

Herbivores in a small world: network theory highlights vulnerability in the function of herbivory on coral reefs

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Summary

1. The application of network theory within the field of ecology has predominantly been based around the examination of species interactions (e.g. food webs). Extension of networks to spatial ecology is currently limited, yet the approach has significant potential as a framework for analysing habitat connectivity and ecosystem stability. Examination of network structures characterizing the spatial dynamics of organisms has the potential to highlight the relative robustness or vulnerability of the ecosystem processes they support.

2. On coral reefs, grazing by large herbivorous fishes is critical in maintaining the balance between coral and algae and is widely recognized as a key process in reef ecosystem functioning. However, the spatial dynamics exhibited by roving herbivores, and the implications of these dynamics for the overall stability and resilience of herbivory on reefs are not well understood.

3. Here, we present a novel extension of network theory to the analysis of movements of marine herbivorous fishes within a reef system. Using an array of remote acoustic receivers, over a period of 12 months, we tracked the movements of fishes belonging to the three dominant species of roving herbivore within a particular coral reef community.

4. Analysing these movements in terms of network graph theory, we found that individual fishes clustered their activities within small sections of the available linear reef habitat, and movements within and outside of these home ranges were made along predictable routes. All three species were heavily reliant on particular, well-connected parts of the reef (nodes), mirroring an ‘ultra-small-world’ network. This underlying dynamic creates vulnerability in the system, making targeted removal by fishing or the degradation of individual pockets of reef habitat more likely to result in a complete collapse in the overall process of herbivory at that particular area of reef.

5. Our results highlight an inherent vulnerability in the movement dynamics of herbivorous fishes and, by extension, in the overall process of herbivory in reef ecosystems. They suggest that maintaining high herbivore abundances across all reef habitats is critical in preserving the integrity of the grazing function on reefs. The approach of using network graph theory to analyse acoustic telemetry data is illuminating and is likely to have a range of applications across diverse ecosystems.

Key-words: acoustic telemetry, coral reef resilience, ecosystem function, parrotfishes, rabbitfishes, roving herbivores, small-world networks, spatial ecology

Introduction

The science of networks, previously the realm of graph theory in mathematics, has now become a cross-disciplinary subject, with an ever-growing list of applications (e.g. Jeong *et al.* 2000; Cancho & Sole 2001; Montoya & Solé

2002; Goldberg & Roth 2003). Within the field of ecology, the application of networks has most frequently been in the examination of interactions between species, for example food webs, host–parasitoid relationships and mutualisms (reviewed by Ings *et al.* 2009) where the approach has provided a useful framework within which to examine the potential effects of disturbances to these networks (Memmott *et al.* 2007). The application of network graph theory

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to spatial ecology has tended to lag behind its usage within the field of trophic interactions, yet the approach has significant potential as a framework for analysing habitat connectivity and the potential impacts of habitat and environmental changes on organisms (Cantwell & Forman 1993; Urban & Keitt 2001; Fagan 2002; Fortuna, Gomez-Rodríguez & Bascompte 2006; Fall *et al.* 2007; Fortuna *et al.* 2009; Urban *et al.* 2009). In the same way that individual properties of ecological networks of species interactions have been linked to varying degrees of ecosystem stability (Pimm, Lawton & Cohen 1991; Montoya, Pimm & Solé 2006; Okuyama & Holland 2008; Thébault & Fontaine 2010), an examination of the underlying structure of networks that characterize the movements and spatial dynamics of organisms can allow us to examine the relative robustness or vulnerability of the ecosystem processes they support.

Within coral reef ecosystems, accumulating evidence of declines in the health of individual coral reefs (Hughes 1994; McClanahan 1999; Lindahl, Öhman & Schelten 2001) or, in extreme cases, the collapse of entire regional systems (Gardner *et al.* 2003; Pandolfi *et al.* 2005) has prompted debate on the degree to which direct (Roberts 1995; Jennings & Polunin 1997; Mora 2008) and indirect (Knowlton 2001; Pandolfi *et al.* 2003; Hoegh-Guldberg *et al.* 2007) anthropogenic impacts on reefs may have compromised the functioning of these ecosystems (Roberts 1995; Jackson 2008; Bellwood, Hoey & Hughes 2012). The documentation of these declines in reef health has highlighted the need for improved management of critical functional groups that support ecosystem processes contributing to coral reef resilience (Bellwood *et al.* 2004; Hughes *et al.* 2005; Nyström *et al.* 2008). Herbivorous fishes, via the impact of their grazing, are known to play a critical role in maintaining the standing crop of algae on reefs (Randall 1965; Hay 1981; Lewis 1986; Hughes *et al.* 2007), thereby enhancing coral recruitment and facilitating a healthy equilibrium between coral and algal growth. The removal of herbivorous fishes from reefs, either experimentally or through overfishing, has been shown to result in the proliferation of macroalgae and a shift of the system into a less-valuable, algal-dominated state (Lewis 1986; Stockwell *et al.* 2009; Rasher, Hoey & Hay 2013). Improved management of this key functional group will therefore be fundamental to strategies designed to help reefs cope with further anthropogenic stressors such as pollution and climate change. Although we know much of the trophic functional ecology of individual species of herbivore (Bellwood & Choat 1990; Choat, Clements & Robbins 2002; Burkepile & Hay 2008), knowledge of their spatial ecology is much more limited and spatial models of the dynamics of herbivores on coral reefs are currently lacking.

To date, extensions of the network approach to spatial ecology have tended to be limited to the examination of movements patterns of terrestrial organisms and ecosystem processes (Fortuna, Gomez-Rodríguez & Bascompte 2006;

Fortuna *et al.* 2009). This is likely due, in part, to the obvious observational challenges imposed on the collection of spatial data for aquatic organisms. However, over the last decade, advances in the field of acoustic telemetry (reviewed by Costa, Breed & Robinson 2012) have opened up new possibilities in terms of the ability to collect direct and continuous information on the movement of marine organisms. The process of remote acoustic monitoring (Heupel, Semmens & Hobday 2006) now allows for the collection of data on the movement patterns of tagged individuals, similar to the process of radiotracking within terrestrial or freshwater habitats. Recent advances in the manufacture of smaller transmitters have opened up the field to a wider array of marine species, including the smaller species of herbivorous fishes that inhabit coral reefs.

Coupled with the data collection opportunities now afforded by remote acoustic telemetry, examination of the movements of herbivorous reef fishes through the lens of network topology has the potential to offer insights into the resilience of the ecosystem process of herbivory on reefs. In this study, our aim was to examine the movement dynamics of individual species of herbivorous fishes within a particular coral reef ecosystem in terms of their network structure. Using remote acoustic telemetry, we collected data on the movements of individuals from a community of herbivorous fishes on the western side of Orpheus Island, Great Barrier Reef (18°35'S, 146°20'E), a reef known to be dominated by three species of roving herbivore: the rabbitfish *Siganus doliatus*, and the parrotfishes *Scarus rivulatus* and *Chlorurus microrhinos* (Fox & Bellwood 2007). Over a period of 12 months, we tracked individuals belonging to these three species along a 3-km stretch of reef using an array of remote acoustic receivers ('listening stations'). From the detections recorded, we analysed the journeys made by individual fish between parts of the reef in terms of a series of edges (migrations) between nodes (parts of the ecosystem), with the specific aim of (i) assessing the underlying network structure of their movements and (ii) determining the associated consequences of this network structure for the dynamics of herbivory at the whole reef scale.

Materials and methods

STUDY SITE AND ACOUSTIC MONITORING ARRAY

A linear array of acoustic receivers (Vemco™ VR2W, 69 kHz frequency, 308 mm × 70 mm; Amirix Pty Ltd, Bedford, Nova Scotia, Canada,) was deployed on the leeward side of Orpheus Island, Great Barrier Reef, Australia (18°35'S, 146°20'E; Fig. 1a,b). The array of 13 receivers encompassed a 3-km stretch of continuous fringing reef habitat (Fig. 1b) and was designed to monitor the linear movement of acoustically tagged herbivorous fishes within Pioneer and Little Pioneer Bays. Based on the results of preliminary range testing, receivers were moored 150–200 m apart (average 180 m) just off the reef crest at a depth of 1–3 m (although due to the presence of a boating channel at the southern end of Pioneer Bay and a limit to the number of available receivers, the distance between the two most northerly and two of the southerly receivers

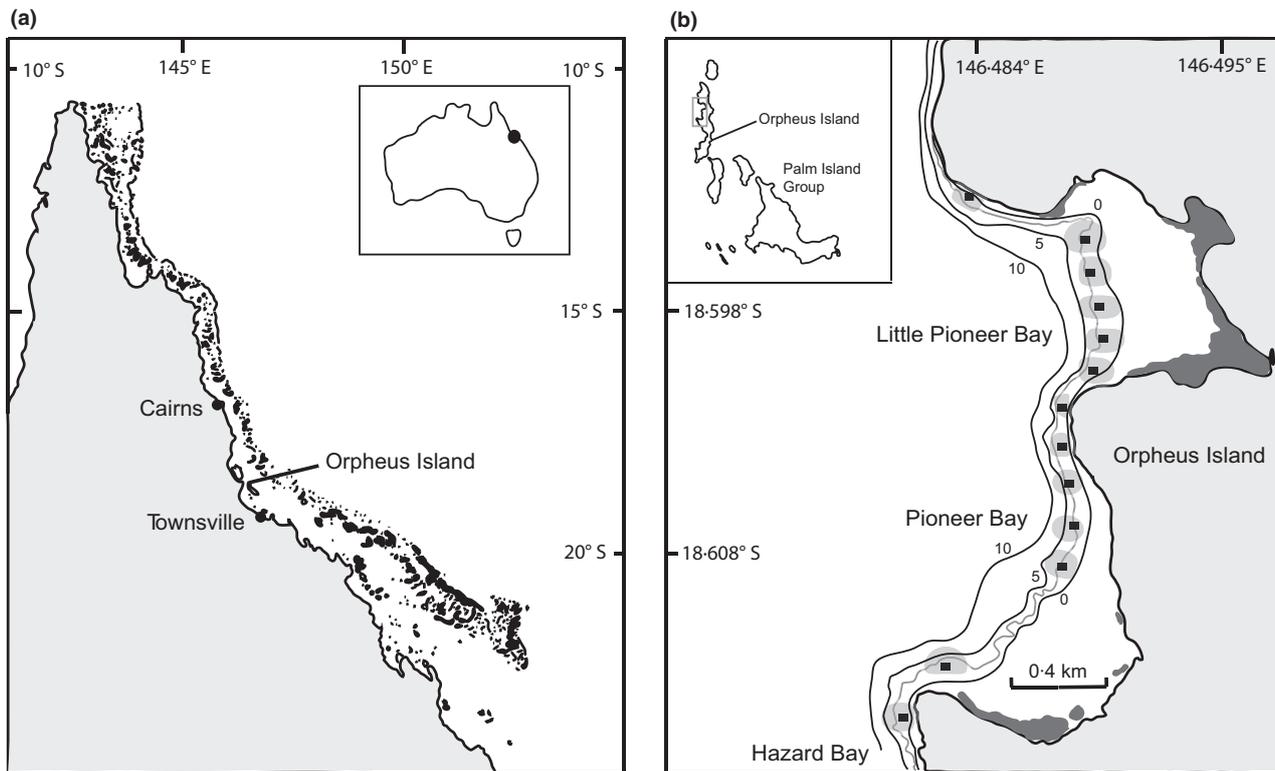


Fig. 1. (a) Location of the study site, Orpheus Island, on the inner part of the Australian continental shelf, within the mid-section of the Great Barrier Reef, Australia. (b) Positioning of linear array of remote acoustic receivers (black squares) within Pioneer and Little Pioneer Bays, on the leeward side of Orpheus Island (receivers were numbered 1–13 from south to north). Grey line running through receivers shows position of reef crest, black lines represent approximate depth contours. Shaded areas around receivers show experimentally determined detection ranges. Dark grey areas represent neighbouring mangrove habitat.

exceeded 200 m). The array resulted in a linear detection corridor along the outer reef flat and upper section of reef slope designed to encompass the primary habitat of the three study species, as confirmed through underwater visual censuses conducted by both divers and remote video recorders (Fox & Bellwood 2007, 2008). Movements by the three species at this location at 6–10 m depth were assumed to be negligible, based on extrapolation of the census data contained in Fox & Bellwood (2007, 2008). The detection range of each receiver was empirically tested by towing a coded transmitter (Vemco™, V9-1L, 5 s repeat rate, power output 142 dB re 1 μ Pa at 1 m) in the water column at a height of *c.* 0.5 m above the substratum to mirror the behaviour of the study species. Starting at the moored receiver, replicate transects were performed towing at a constant rate of 8 m min^{-1} (monitored via a handheld GPS unit) for a distance of 200 m along four bearings (0° north, 90° east, 180° south, 270° west), and detection ranges subsequently calculated by cross-referencing time-stamps at which no further transmitter detections were logged by the receiver. Detection ranges were non-symmetrical around the receiver and varied from 16 to 100 m (Fig. 1b), much lower than manufacturer's estimates due to the topographical and acoustic limitations imposed by the coral reef habitat (Welsh *et al.* 2012). Array coverage was therefore not 100% and, the potential impacts of this aspect of the study design are addressed below (see Discussion).

FISH TAGGING

A total of 20 fishes belonging to the three species, *S. doliatus* ($n = 10$), *Sc. rivulatus* ($n = 6$) and *C. microrhinos* ($n = 4$), were caught within Pioneer and Little Pioneer Bay using barrier nets and tagged with acoustic transmitters. Sample sizes were limited

by logistic considerations (the need to minimize the potential for signal collision and associated rejection of code detections at individual receivers) and legislative (permit) constraints. Coded transmitters (Vemco™ V7-2L, 20×7 mm or Vemco™ V9-1L, 24×9 mm; Amirix Pty Ltd) were surgically implanted into the peritoneal cavity of fishes whilst under anaesthesia (0.1 g L^{-1} salt-water solution of MS-222, FINQUEL, Argent Chemical Laboratories, Inc., Redmond, WA, USA). Following surgery, fish were held overnight in 1000 L aquaria with running sea water to allow for recovery and then released back at point of capture the next morning. The VR2W receivers logged the presence (time and date stamp) of individual fish passing within detection range of the unit, and data were downloaded from receivers at 8-week intervals over the 12-month deployment period.

NETWORK ANALYSIS

Logged detection sequences of tagged fish were viewed in VUE software version 1.4 (<http://vemco.com/downloads/>). Characterizing the experimental acoustic array as a line of 13 nodes or vertices (the receivers) connected to each other by links or edges (representing movements of the fishes between receivers), the detection sequences for each fish were broken down into constituent links between nodes. Movements detected along the receiver array were assigned to one of the 78 possible combinations of vertex pairs within the 13 node network (movement between receiver 1 and 2, between receiver 1 and 3, between receiver 1 and 4 etc.) based on the following criteria: a journey was considered to end at a particular node if the individual was detected on the same receiver for a period >15 min; otherwise, the fish was assumed to be passing through the detection range of that vertex en route to an alternative node in the array.

The selection of the 15-min period was based on the lower end of the range of published swimming speeds for reef fishes of the family Labridae (Fulton, Bellwood & Wainwright 2005) to which two of the three study species belonged. To simplify the model, links between nodes were treated as unidirectional and unweighted by actual distance between receivers. For each individual, the number of journeys made between particular pairs of nodes was calculated as a proportion of the total and plotted as a series of network graphs, with the thickness of the link or edge between nodes representing its relative use by that individual.

The structural properties of the individual network graphs generated by the categorization of movement sequences were then quantified by calculating their characteristic path length (L) and clustering coefficient (C), following the approach of Watts & Strogatz (1998). The characteristic path length was defined as the number of links (edges) in the shortest path between two nodes, averaged over all pairs of nodes. In the context of the present study, L therefore represented a measure of the directedness of an individual's mobility along the reef, that is, whether fishes tend to move from one area to another in a single motion or whether they impacted on many areas (nodes) in the course of moving along the reef. The clustering coefficient, $0 \leq C \leq 1$, was calculated as the fraction of possible edges between neighbouring nodes that actually exist. The variable quantified the degree to which groups of neighbouring nodes were linked to each other and therefore reflected the degree to which fishes' movements were fractioning off the reef into smaller clusters or enclaves. Variables L and C were calculated for individual fishes and at the species level, with species variables based on the aggregated network graphs of all conspecifics. For each species, we also calculated L_{regular} , C_{regular} , L_{rand} and C_{rand} , the values of L and C that would pertain to theoretical regular and random network graphs with the same number of vertices (n) and mean number of edges per vertex (k) as that species aggregate. The formulas used for L_{regular} , C_{regular} , L_{rand} and C_{rand} were those approximations reported by Watts & Strogatz (1998) for a network with sparse connections, but for which $n \gg k \gg \ln(n) \gg 1$.

Results

The period over which each fish was detected within the array of listening stations ranged from 14 to 334 days (overall median 164 day; Table 1). For all but one individual (a male parrotfish *Sc. rivulatus*), the total detection span corresponded with the expected battery life of the acoustic transmitter. Within the total detection span, the majority of individuals were detected daily within the 3-km study site (residency range 16–100%, median 97%), meaning that residency levels were universally high for all three species (Table 1). The only exception to this was an individual rabbitfish (*S. doliatus*) who went undetected for a

continuous period of 134 days within its 243 days detection span and thereafter was only detected within the array around the time of the new moon each month. No individuals were detected on the two most southerly receivers (receivers 1 and 2, Fig. 1b), suggesting that there were no excursions out of Pioneer Bay in a southerly direction. There were migrations by some individuals out of the bay in a northerly direction, with detections showing these individuals exiting and re-entering Pioneer Bay via receiver 13. As most of these migrations were tied to the lunar cycle, they were assumed to be associated with reproductive behaviour, rather than functional grazing impact, and were discarded from the analysis of ecosystem impact. Most individuals also showed high levels of local site attachment (Table 1), being most frequently detected on the receiver closest to where they were caught and released. Local site attachment was at, or close to, 100% for both *C. microrhinos* and *S. doliatus* (Table 1). The lower value of local site attachment for *Sc. rivulatus* as a species was driven by the behaviour of two male (terminal phase) individuals who were detected at their 'home' receiver on only an average of 60% of the days detected within the array. For initial phase individuals of this protogynous sequential hermaphroditic species, average levels of site attachment were 99% (± 0.1 SE), mirroring the results obtained for *C. microrhinos* and *S. doliatus*.

The pattern of movements exhibited by individuals between nodes of the array was highly directed, with fish using only 5–23% of the 78 potential routes available within the network (Table 2). Network graphs revealed the directed nature of individuals' movements and a limited degree of connectedness between nodes (Figs 2 and S1, Supporting information). Movements to points along the reef tended to be made via long-range short cuts, rather than via a regular sequence of moves through neighbouring nodes, with fishes returning to their 'home' node (receiver closest to where they were captured and released) between excursions. This resulted in a 'hub-and-spoke' pattern of connections between vertices (hubs being those nodes in the network with a high number of connections), in complete contrast to the 'nearest neighbour' pattern of connections (where movements are between adjacent or semi-adjacent nodes) that would be observed in a 'regular' network (Fig. 2a).

Table 1. Summary of detections recorded for herbivorous fishes tagged at Orpheus Island, Great Barrier Reef. Residency is defined as the number of days an individual was detected within the 3 km array as a percentage of the total detection span. Site attachment is defined as the number of days an individual was detected at the receiver closest to its capture and release point as a percentage of the number of days detected within the 3 km array

Family	Species	n	Size (cm) Median	Total detection span (days)			Days detected in array			Residency (%) Mean (\pm SE)	Site attachment (%) Mean (\pm SE)
				Min	Max	Median	Min	Max	Median		
Siganidae	<i>Siganus doliatus</i>	10	21.3	149	243	167	39	165	163	88.3 (8.1)	100 (0)
Labridae	<i>Scarus rivulatus</i>	6	23.9	14	249	245	13	244	223	92.5 (5.4)	78.0 (13.6)
Labridae	<i>Chlorurus microrhinos</i>	4	40.6	127	334	246	123	257	230	90.1 (5.2)	98.7 (0.5)

Table 2. Structural properties of herbivore networks. Characteristic path length (L) and clustering coefficient (C) values for individual species of herbivore compared to approximate values of these structural variables for a regular network with the same number of vertices (n) and average number of edges per vertex (k) (*Chlorurus microrhinos*: $n = 13$, $k = 3.154$; *Scarus rivulatus*: $n = 13$, $k = 3.462$; *Siganus doliatus*: $n = 13$, $k = 1.846$)

Species	Routes used (%)	Characteristic path length			Clustering coefficient		
		L_{actual}	L_{regular}	L_{rand}	C_{actual}	C_{regular}	C_{rand}
<i>C. microrhinos</i>	23	1.244	4.072	2.233	0.462	~0.75	0.243
<i>Sc. rivulatus</i>	15	1.013	5.511	2.065	0.692	~0.75	0.266
<i>S. doliatus</i>	5	0.731	11.118	4.184	0.154	~0.75	0.142

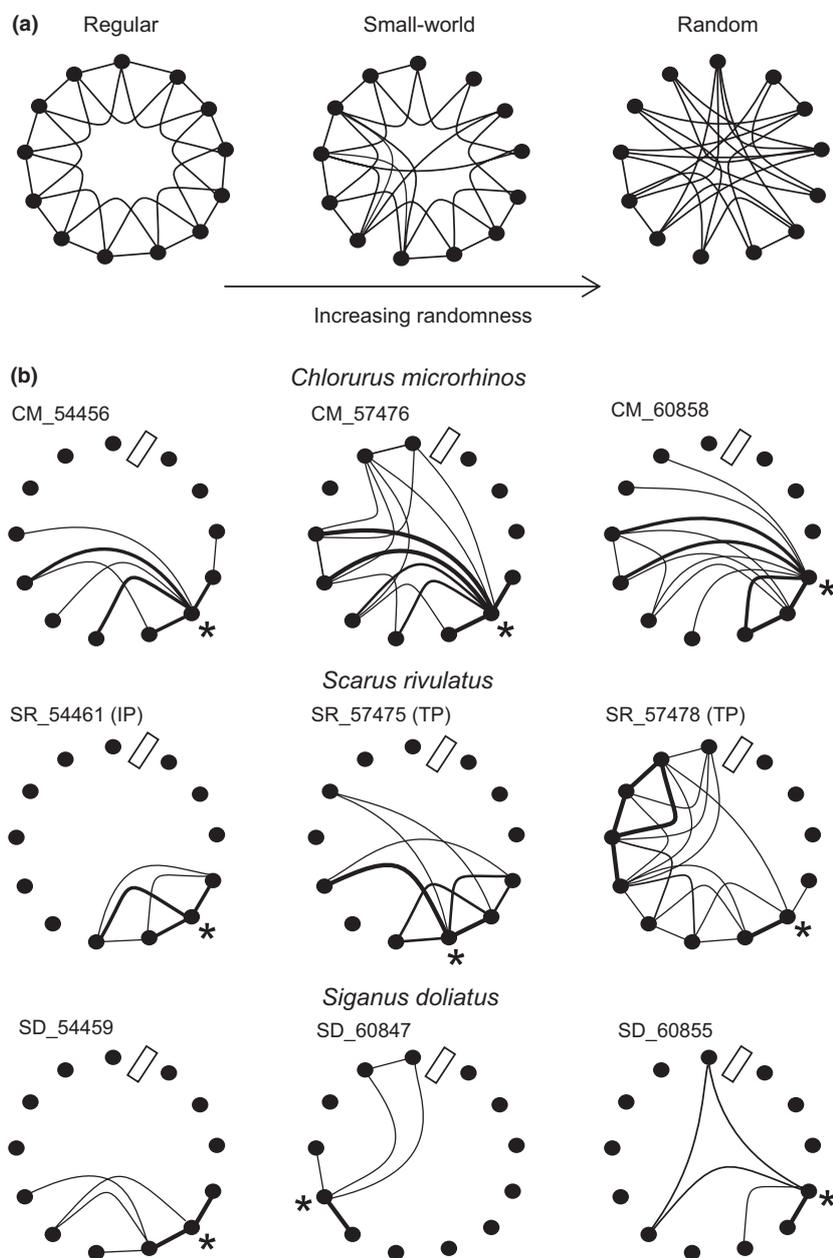


Fig. 2. (a) Theoretical lattice graphs for regular, random and 'small-world' networks showing graphical representation of the properties of a small-world network (highly clustered-like regular network but with low characteristic path length). Adapted from Watts & Strogatz (1998, Fig. 1). (b) Network lattices summarizing movements between receivers (nodes) over the total detection span for three representative individuals belonging to the species *Chlorurus microrhinos*, *Scarus rivulatus* and *Siganus doliatus*. Thickness of edges connecting receivers relates to the proportion of total movements made between those nodes. *The receiver closest to where individuals were caught and released. The open rectangle between nodes in top right hand corner denotes the fact that receivers 1 and 13 are not nearest neighbours. See Fig. S1 (Supporting information) for remainder of network graphs.

The network of movements displayed by most individuals was characterized by low path length and a relatively high degree of clustering, properties associated with the class of 'small-world' networks (*sensu* Watts & Stro-

gatz 1998) that lie intermediate between random and regular network lattices (Fig. 3a). Characteristic path lengths of overall species' networks were lower than those of equivalent regular and random networks

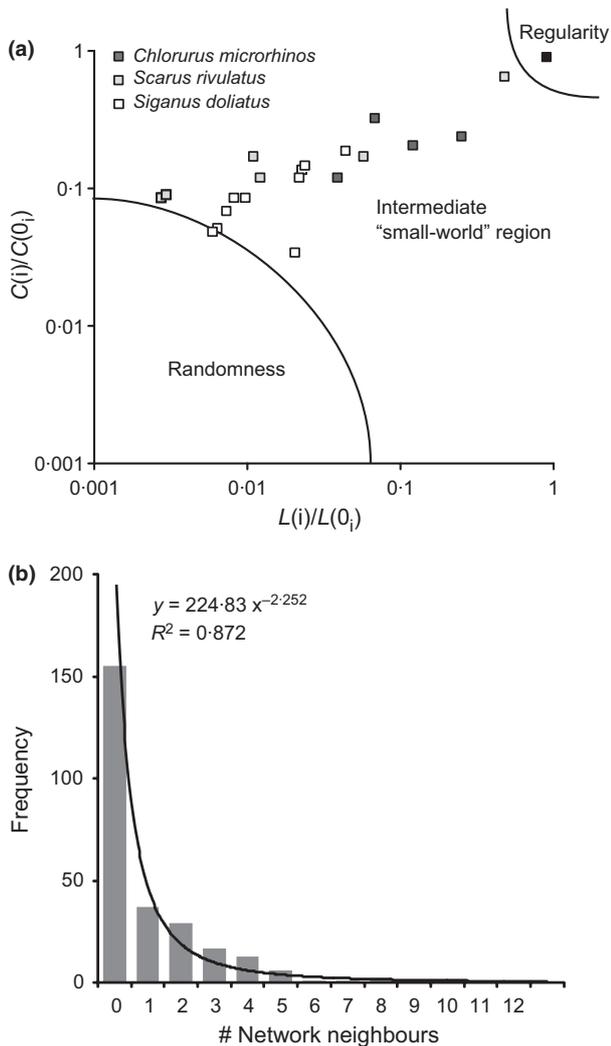


Fig. 3. Properties of individual network graphs summarizing movements of individual herbivorous fishes within Pioneer and Little Pioneer Bay, Orpheus Island over periods of 14–334 days. (a) Characteristic path length [$L(i)$] and clustering coefficients [$C(i)$] of network graphs based on the long-term movement patterns of individual herbivorous fishes belonging to the species *Chlorurus microrhinos*, *Scarus rivulatus* and *Siganus doliatus*. Calculations of $L(i)$ and $C(i)$ for each fish have been normalized by their respective values of $L(0)$ and $C(0)$ for a regular lattice and black square (■) therefore represents normalized values for a regular network. Logarithmic scales are used for both axes. (b) Distribution of the number of network neighbours (i.e. number of edges linking each node) across all individuals tracked within Pioneer and Little Pioneer Bay. Like the class of ultra-small-world ‘scale-free’ networks, the distribution decays as a power law ($y = x^{-\alpha}$), with $\alpha = -2.25$.

($L_{\text{regular}} \gg L_{\text{rand}} > L_{\text{actual}}$), whilst clustering coefficients were greater than those associated with equivalent random networks ($C_{\text{regular}} > C_{\text{actual}} > C_{\text{rand}}$; Table 2). The strong site attachment of individuals and the directedness of their movements were also reflected in the frequency distribution of the number of network neighbours. The degree distribution was heavily right-skewed, meaning that the majority of nodes had fewer-than-average connections to other parts of the reef, and a small number of nodes had better-than-average connectedness (Fig. 3b). The

distribution decayed as a power law ($y = x^{-\alpha}$) with $\alpha = -2.25$, exhibiting the properties of a scale-free network.

Discussion

In this study, we present an analysis of the spatial dynamics of three species of herbivorous coral reef fishes based on the application of network graph theory to movement data collected via remote acoustic telemetry. Sample sizes for the two of the three species were limited; however, we obtained consistent within-species results showing that the movements of *C. microrhinos*, *Sc. rivulatus* and *S. doliatus* are directed and highly localized. The majority of individuals studied had limited linear extensions of movement (average linear movement was just a 180–240 m portion of the 3 km length of continuous reef habitat), with a high level of local site attachment and a fixed pattern of reef usage. Only one individual (a male parrotfish, *Sc. rivulatus*) appeared to display the sort of behaviour that might be expected of a ‘roving’ herbivore in the sense of providing regular, ongoing connections between all parts of the reef within Pioneer Bay. The remainder of individuals moved between limited numbers of areas along the extent of available reef habitat and did so along consistently used, direct routes. Although the limited detection ranges of receivers meant that array coverage was not 100%, the fact that the array was able to document the range of movement dynamics from random to regular (Fig. 3) suggests that the results presented here are robust to the detection range issues necessarily imposed by the topography and acoustics of the coral reef habitat. The behaviour of most individuals approximated to the small-world class of ‘scale-free’ networks (Amaral *et al.* 2000) that have been labelled as ‘ultra’-small worlds (Cohen & Havlin 2003). In an ‘ultra’-small world, even distant areas of the reef will be joined by just one edge or pathway. These pathways effectively acted as short cuts between parts of the ecosystem, meaning that neighbouring areas are bypassed. This resulted in a high degree of clustering of parts of the reef (node clustering), a common property of ecological networks (Dunne, Williams & Martinez 2002a; Olesen *et al.* 2006).

The finding of limited spatial impact by the species tracked in our study is unsurprising, given that all three have been observed to exhibit varying degrees of either home-ranging or defence of territory against conspecifics. In the case of the two species of parrotfishes studied here, this behaviour is likely to be based on the complex social and mating systems displayed by members of this family of reef herbivores (Ogden & Buckman 1973; Thresher 1984; Van Rooij, Kroom & Videler 1996). For the rabbitfish, *S. doliatus*, social systems are little studied; however, individuals can be observed giving displays of aggression to conspecifics (R. J. Fox, pers. obs.). The documentation of limited home ranges for species of herbivorous reef fishes is therefore not novel (Robertson & Gaines 1986;

Mumby & Wabnitz 2002), and the fact that territorial species view the reef as a segmented entity, rather than a continuous whole is arguably to be expected (cf. Meyer & Holland 2005; Meyer, Papastamatiou & Clark 2010; Claisse *et al.* 2011; Marshall *et al.* 2011). Instead, the significance of this aspect of our findings lies in the contrast it reveals to the view of all herbivorous fishes as 'mobile-link' organisms (*sensu* Lundberg & Moberg 2003) providing ongoing connections between parts of the reef and actively moving between habitats (Moberg & Folke 1999; Nyström *et al.* 2008). Our results demonstrate that, even over long-term periods, the movements of particular species of herbivore are indicative of a fundamental lack of continuity in individual functional impact along reef. In terms of the spatial dynamics of herbivorous fishes on coral reefs, our results add weight to the view that social structure may be a significant constraint on the spatial impact of certain species of herbivorous fishes (Afonso *et al.* 2008) and, by extension, the overall dynamics of herbivory.

Along with the impacts of social structure, it is likely that the movement and foraging patterns of the species of herbivore documented here were influenced by the benthic habitat characteristics of the study site. Several studies have documented the impact of both substrate type (Fox & Bellwood 2007; Nash *et al.* 2012) and structural complexity (Wilson, Graham & Polunin 2007; Graham & Nash 2013) on the distributions and feeding patterns of reef fishes. It is therefore important to consider how the influence of benthic characteristics and level of topographical complexity at our study site may relate to the observed small-world dynamics, and the potential sensitivity of our results to the individual characteristics of the study site. Nash *et al.* (2012) found that coral cover and abundance of congenics were key explanatory variables in a short-term (2-min sampling period) model of feeding behaviour of parrotfish species on five mid-shelf reefs of the Great Barrier Reef, with lower coral cover leading to greater linear foraging ranges and greater distances travelled between feeding forays. At the level of coral cover characteristic of the reef crest at Pioneer Bay (*c.* 20%, see Table 3 of Fox & Bellwood 2007), Nash *et al.* (2012) suggest that the foraging ranges of parrotfishes lie towards the more elongate end of the scale, with greater interforay distances. At sites with higher levels of coral cover than that of Pioneer Bay, therefore, we could potentially expect a compacting of the foraging range. The associated implications for the spatial dynamics of the individual would then be an increase in the clustering coefficient of the network of movements and a shift to the more extreme end of the scale of ultra-small-world networks, with their inherent structural vulnerabilities. The caveat to this being, as Nash *et al.* (2012) themselves point out, that the small-scale movement patterns documented in their study may not necessarily scale up in this way. It is likely that further examination of the spatial dynamics of herbivorous fishes under varying benthic habitat conditions will be required to test the hypothesis presented here.

Individual properties of ecological networks of species interactions such as food webs have been linked to varying degrees of ecosystem stability (Pimm, Lawton & Cohen 1991; Montoya & Solé 2002; Okuyama & Holland 2008; Thébault & Fontaine 2010), and the network properties of the spatial dynamics of herbivorous reef fishes described here will therefore have implications for the relative stability of the overall ecosystem process of herbivory in the face of natural and anthropogenic disturbances. Within the context of the sample size that was possible for the current study, the implications drawn out here are obviously of a preliminary nature. However, the consistency of results obtained across individuals within species do allow for some preliminary observations to be made on the relationship between network properties and the process of herbivory. For example, the fact that the majority of nodes within species' movement networks had only limited connection means that the random deletion of a node (e.g. habitat patch loss due to natural, randomized events) is probabilistically less likely to cause disturbance (i.e. alter the characteristic path length or clustering coefficient) than for a regularly structured network. Scale-free networks are therefore more robust to random disturbances (Dunne, Williams & Martinez 2002b), a feature which, in the ecological context, has been suggested to confer evolutionary advantage (Barabási & Albert 1999). This could be good news for coral reefs in the sense that it suggests a certain degree of resilience to random perturbations or disturbance events. However, the problem for such networks lies not in the effect of random disturbances, but in the impact of targeted attacks.

Small-world networks, by virtue of the over-abundance of connections through hub nodes, are extremely vulnerable to targeted attacks on those hubs, and such attacks will result in catastrophic network failure (Dunne, Williams & Martinez 2002b; Allen, Gunderson & Johnson 2005). For a coral reef ecosystem, targeted attacks might be thought of as the concentration of fishing effort at known aggregation sites, for example the practice of collecting *C. microrhinos* and other large parrotfishes from their habitual nocturnal resting spots (Bellwood *et al.* 2004), or the fishing of spawning aggregations (Sadovy & Domeier 2005). Our results provide a mechanistic explanation of why herbivores are more closely aligned with fishing vulnerability than climate change in assessments of extinction vulnerability of individual groups of fishes on coral reefs (see Graham *et al.* 2011). They also suggest that the overall process of herbivory at this site contains an inherent structural vulnerability in terms of the heavy reliance of individuals on particular nodes. In contrast to individuals that display 'random' network dynamics, the majority of herbivores within Pioneer Bay are likely to be vulnerable to the loss or degradation of particular parts of the reef. The result provides a theoretical basis for the connection between mobile-link organisms (Lundberg & Moberg 2003) and the robustness of ecological systems. By virtue of their mobility and lack of direct attachment to particular 'nodes' of the reef, such organisms provide a degree of insurance against attacks on the system.

Essentially, they reduce the system's dependence on individual nodes and in doing so promote the overall stability of the ecosystem by ensuring the network is highly connected and that propagation of cascading failures is limited (Watts 2002). In conservation terms, this suggests that true mobile-link or roving species of herbivore represent a key (but potentially scarce) component of ecosystem resilience and therefore merit special levels of protection by management. In our system, this behaviour was only observed in a single individual (a male *Sc. rivulatus*), whose movement was probably underpinned by his reproductive status and lack of territory, but may be characteristic of other species of herbivore not examined in the current study. Determination of the behavioural dynamics of other species of reef herbivore must therefore be a priority.

But what do these results suggest for management of herbivore populations? If social structure really is the ultimate constraint on herbivore dynamics, the question is whether the selective removal of neighbouring conspecifics will result in the remaining individuals extending their foraging range, liberating them from the constraints of their ultra-small world and allowing them to behave more randomly? If so, then this may suggest that the system contains some degree of compensatory mechanism with which to offset patchy declines in population numbers. The alternative is that the foraging dynamics presented here are the pattern that adult individuals will adopt, regardless of neighbour presence. Further experimental work will be required to distinguish between these competing hypotheses and to tease out potential compensatory mechanisms within the process of herbivory at the whole reef scale. Nevertheless, even selective removal of herbivores under the assumption of compensatory foraging dynamics must be viewed with caution. The spread of an individual's grazing impact over a larger area of reef following removal of a neighbour will necessarily yield a lower level of grazing disturbance per unit area of reef, potentially allowing the benthic community to reach a later stage of succession (Steneck & Dethier 1994). This, in turn, may increase the potential for the benthic algal community to reach a stage at which positive feedback loops allow the development of late-stage unpalatable (Paul & Hay 1986; Hay, Fenical & Gustafson 1987) or physically unappealing (Hoey & Bellwood 2011) macroalgae that can persist even in the presence of significant numbers of herbivores (cf. Williams, Polunin & Hendrick 2001).

By examining the long-term movement patterns of herbivorous reef fishes through the lens of network topology, this study presents a framework for examining the implications of individuals' spatial dynamics on the stability of particular ecosystem processes. The method is one that has potential applications across a wide range of aquatic and terrestrial ecosystems in the analysis of the impact of organisms' spatial ecology on the stability and functioning of individual system processes. In the particular case examined here, a network approach to classifying the movement patterns of individual species of coral reef herbivore determined via remote acoustic telemetry revealed that

individual fishes display properties of the ultra-small-world class of scale-free networks that are likely to be vulnerable to targeted attack. As one of the key ecological processes that support the health and resilience of reefs, this vulnerability must be taken into account when evaluating the status of herbivore populations on coral reefs. Our results suggest that maintaining high herbivore abundances along the linear extent of a reef will be critical in terms of preserving the integrity of the grazing function.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Network lattice graphs of remaining individuals of the species *Chlorurus microrhinos*, *Scarus rivulatus* and *Siganus doliatus*.