

Herbivorous fishes, ecosystem function and mobile links on coral reefs

J. Q. Welsh · D. R. Bellwood

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Abstract Understanding large-scale movement of ecologically important taxa is key to both species and ecosystem management. Those species responsible for maintaining functional connectivity between habitats are often called mobile links and are regarded as essential elements of resilience. By providing connectivity, they support resilience across spatial scales. Most marine organisms, including fishes, have long-term, biogeographic-scale connectivity through larval movement. Although most reef species are highly site attached after larval settlement, some taxa may also be able to provide rapid, reef-scale connectivity as adults. On coral reefs, the identity of such taxa and the extent of their mobility are not yet known. We use acoustic telemetry to monitor the movements of *Kyphosus vaigiensis*, one of the few reef fishes that feeds on adult brown macroalgae. Unlike other benthic herbivorous fish species, it also exhibits large-scale (>2 km) movements. Individual *K. vaigiensis* cover, on average, a 2.5 km length of reef (11 km maximum) each day. These large-scale movements suggest that this species may act as a mobile link, providing functional connectivity, should the need arise, and helping to support functional processes across habitats and spatial scales. An analysis of published studies of home ranges in reef fishes found a

consistent relationship between home range size and body length. *K. vaigiensis* is the sole herbivore to depart significantly from the expected home range–body size relationship, with home range sizes more comparable to exceptionally mobile large pelagic predators rather than other reef herbivores. While the large-scale movements of *K. vaigiensis* reveal its potential capacity to enhance resilience over large areas, it also emphasizes the potential limitations of small marine reserves to protect some herbivore populations.

Keywords Home range · Ecosystem function · Coral reefs · Functional connectivity · *Kyphosus vaigiensis* · Cross-scale interactions

Introduction

Many studies have emphasized the need to increase resilience to help limit or prevent ecosystem decline (Vitousek et al. 1997; Scheffer et al. 2001). The resilience of an ecosystem refers to the capacity of the system to respond to, and recover, after a disturbance event (Folke et al. 2004; Hughes et al. 2003, 2007). To be resilient, a system must have the ecological capacity to maintain critical ecosystem processes (Hughes et al. 2003; Carpenter et al. 2006). One key component of resilience is connectivity via mobile links (Lundberg and Moberg 2003; Rico et al. 2012). Mobile links are described as those taxa which have the capacity to move between systems, particularly where they supplement functional processes by moving from a relatively intact system to one degraded by exploitation or natural disturbances (Lundberg and Moberg 2003). Mobile links may be passive (e.g., marine invertebrate larvae) or active (e.g., bats, birds and large terrestrial herbivores),

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J. Q. Welsh (✉) · D. R. Bellwood
Australian Research Council Centre of Excellence for Coral Reef Studies, and School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia
e-mail: Justin.Welsh@my.jcu.edu.au

depending on their capacity for movement (Lundberg and Moberg 2003; Couvreur et al. 2004; Kremen 2005; Serkercioglu 2006).

In the marine environment, the passive mobile links of invertebrates and the more active larval fishes have been widely studied, and their ability to interconnect reefs is well established (e.g., Jones et al. 1999; Patterson and Swearer 2007; Almany et al. 2009). These larval connections are usually over large spatial and temporal scales (regional to biogeographic scales, over weeks to years) (Patterson and Swearer 2007; Shanks 2009). In contrast, at the reef-scale, short-term movement or connectivity of adults has received less attention, and the extent and nature of active mobile links in the marine environment is poorly understood. This is especially troubling on coral reefs given the potential importance of ecological interactions conferred by one of the key active mobile links, roving herbivorous reef fishes (e.g., Nyström and Folke 2001; Ceccarelli et al. 2011).

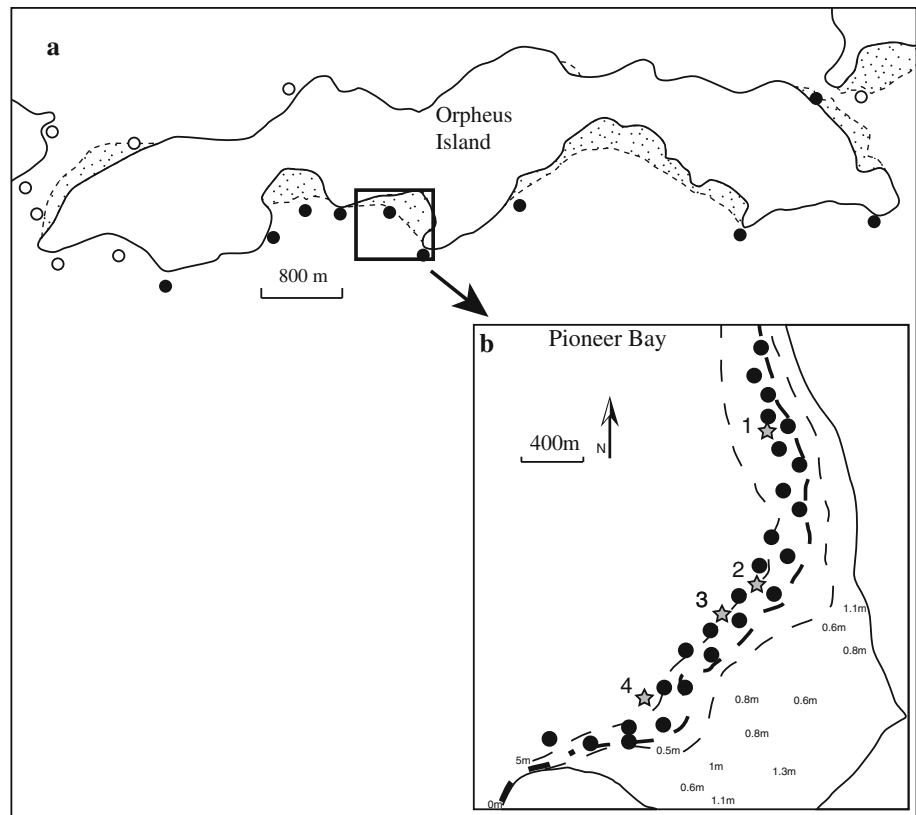
Reef fishes have a number of functional roles, which support the resilience of coral reef ecosystems (Bellwood et al. 2004; Folke et al. 2004). One key process is herbivory, where the feeding activities of herbivorous fish mediate coral–algae interactions and help maintain a coral-dominated state (McCook 1997; Bellwood et al. 2004; Burkepile and Hay 2010). Within the herbivore guild, separate functional groups have been identified, each important in maintaining different components of reef resilience. Scrapers (e.g., *Scarus* spp.), excavators (e.g., *Chlorurus* spp.), and croppers (e.g., *Acanthurus* spp.) are responsible for grazing the reef's epilithic algal matrix and keeping algal growth in check (Fox and Bellwood 2007). Browsers (e.g., *Kyphosus* spp.) are unusual in that they feed directly on adult leathery macroalgae and play an important role in the removal of macroalgae (Bellwood et al. 2004; Burkepile and Hay 2008; Hoey and Bellwood 2009; Rasher et al. 2013). Given its importance in regenerating degraded ecosystems, a great deal of research has recently been focused on quantifying browsing (e.g., Burkepile and Hay 2010; Michael et al. 2013), especially on the Great Barrier Reef (GBR) (McCook 1997; Hughes et al. 2007; Hoey and Bellwood 2009). This research has found that the process is overwhelmingly dominated by a limited number of species (predominantly *Naso unicornis* and *Kyphosus vaigiensis*) and that it is highly variable both spatially and temporally (Cvitanovic and Bellwood 2009; Bennett and Bellwood 2011; Lefèvre and Bellwood 2011). Understanding the nature of this variability is key to understanding how browsing herbivores interact with their environment, support its resilience, and offer a capacity to regenerate or recover from degradation. However, the factors that underpin this variability remain to be determined and are likely to be strongly influenced by the spatial scales over which browsing herbivores feed.

In the terrestrial environment, large-bodied herbivorous mammals will travel several hundred kilometres in search of food. They act as mobile links, delivering both their grazing activities and ingested plant seeds to distant, spatially separated locations, and thus interconnect metapopulations (Couvreur et al. 2004; Owen-Smith et al. 2010). On coral reefs, there is no evidence of similar widespread feeding behaviour, and thus little evidence that fishes act as mobile links in this manner (but see Vermeij et al. 2013). Indeed, most reef fishes, including roving herbivores, appear to have extremely limited movements (Eristhee and Oxenford 2001; Meyer and Holland 2005; Fox and Bellwood 2011; Welsh and Bellwood 2012a, b). The basic question in understanding functionally important mobile links on coral reefs is: at what point is an individual's home range large enough for them to act as a significant vector for functional connectivity (i.e., a mobile link)?

Evidence of a relationship between body length and a fish's home range length has been used to identify the size range of fishes which are expected to be protected by a marine protected area (MPA) of a given size (Kramer and Chapman 1999). This relationship highlights the limited movement of many smaller species, a finding that has been strongly supported by recent studies, which have employed acoustic telemetry to assess the movement patterns of individual herbivorous fish species. These studies have invariably found that the movements of reef species are constrained to relatively small areas of reef, regardless of the fish's social characteristics (e.g., harem or schooling), and thus, these species may contribute little to functional connectivity (Afonso et al. 2008; Hardman et al. 2010; Welsh and Bellwood 2012a, b). Indeed, the traditional distinction between small solitary and large roving herbivores appears to be largely a reflection of size, and even the largest 'roving' herbivores do not move very far, even when foraging in schools (Welsh and Bellwood 2012a). Therefore, most fishes on coral reefs may not be mobile links at all, a sobering notion given that large-scale movements by herbivores have been described as being among the most important mobile links on coral reefs (Nyström and Folke 2001).

Our goal, therefore, was to (a) determine whether all major nominal reef herbivore groups show comparably small range sizes and (b) contextualize the movements of a functionally important herbivorous species, *K. vaigiensis*, with those reported for other coral reef species in the primary literature. To evaluate the first objective, we assess home range data on a largely overlooked family of coral reef herbivores, the Kyphosidae. We then compare these home range data to published home range sizes of representative species from every major herbivore family and to a broad range of non-herbivore species. With this information, we provide an overview of herbivorous mobile

Fig. 1 Orpheus Island receiver (VR2W, Vemco) deployment sites. *Black circles* mark the location of each receiver. *Filled in circles* represent receivers with >5 % of at least one individual *K. vaigiensis*' detections; *open circles* had no significant detections. **a** Map of Australia showing the location of Orpheus Island along the Queensland coast. **b** Array in Pioneer Bay showing depth contours and numbered stars representing capture and release sites of individuals (capture site 1 K40, K41, K42, K43, K44; capture site 2 K31, K32, K35; capture site 3 K36, K37, K38, K39; capture site 4 K33, K34). *Dotted lines* represent reef area



links on coral reefs in order to better understand potential connectivity of functional processes on an inter- and intra-reef scale and discuss the implications of how this may influence the predicted local-scale ecosystem benefits of MPAs.

Methods

Home range of *Kyphosus vaigiensis*

This study took place between September 2011 and January 2012 on the fringing reefs surrounding Orpheus Island (18°350'S, 146°200'E), an inshore island on the GBR. The majority of the spatial sampling effort occurred within Pioneer Bay, on the leeward side of Orpheus Island, with an extensive reef flat and a moderately complex reef structure (detailed descriptions of Pioneer Bay are given in Welsh et al. 2012).

Acoustic monitoring

The movements of *K. vaigiensis* around Orpheus Island were quantified using acoustic monitoring. This involved the construction of an array of 46 acoustic receivers (VR2W; Vemco, Halifax, Canada), deployed around Orpheus Island (Fig. 1a). The majority of the receivers

(25 × VR2Ws) were placed within Pioneer Bay to provide a high-resolution indication of tagged individual's activities within the bay (Fig. 1b). The remaining receivers (15 × VR2Ws) were moored at key monitoring positions around the island i.e., the points and centres of nearly every bay (Fig. 1a). Six additional receivers on adjacent islands (three on Pelorus and three on Phantom) had no detections. The effective detection range (where 50 % of acoustic signals are detected) of the receivers was assessed and found to be approximately 55 m throughout the duration of the study (Welsh et al. 2012).

Prior to tagging, the population size of *K. vaigiensis* was estimated. To ensure an accurate estimation of the proportion of the population of *K. vaigiensis* being sampled, five 1.4 km × 15 m snorkel transects (spanning the entire length of Pioneer Bay) were conducted along the reef crest. A 15 m width was selected to ensure that widths could be maintained regardless of visibility over the census days. Each census was undertaken on non-consecutive days.

Individual *K. vaigiensis* were captured by divers on SCUBA from four separate sites over a 1.4 km stretch of reef within Pioneer Bay using barrier nets in September 2011 (Fig. 1b). Four capture sites were used to maximize the chances of sampling fish from separate schools. Once captured, fish were transported to the Orpheus Island Research Station where they were held in 3,300-L flow-through tanks prior to surgical tagging. To tag the fish,

individuals were first anaesthetised in a tricaine methanesulfonate (MS-222) seawater solution (0.13 g L^{-1}). Once the fish was sedated, the fork length (FL) was recorded and a small incision was made in the body wall. An ultrasonic transmitter (tag; V9-1L, random delay interval 190–290 s, power output 146 dB re $1 \mu\text{Pa}$ at 1 m, Vemco) was then inserted into the peritoneal cavity of the individual, and the incision was sutured, closed, and treated with antiseptic. Following surgery, individuals were held in captivity for 12–24 h to recover before being released back at their site of capture.

Before the data were analysed, each individual's detection plots were inspected using the VUE software package (Vemco) to check for signs of mortality. Mortality was identified by an obvious change in an individual's movement patterns to long periods of inactivity. If mortality was suspected, all subsequent detections were excluded from the analyses (one individual was excluded on this basis; Electronic Supplemental Material, ESM Tables 1, 2). For analysis, the first 24 h of data from each individual following release were excluded to remove any unusual behaviour, which may arise from tagging. Each individual's detection data were then separated into diurnal and nocturnal sampling periods. Diurnal periods were set from 0530 to 1930 hrs to incorporate crepuscular movements, and nocturnal periods were defined as 1931 to 0529 hrs. The frequency and variability of large-scale movements were analysed using the *adehabitatLT* package for R (Calenge 2006). The home range length of each individual was calculated for diurnal and nocturnal periods using two metrics: the minimum linear dispersal (MLD) and the median distance travelled (MDT). Both metrics were calculated using *adehabitatLT*. The MLD is defined as the shortest possible distance between the two most distant receivers where an individual has been detected (Murchie et al. 2010). For the purposes of this study, this metric will be used to represent the minimum home range length. The MDT provides a metric of the median dispersal of an individual from its principal area of residence. Individual's MDT values were quantified by first determining the receiver on which an individual is most frequently detected, and then calculating the median distance between that receiver and all other receivers where the fish was detected (Murchie et al. 2010). The proportion of detections at an individual's principal detection location was also calculated for each individual in diurnal and nocturnal periods to compare how stationary or site-attached individuals are at night versus the day. To meet the assumptions of the parametric *t* test, MLD data were log-transformed and a logit-transformation was applied to the proportion data (Warton and Hui 2011). To further explore individual movement patterns, we calculated the average number of detections per day for each individual at each of

the VR2W acoustic receivers. These detection frequencies were calculated for diurnal and nocturnal periods. The distribution of detections (expressed as a coefficient of variation [CV = standard deviation/mean] for each individual) provides a representation of the spread of the movements of each individual *K. vaigiensis* throughout their home range. High CV values indicate a heterogeneous distribution of an individual's detections throughout the acoustic array, while low CV values suggest that the distribution is more homogeneous. All the above metrics were calculated using the data set for the entire study period. However, for each individual, the average MLD was also calculated over five separate randomly selected days to quantify the average size of an individual's daily movements.

A *t* test for matched pairs was used to compare the diurnal and nocturnal sampling periods for the overall MLD, the daily MLD, and the proportion of detections at individual principal detection locations. The CV values for each individual were also compared between diurnal and nocturnal samples using a *t* test for matched pairs.

Data for general home range relationship

To evaluate the potential of herbivorous reef fishes to act as mobile links, a data set of published coral reef fish home range length data was assembled by searching the ISI Web of Science and Google Scholar for primary research articles using the following keywords: fish, coral reef, home range, movement, and spatial. Studies were limited to those conducted on adult coral reef taxa that provided an estimation of the linear movements of focal taxa. Studies on adult reproductive migrations were excluded. The selection criteria avoided confounding factors associated with ontogenetic home range expansion and reproductive behaviour. Furthermore, data were excluded if individuals did not survive for >24 h following release after tagging and/or if based on homing studies, as these cases would most likely represent unusual behaviour. From each study, the maximum distance moved by any individual of each species was recorded along with the individual's corresponding body size (measured as FL) following Freiwald (2012). The functional group was also noted and classified as either carnivore or herbivore. If several studies were available for the same species, the study that reported the largest movement, meeting the aforementioned criteria, was used.

Body size data exhibited a non-normal (positively skewed) distribution. Data were therefore square-root-transformed to normalize the data. The relationship between body size and home range length was analysed using GLMs in lme4 package in R (Bates and Maechler 2009; R Development Core Team 2011). Initially, an overall model was constructed irrespective of functional

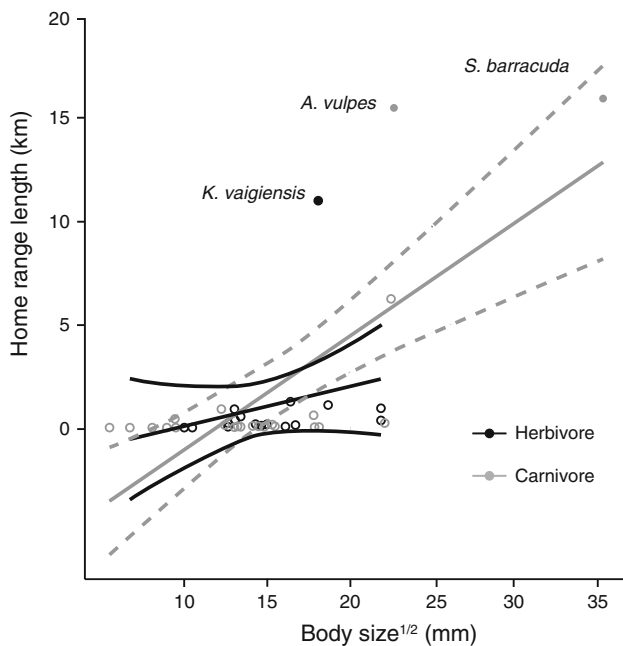


Fig. 2 Relationship between home range length (m) and fish body length ($\sqrt{\text{fork length}}$; mm) for carnivorous and herbivorous taxa with 95 % confidence intervals for each trend line. Species with a Cook's distance value of >0.5 are labelled and have solid circles

group. Separate models were then constructed for each functional group. To test for deviations from each model, an analysis of each species' Cook's distance was used (Quinn and Keough 2002).

Results

Home range of *Kyphosus vaigiensis*

In total, 14 individual *K. vaigiensis* (average length 29.4 ± 0.7 cm SE; range 23.4–32.6 cm) were tagged. This represented approximately 10 % of the total within-bay population size, which was estimated to be 148.4 ± 8.8 individuals. Over the 5-month study, individual *K. vaigiensis* exhibited consistently large home ranges regardless of capture site. Individuals travelled an average minimum linear distance (MLD) of $2,521.4 \pm 713.7$ m during the day and $2,625.9 \pm 880.1$ m at night (and ranging from 784 to 13,352 m; Fig. 2; Table 1; ESM Table 2). These values were extensive and, on average, covered over 10 % of the available coastline of Orpheus Island for both diurnal and nocturnal periods (and ranged from 2 to 53 %). No significant difference was detected between the diurnal and nocturnal MLDs over the whole study ($t_{11} = 0.62$, $p = 0.55$). Assuming a constant home range width of 50 m (the approximate width of the reef from base to outer flat on Orpheus Island), a conservative estimate of the potential

home range area of *K. vaigiensis* was $126,070 \pm 35,683$ m² in the day and $131,294 \pm 44,000$ m² at night.

The patterns for the MLD were mirrored by the median distance travelled (MDT), with almost every fish moving large distances away from their principal area of detection. Individuals had an average MDT of 442.5 ± 49.4 m during diurnal periods and 333.6 ± 26.7 m during nocturnal periods. Despite individuals being detected over the majority of the array, individuals had significantly higher proportions of their total detections at their site of principal detection during nocturnal periods, when compared to diurnal periods (30.2 % and 15.8 %, respectively) ($t_{11} = -5.0$, $p < 0.001$). The values reported for the MLD and MDT are likely to be conservative, with a much larger actual movement range of *K. vaigiensis* as the residency index was on average 76 ± 0.8 %, indicating that individuals were beyond the detection regions of the array 24 % of the time on the days analysed (Table 1).

The distributions of an individual's average daily detections were highly variable, with detections over 24 h spread across the majority of the acoustic array. However, when evaluated in diurnal versus nocturnal subsections, it was clear that species were generally more mobile in diurnal sampling periods (ESM Fig. 1). Diurnal samples were characterized by records at a number of receivers. Nocturnal samples usually had a major location and relatively few records at other receivers. This is supported by CV values, which were significantly lower over diurnal samples (mean = 1.76) compared to nocturnal samples (mean = 2.50; $t_{13} = -3.22$, $p < 0.01$).

Daily movement patterns

When only a single 24-h period was considered (with five random days used for replication), an individual's MLD values were quite large, with an average of $1,091.6 \pm 103.7$ and 875.7 ± 65.4 m, during diurnal and nocturnal periods, respectively. An individual's 24-h subsample movement values were, on average, 59 % of an individual's total diurnal MLD and 57 % of an individual's total nocturnal MLD (Table 1; ESM Table 1). The average 24-h MLD values of each individual were significantly different when comparing diurnal and nocturnal movements ($t_{11} = 3.02$, $p = 0.01$), with most individual's diurnal movements being larger (ESM Table 2).

General home range relationship

The overall model of body length versus home range length for both herbivores and carnivores was significant and positive ($F_{1,38} = 28.77$, $p < 0.001$; $r^2 = 0.76$). There was also a significant positive relationship between body size

Table 1 Average metrics of *Kyphosus vaigiensis* movement data separated by diurnal and nocturnal sampling periods

Diel period	Minimum linear distance (m)		Home range estimate (m ²)	Median distance travelled (m)	Residency index
	Total study period	Five day average (with per cent of total)			
Diurnal	2,521.4 ± 713.7	1,091.6 ± 103.7 (59 % ± 5)	126,070 ± 35,683	442 ± 49.4	0.76 ± 0.1
Nocturnal	2,625.9 ± 880.0	875.7 ± 65.4 (57 % ± 7)	131,293.9 ± 44,000	333.6 ± 26.7	

For individual data, please see Table S2

and home range length ($F_{1,15} = 5.47$, $p < 0.05$; $r^2 = 0.51$) for all herbivores, excluding *K. vaigiensis*. However, when *K. vaigiensis* was included, there was no longer a significant relationship between body size and home range length for herbivores ($F_{1,16} = 1.48$, $p > 0.05$). Of all the herbivores, only *K. vaigiensis* had a significant Cook's distance value of >0.5 , indicating that the inclusion of this outlying data point had a significant effect on the modelled relationship (Fig. 2). There was also a positive, significant relationship between body size and home range length for carnivorous fish taxa ($F_{1,20} = 26.40$, $p < 0.001$; $r^2 = 0.74$). Based on the Cook's distance analysis, two species, *Sphyaena barracuda* and *Albula vulpes*, were exceptional and significantly influenced the carnivore model, with Cook's distance values >0.5 (Fig. 2).

Discussion

Despite our rapidly increasing knowledge of the spatial ecology of marine taxa, no herbivorous species on coral reefs have been quantitatively identified as mobile links as adults. Most reef fishes remain close to the structure provided by the reef and have been shown to be less willing than their terrestrial counterparts to cross gaps in shelter of more than 20 m (Turgeon et al. 2010). Among herbivores, *K. vaigiensis* appears to be an exception to this rule, being sufficiently vagile to travel large distances, not only across the reef within a single bay, but also between fringing reefs up to 11 km apart. It is, to our knowledge, the only documented coral reef herbivore to date capable of providing short-term reef-scale connectivity of functional processes.

The association between body size and home range length highlights the site-attached nature of reef fishes, especially the herbivores, the presumed mobile links. Even one of the largest herbivores, *N. unicornis*, is predicted by the herbivore model to occupy a range of just 1,024 (± 381.84) m (linear home range). This finding is strongly supported by several studies of the species (estimating its range to be between 240 and 940 m long) and highlights its site-attached behaviour (e.g., Meyer and Holland 2005; Hardman et al. 2010). Most herbivores, therefore, appear to contribute little as mobile links. However, *K. vaigiensis*, a

functionally important herbivorous reef fish (Cvitanovic and Bellwood 2009; Hoey and Bellwood 2011), appears to depart significantly from the expected body size—home range length relationship. It is a significant outlier for an herbivorous species, with a range over three times larger than expected based on its size. The distances moved by this species are more similar to those of the pelagic carnivorous species, *S. barracuda* (O'Toole et al. 2011) and *A. vulpes* (Murchie et al. 2013), which were likewise the only other taxa that deviated significantly from the predicted relationship for non-herbivore fishes. It is by virtue of these unusual, large-scale (i.e., >2 km) daily movements that *K. vaigiensis* may be important for the functional connectivity within reefs, serving as an active mobile link and thereby able to contribute significantly to reef resilience across a range of spatial scales.

The importance of the unique, large-scale movement of *K. vaigiensis* is most apparent when placed in context of its functional role. The role of browsing herbivores is one in which functional redundancy (i.e., niche overlap of several taxa performing the same functional role) is extremely limited (Hoey and Bellwood 2009). On the GBR, the removal of adult macroalgae is restricted to between two and six species (Bellwood et al. 2006; Mantyka and Bellwood 2007), although often only one or two species are predominant in a single area (Cvitanovic and Bellwood 2009; Hoey and Bellwood 2010). Among these few species, *K. vaigiensis* stands out consistently as a significant consumer of macroalgae (Cvitanovic and Bellwood 2009; Lefèvre and Bellwood 2011). Indeed on several occasions, this species and its congeners have been noted to play a vital role in coral reef resilience through intense predation of macroalgae (Downie et al. 2013; Michael et al. 2013). The exceptional mobility of a single species within this vitally important ecological role for reef health suggests that short-term mobile links in adult herbivores may be particularly rare on coral reefs.

Home range size in reef fishes

Herbivorous fishes have previously been recognized as important mobile links for functional processes (Nyström and Folke 2001; Lundberg and Moberg 2003). However,

this may not be the case for most species. Only *K. vaigiensis* exhibited attributes that would enable it to act as a mobile link, providing large-scale ecosystem connectivity by interconnecting ecological processes on reefs up to 11 km apart. Observations on the behaviour of *K. vaigiensis* at this site found that it invariably travels in large schools (>20 individuals). Therefore, the large home ranges exhibited by the tagged individuals are likely to be representative of a significant proportion of the population.

On average, *K. vaigiensis* occupies a stretch of reef 2,521 m long. This is approximately 2–100 times larger than other roving herbivorous species. In comparison, the home ranges of several similar-sized territorial or harem herbivorous species, such as *Chlorurus microrhinos* from the GBR (Welsh and Bellwood 2012b), *Sparisoma cretense* in the mid-Atlantic (Afonso et al. 2008), and *S. viride* from the Caribbean (van Rooij et al. 1996), have been found to be relatively small, with home range lengths of just 266, 460, and 25 m, respectively. These restricted ranges likely occur as a result of the trade-off between the energetic expenditure of territorial defence and the benefits of exclusive access to a territory's resources. These benefits become unfavourable when too large an area must be defended (Bonaldo et al. 2006; Laguë et al. 2012). We would therefore expect smaller, limited home ranges in territorial or harem species. However, even schooling, non-territorial species also seem to have quite limited home range sizes. The schooling parrotfish *Scarus rivulatus* in the GBR (Welsh and Bellwood 2012a) and *Sparisoma chrysopterum* from the Caribbean (Muñoz and Motta 2000) both appear to have restricted home range sizes (albeit slightly larger than those of territorial species). Small home ranges in schooling species have been attributed to a need for familiarity with sites used as shelter from predators (Wittenberger 1981; Welsh and Bellwood 2012a, b). Even herbivore species with similar diets and behaviour to *K. vaigiensis*, such as *N. unicornis*, *N. lituratus*, and *K. setatrix*, are reported to have restricted spatial ranges, regardless of geographic location (e.g., Eristhee and Oxenford 2001; Meyer and Holland 2005; Hardman et al. 2010). The question remains as to why *K. vaigiensis* appears to be unique among reef herbivores in regards to its movement patterns.

The explanation for the relatively large home range in *K. vaigiensis* may lie in their feeding behaviour. Ecological theory suggests that there is a trade-off between the risks (i.e., increased exposure to predation while moving across habitats and energetic expenditure on swimming) and the benefits of having a large home range (i.e., access to higher-quality food resources) (Lindstedt et al. 1986; Kramer and Chapman 1999; Owen-Smith et al. 2010). The available evidence for *K. vaigiensis* suggests that, when encountered, it preferentially targets brown leathery

macroalgae (Cvitanovic and Bellwood 2009; Lefèvre and Bellwood 2011). Indeed, it is one of the few species to ingest adult macroalgae (Green and Bellwood 2009). Previous studies on the diet and gut physiology of *K. vaigiensis* found a dominance of brown macroalgae in their guts, even when collected in areas with very low abundances of the algae (McCook 1997; Choat et al. 2004). Hoey and Bellwood (2010) suggest that this species may be highly effective at locating cryptic or isolated strands of macroalgae. If so, large home ranges in this species would increase encounter rates with macroalgae and facilitate a selective diet dominated by macroalgae. Such larger-scale movements for the purpose of food acquisition have been noted for other kyphosid species on Ningaloo Reef. *K. sydneyanus*, for example, was found to travel significantly further from patch reefs to prey on macroalgae than other browsing species (Downie et al. 2013). This movement is attributed to large body size and schooling behaviour in this species, which may reduce an individual's predation risk while feeding far from the shelter of the reef (Downie et al. 2013). It may be a similar behaviour in *K. vaigiensis* that facilitates the large-scale movement patterns recorded herein.

The large-scale movements of *K. vaigiensis* appear to occur over both diurnal and nocturnal periods. However, diurnal movements are largest with longer times spent away from the main receiver, which may reflect foraging activities. This foraging and the associated searching for macroalgae appear to occur mainly during the day. This is supported by gut content analysis, which suggests that the majority of gut filling in *K. vaigiensis* occurs during the day (Choat et al. 2004). Nocturnal movements, however, (excluding potential crepuscular movements) were also found to be quite extensive and cannot be ignored. For the browsing herbivore species *N. unicornis*, nocturnal forays have been reported away from shelter sites, and it was suggested that these movements most likely represent foraging forays (Meyer and Holland 2005). This may also be the case for *K. vaigiensis* with higher peak nocturnal detections at a single receiver, likely representing a resting site, but with significant movements away from that location at night (this may be to feed as in the grazer *Siganus lineatus*; Fox and Bellwood 2011). Overall, *K. vaigiensis* appears to be a diurnal browser with the possibility of some nocturnal feeding activity.

Significance of mobile links in reef systems

The large (>2 km) home ranges and selective feeding behaviour of *K. vaigiensis* hold promise for the connectivity of ecological processes between areas of a reef and for the capacity of fish taxa to act as mobile links. Localized macroalgal outbreaks do occur on coral reefs (Burgess

2006). In the event of an outbreak, *K. vaigiensis* from neighbouring parts of the reef have the capacity to travel to the affected areas and consume macroalgae within hours or days. This is especially important as a reliance on larval connectivity may be insufficient to respond to a pulse disturbance, especially given the stochastic nature of larval recruitment (Siegel et al. 2008). Even if larvae recruit to an area immediately following an algal outbreak, the ability of these fishes to consume algae is limited since the ecological impact of fishes is size dependent (Bonaldo and Bellwood 2008). Given that an experimentally induced phase-shift exhibited dramatic increases in algal cover after only six months (Hughes et al. 2007), the growth rate of fishes from larvae may not be sufficient for functionally important taxa to reach a large enough size to reduce algae after it has taken hold. Following an initial increase in algal colonization, negative feedbacks described by Hoey and Bellwood (2010) may further reduce the capacity of herbivores to remove macroalgae, thus increasing the likelihood of a large-scale phase-shift. *K. vaigiensis* may, therefore, provide a vital first response linking large spatial scales, ultimately supporting system-wide resilience on coral reefs.

It must be noted that mobile links are always scale dependent. *K. vaigiensis* is the only known herbivorous reef fish capable of regular movement over 2 km. However, it still moved around a single island, and all reefs and bays were connected by hard ground, not open sand or deep water. Movement between widely spaced reefs may require mobile links operating on even larger scales. Although such movement is possible in turtles (Goatley et al. 2012), functional connectivity and mobile links by adult fishes, at present, appear to be predominantly a within-reef phenomenon. At present, *K. vaigiensis* appears to be unique among reef herbivores and is the first fish to be identified as a potential mobile link, able to support the large-scale application of herbivory on adult macroalgae on coral reefs. As a specialist feeding on leathery brown macroalgae, this species may be the key to avoiding phase-shifts on coral reefs. However, it is also a species that can gain little protection from small (<1 km) MPAs. For this critical species, gear restrictions or species-specific protection may be a more appropriate management option (Graham et al. 2013).

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