functional groups were present in generally low proportions, varying between day and night transects in different ways, e.g. macrocarnivores (MCAR) and mobile benthic invertivores/cleaners (MINV). Detritivores were found primarily at night, being composed of three species of holothurians (Table 1).

Functional group diversity was examined between day and night transects for each season. There were no significant differences between day/night S (here being the number of functional groups), H' (relative abundance of groups present) and J' (evenness of groups present) in each season (after ANOVA and Tukey's HSD *post hoc* tests). Within functional groups, species overlap between day and night transect pairs was tested using Morisita–Horn index of dissimilarity (Table 4). Particularly low dissimilarity between day and night assemblages was found within the planktivores (PLA) in 2012, due in part to high abundances of juvenile *Paranthias furcifer* in both day and night surveys. However in 2013, there was

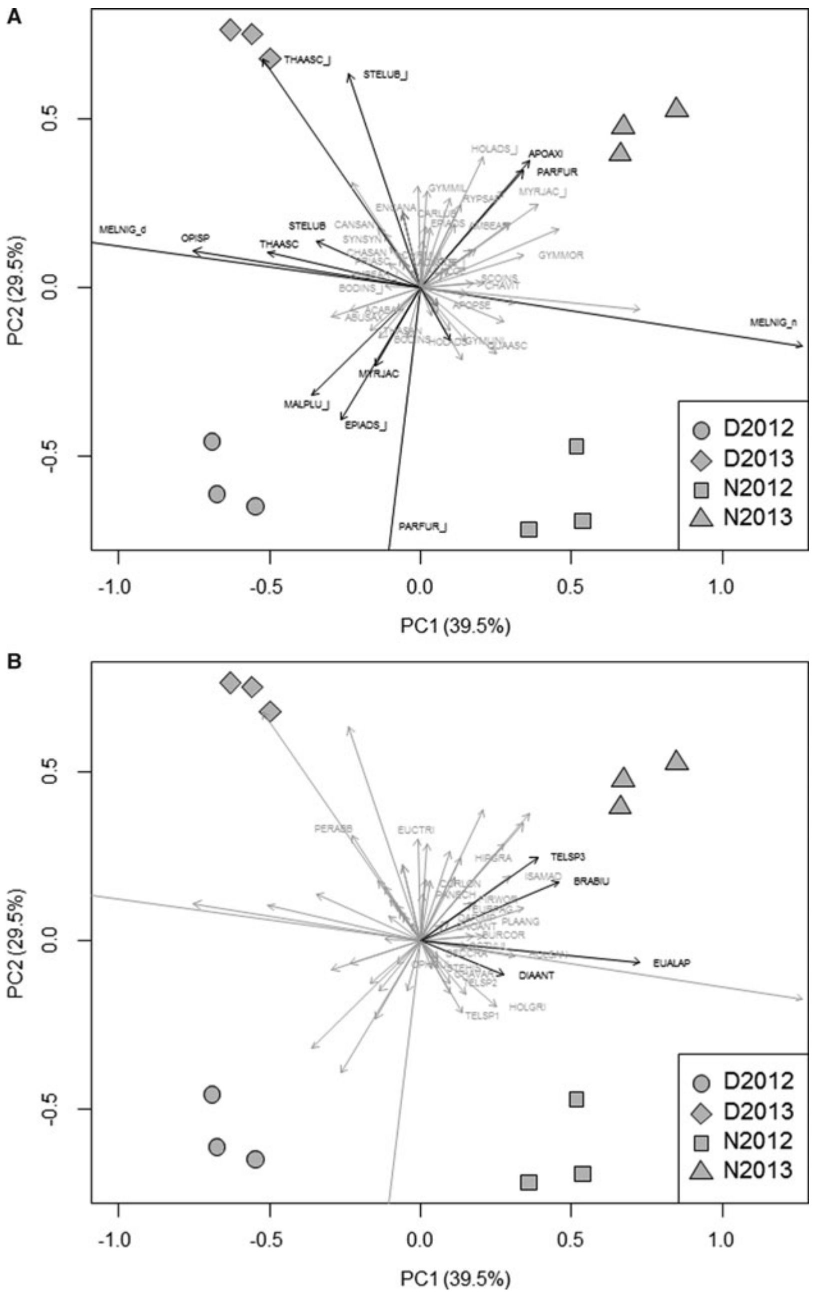

Fig. 3. Day and night species PCA. Top and bottom plots are identical, where the top plot names fish species, and the bottom plot names invertebrates. Species in black are those identified in SIMPER as being in the top 90% of species driving separation of day/night and 2012/2013 pattern.

high dissimilarity between day and night planktivore species, this time driven by the relatively high abundance of juvenile *Thalassoma ascensionis* in the day and high abundance *Apogon axillaris* at night. For mobile benthic invertivores/cleaners (MINV), low dissimilarity was seen in 2012, while high dissimilarity was seen in 2013, possibly driven by the presence of the shrimp *Brachycarpus biunguiculatus* at night, but also the presence or absence of a variety of low abundance species found in night or day surveys. There was a surprisingly low dissimilarity for herbivore species turnover between day and night transects (Table 4), suggesting that in general most herbivore species were found in both day and night surveys, although varying in their abundance only between day and night.

DISCUSSION

We quantitatively show clear differences between the day and night shallow reef assemblages on Ascension Island. Overall, invertebrate density increased by over 50% at night compared with the day, while fish density decreased. The sea urchin *Diadema antillarum* was a large component of this increase, emerging from crevasses at night; this predator avoidance behaviour has been well studied in the tropical Atlantic (e.g. Rodríguez-Barreras *et al.*, 2014). Indeed, the majority of invertebrates surveyed were found exclusively at night. For example, the holothurians *Holothuria* (*Platyperona*) *sanctori, H.* (*Halodeima*) *grisea* and *Euapta lappa* all increased activity

Table 3. SIMPER results for day/night comparison, and 2012/2013 comparison. Results of this analysis are Contr, Average contribution to overall dissimilarity; SD, Standard deviation of contribution; Cumsum, Ordered cumulative contribution.

	Contr	SD	Cumsum		Contr	SD	Cumsum
D2012/N2012				D2013/N2013			
Diadema antillarum	0.14	0.10	0.28	*Diadema antillarum*	0.15	0.06	0.23
Melichthys niger (day)	0.09	0.03	0.46	*Melichthys niger* (night)	0.12	0.03	0.42
Paranthias furcifer (j)	0.09	0.06	0.63	*Melichthys niger* (day)	0.11	0.03	0.59
Melichthys niger (night)	0.08	0.04	0.79	*Thalassoma ascensionis* (j)	0.07	0.03	0.70
Ophioblennius sp.	0.02	0.01	0.83	*Stegastes lubbocki*	0.03	0.00	0.75
Stegastes lubbocki	0.01	0.00	0.86	*Stegastes lubbocki* (j)	0.03	0.01	0.79
Epinephelus adscensionis (j)	0.01	0.01	0.89	*Apogon axillaris*	0.02	0.00	0.82
Malacanthus plumieri (j)	0.01	0.00	0.90	*Ophioblennius* sp.	0.02	0.00	0.84
				Euapta lappa	0.02	0.00	0.86
				Telmatactis sp3	0.01	0.01	0.88
				Brachycarpus biunguiculatus	0.01	0.00	0.89
				Paranthias furcifer	0.01	0.00	0.90
D2012/D2013				N2012/N2013			
Paranthias furcifer (j)	0.21	0.05	0.41	*Paranthias furcifer* (j)	0.18	0.05	0.42
Diadema antillarum	0.09	0.06	0.58	*Diadema antillarum*	0.12	0.06	0.70
Thalassoma ascensionis (j)	0.06	0.03	0.70	*Melichthys niger* (night)	0.03	0.02	0.77
Epinephelus adscensionis (j)	0.02	0.00	0.75	*Apogon axillaris*	0.01	0.01	0.81
Melichthys niger (day)	0.02	0.03	0.79	*Telmatactis* sp3	0.01	0.01	0.82
Stegastes lubbocki (j)	0.02	0.01	0.84	*Epinephelus adscensionis* (j)	0.01	0.00	0.84
Stegastes lubbocki	0.01	0.01	0.86	*Holocentrus adscensionis*	0.01	0.00	0.85
Ophioblennius sp.	0.01	0.01	0.87	*Euapta lappa*	0.01	0.00	0.87
Malacanthus plumieri (j)	0.01	0.00	0.89	*Myripristis jacobus*	0.01	0.01	0.88
Thalassoma ascensionis	0.01	0.00	0.90	*Paranthias furcifer*	0.01	0.00	0.89
				Brachycarpus biunguiculatus	0.00	0.00	0.90

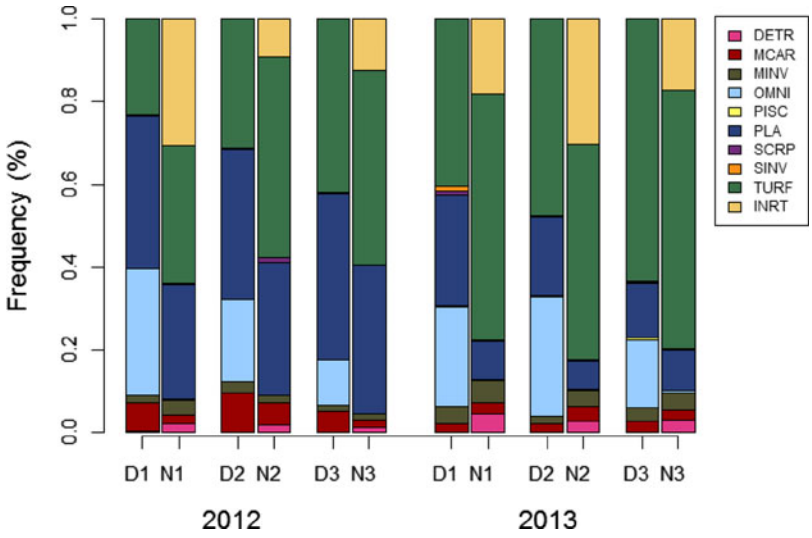

Fig. 4. Proportion of functional groups per transect. Functional group codes are found in Table 1.

at night. These large (10 s of cm in length), soft-bodied, slow-moving species may be particularly susceptible to predation, and their nocturnal emergence may be a predator avoidance behaviour (Hammond, 1982). PCA and ANOSIM analyses indicate significant differences between day and night assemblages, however these analyses also show that there is a great deal of variability not well explained, where the first two PCA axes explained only 69% of multivariate variation in the species matrix. Sample size is relatively low in the present study with limited replication, which may lead to a poorly resolved pattern. This study does provide strong guidance towards developing and testing hypotheses of important ecological gradients within the assemblage (e.g. day/night, depth, season) that can be translated into a more fully replicated and stratified design in the future, spanning a wider spatial extent.

It should be pointed out that day and night survey observations are based on those species that are in fact observable in either the day or night. In other words, with the exception of some fish that may have diurnal depth migrations, the actual assemblage is likely to be similar between day and night, where unobserved taxa are present but hidden. For example,

Table 4. Species overlap (Morisita–Horn index) within functional groups. High values represent high dissimilarity (i.e. low number of shared species). Instances marked 'too few data' mean that there were too few occurrences (many zeros) or the functional group was made up of only one species, meaning that comparison was not possible.

Functional group	**2012**			**2013**		
	DN1	**DN2**	**DN3**	**DN1**	**DN2**	**DN3**
TURF	0.18554	0.05413	0.01351	0.10669	0.12552	0.06537
MCAR	0.11471	0.14544	0.38138	0.58729	0.32151	0.62298
MINV	0.09576	0.03614	0.04261	0.45525	0.56627	0.88471
PLA	0.00717	0.00141	0.00186	0.96602	0.93798	0.89502
DETR	0.70492	Too few data				
SINV	Too few data					
SCRP	Too few data					
PISC	Too few data					
OMNI	Too few data					

M. niger densities were not significantly different between day (observed to be swimming) and night (observed to be resting) transects, suggesting that they are somewhat resident to specific areas. Conversely, *D. antillarum* densities were significantly different between day and night surveys. However in this case, they are simply hidden from view in the day, and this is likely to be the case for all invertebrates observed at night. What this means in terms of trophic dynamics is unclear, however it is thought that species' refuge sites are sub-optimal for food resources (Barnes & Crook, 2001 for review). Therefore it is reasonable to assume that the trophic ecology of the reef is roughly partitioned between day and night, described by a representative turnover of species and related functional groups. What this means in terms of the reef's day and night distribution of biomass and coincident diversity remains unknown; further investigation into the diversity-biomass (i.e. productivity) relationship would offer good insight into the overall ecosystem functioning of tropical reef systems (Gaston & Blackburn, 2000).

Although predator avoidance may be a driver for nocturnal activity in some species, many other reef species have evolved to take predatory advantage of their behaviour. For example, we show that anemone (*Telmatactis* sp. and *Isarachnanthus maderensis*) emergence is exclusively at night. This is likely to be related to feeding on the nocturnal emergence of benthic zooplankton (Sebens & DeRiemer, 1977). Increased zooplankton (e.g. copepods) and other small crustacean (cumaceans and amphipods, etc.) abundance at night has been reported widely for temperate and tropical shallow reefs (Ohlhorst, 1982; Annese & Kingsford, 2005; Nakajima *et al.*, 2009; Heidelberg *et al.*, 2010), where they swarm near the bottom or hide in sediment in the day, and emerge into the water column at night with depth and time of emergence varying with species (Alldredge & King, 1980). Increases in zooplankton at night were not measured in this study, however it can be inferred through the higher abundance of other planktivorous fish such as the cardinalfish (*Apogon axillaris*) (Marnane & Bellwood, 2002) reported in the present study at night, particularly in 2013. Nocturnal feeding on zooplankton may also drive the emergence of benthic decapods found in the present study (e.g. *Brachycarpus biunguiculatus*). Furthermore, the role of other more cryptic trophic associations such as diel patterns of fish parasites, fish, and their mutualistic cleaner fish and invertebrates commensals (Chambers & Sikkel, 2002) cannot be ignored.

In addition to day/night patterns of species abundance, there is also a strong seasonal pattern in both day and night assemblages. This pattern was driven primarily by the presence or absence of juveniles of a variety of fish species, where principal component analysis and rank abundance analyses show a difference in juvenile night assemblage between surveys (spanning 9 months) as well as differences in the day assemblages. Timing and location of, for example, spawning aggregations in reef fish are known to be highly precise and variable among species (Domeier & Colin, 1997). In particular, species of the Serranidae (e.g. *Paranthias furcifer* and *Epinephelus adscensionis* highlighted in the present study), are known to form seasonal spawning aggregations; their differences in reproductive timing may account for the seasonal variation in their presence or absence shown in Ascension Island. Difference in length of larval stages will also determine when the juveniles are visible in abundance counts. Certainly, variability between seasons in other species may be due to those species being rare or found in particularly low abundances in the area surveyed (i.e. those having low rank abundance). As such, sampling error may account for at least some of this variability. More comprehensive sampling is needed to find true seasonal or inter-annual differences in rare species. In addition, seasonal patterns related to reproductive timing also need to be considered in future trophic studies.

Herbivorous and planktivorous species dominated the functional group profile in all the day and night surveys. There was no difference in the diversity of functional groups between day and night, although there was significant turnover in species within each functional group between day and night assemblages. Given this high species turnover, this suggests that there may be a degree of 'functional redundancy' (*sensu* Rosenfeld, 2002) in this system. That is, because species within the group share a similar functional role, some species loss may have little effect on the overall functioning of the ecosystem. Functional redundancy, therefore, offers the ecosystem some resilience to perturbations. This has been studied in herbivorous reef fish (e.g. Hamilton *et al.*, 2014), and in cases where there is significant exploitation of reef fish, the consequences of reduced functional redundancy can have significant negative effects on the reef system (e.g. Bellwood *et al.*, 2003). Although we define functional diversity solely by the presence and relative abundance of trophic groups, true functional diversity of an assemblage may integrate a wider range of ecological traits including species abundance, body size, behaviour and habitat characteristics (e.g. Stuart-Smith *et al.*, 2013; Whittaker *et al.*, 2014). In the present study, we found numerical dominance in a few species, but low abundance (local rarity) in others, drawing into question how much effective redundancy there actually is within functional groups. Indeed, our interpretation of functional redundancy in the present study can be an artefact of how we have defined our functional groups (Bellwood *et al.*, 2003, Halpern & Floeter, 2008), where our functional group might be too broad, thereby being more descriptive of the species' fundamental niche space, when the reality is that each species occupies a very narrow realized niche space (Hutchinson, 1957; Morlon *et al.*, 2014), which would result in a reduced functional redundancy overall. Future trophic studies in Ascension Island should focus on the importance of abundant versus rare species, their relationship to habitat type, and species' morphological features as has been shown to be important in other reef systems (e.g. Ellingsen *et al.*, 2007; Stuart-Smith *et al.*, 2013; Aguilar-Medrano & Calderon-Aguilera, 2015).

The presence/absence and abundance of species in the day compared with night, and hence the trophic profile of the reef, will likely be strongly correlated with habitat complexity as it relates to refuge space for fish and invertebrates (e.g. Beukers & Jones, 1997; Wilson *et al.*, 2007 for review). The subtidal rocky seabed of Ascension Island can be extremely complex, with non-geniculate coralline red algae creating formations that add significantly to benthic rugosity. Such complexity will vary spatially throughout the island and at varying depths; in the present study the same habitat was surveyed in both seasons. However, future studies of trophic complexity or other ecological studies of assemblages across wider spatial scales should include habitat complexity as a co-variable. Furthermore, there is evidence of important yet highly cryptic habitats such as in the internal spaces of maerl balls and reef-forming coralline tower formations (SMSG unpublished observations) that should be more thoroughly explored.

Trophic processes of tropical marine communities can be placed on a spectrum of top-down (e.g. predation pressure) versus bottom-up (e.g. physical forcing) control of trophic dynamics, where placement along this spectrum is dependent on biotic and abiotic processes acting across a broad range of spatio-temporal scales (Vinueza *et al.*, 2014). Moreover, in these systems dynamics are not static and can be modified by, for example, spatio-temporal variability in oceanographic processes (e.g. Vinueza *et al.*, 2014). Our data show that there is significant daily and seasonal variability in species composition, abundance and functional group profile in Ascension Island. This suggests that there are a very wide range of species and processes that contribute to the trophic dynamics of the reef system. For example, at this location there have been significant seasonal cold-water upwellings detected compared with near-by sites (SMSG, unpublished data). Future research should examine interactions of such bottom up-processes with potential top-down processes (herbivory and predation on herbivores) for better understanding of reef assemblages and ecosystem function across local and wider-spatial scales in this highly isolated tropical reef system.

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