

Habitat effects on home range and schooling behaviour in a herbivorous fish (*Kyphosus bigibbus*) revealed by acoustic tracking

R. D. Pillans^A, R. C. Babcock^{A,D}, D. P. Thomson^B, M. D. E. Haywood^A,
R. A. Downie^C, M. A. Vanderklift^B and W. A. Rochester^A

^ACSIRO Marine and Atmospheric Research, GPO Box 2583, Brisbane, Qld 4001, Australia.

^BCSIRO Marine and Atmospheric Research, Private Bag 5, Wembley, WA 6913, Australia.

^CCSIRO Marine and Atmospheric Research, GPA Box 1538, Hobart, Tas. 7001, Australia.

^DCorresponding author. Email: russ.babcock@csiro.au

Abstract. Large mobile herbivorous fish that specialise in browsing large brown algae are particularly important on coral reefs because their activities mediate algal–coral competition. Despite this important ecological role, we have a poor understanding of the movement patterns of such large herbivorous fish, including *Kyphosus bigibbus*. Nineteen *K. bigibbus* captured near adjacent but distinct patch reefs were tagged with internal acoustic tags and their movements monitored for up to 20 months by an array of 60 acoustic receivers. Home-range estimates showed that movements of individuals from each patch reef encompassed different spatial extents and resulted in differences in habitat used by the two groups of fish. The average 50 and 95% kernel utilisation distribution for long-term resident fish was 0.27 ± 0.03 and 1.61 ± 0.30 km² respectively, ranges that represent the largest values for a herbivorous coral reef fish recorded to date. There was a significantly higher degree of fidelity among fish from the same school, and to particular patch reefs, despite the proximity of the reefs and substantial overlap between schools of conspecifics. A coefficient of sociality was used on pairs of fish and showed that there was no evidence that individuals were consistently detected together when they were detected by receivers away from their home reef. The variability of movement patterns among individuals of *K. bigibbus* results in an increased niche footprint for this important browser, potentially increasing reef resilience.

Additional keywords: acoustic telemetry, algae, coral reef, herbivorous fish, marine protected area, movement, Ningaloo Reef.

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Introduction

The removal of algae by herbivorous coral reef fish has been identified as a key process in maintaining reef resilience (Bellwood *et al.* 2004; Mumby *et al.* 2006; Hughes *et al.* 2007). Herbivorous coral reef fish are often classified into two functional groups, grazers and browsers (Horn 1989), but diet does not always reflect taxonomic relationships (Choat *et al.* 2002). Grazers primarily consume epilithic algal matrix (EAM), organic detritus and calcareous sediments and include scrapers, excavators and detritivores (Bellwood and Choat 1990; Choat *et al.* 2002). Browsers consume large brown algae and small foliose and filamentous red and green algae (Choat *et al.* 2002). Grazers and browsers play important roles in preventing phase shifts on coral reefs by consuming algae that would otherwise compete with corals. Grazers typically consume early life history stages of algae, like newly settled spores or zygotes and new recruits, and through this they can prevent the establishment of adult plants, whereas browsers consume adult plants and can prevent the overgrowth and shading of corals by large erect

stands of macroalgae (McCook *et al.* 2001). Browsers may also reverse phase shifts if feeding intensity is sufficiently high (Bellwood *et al.* 2004).

Although the critical role that herbivorous fish play in maintaining or restoring high abundances of corals has been clearly demonstrated (McCook 1997; Bellwood *et al.* 2004; Hughes *et al.* 2007; Burkepile and Hay 2010; Vergés *et al.* 2011), the intensity of algal consumption by fish on coral reefs varies considerably. Habitat complexity, habitat type, the species composition of the fish assemblage, fish behaviour and the area studied can all affect rates of consumption (McCook 1997; Hoey and Bellwood 2008, 2010; Vergés *et al.* 2011; Michael *et al.* 2013). Studies investigating long-term movement patterns and habitat use of key herbivorous species are only recently beginning to provide insights into the spatial extents of movements and home ranges, and their relative importance in shaping coral reef ecosystems (Marshall *et al.* 2011; Welsh and Bellwood 2012a, 2012b, 2014). This information is essential to understanding how movements of individuals among different habitat

types within and among reefs affect the relative abundance of corals and macroalgae, and ultimately the resilience of coral reefs to disturbance. However, compared with studies on coral reef predatory fish, there remain relatively few data on the movement patterns of large herbivorous species on coral reefs.

Rates of algal consumption, and by extension the abundance of erect macroalgae on both the Great Barrier Reef and Ningaloo Reef, is affected by the structural complexity of the surrounding reef, which appears to be a consequence of the availability of refugia from predatory fish (McCook 1997; Vergés *et al.* 2011; Downie *et al.* 2013). Vergés *et al.* (2011) and Downie *et al.* (2013) demonstrated that rates of consumption of tethered algae declined rapidly with distance from corals; the latter study demonstrated how this yields emergent patterns across the landscape, showing that algal biomass decreases rapidly with increasing distance from structurally complex *Porites*-dominated patch reefs. Therefore, the movement patterns and habitat use of herbivorous fish on coral reefs can have important implications to the functional processes at a landscape level.

Large-scale landscape changes in the form of areas largely devoid of macroalgae (termed 'halos') around patch reefs along the Ningaloo Reef system have been attributed primarily to *Kyphosus bigibbus* (previously identified as *Kyphosus sydneyanus*; Downie *et al.* 2013). The relatively small scale of these halos, together with video evidence showing that *K. bigibbus* are rarely observed at distances greater than 30 m from the patch reefs, suggest that this species may be confined to the protection offered by patch reefs (Downie *et al.* 2013). However, during underwater visual census (UVC) surveys of fish at Ningaloo Reef, this species has frequently been observed on the reef flat and reef slope (R. D. Pillans and R. C. Babcock, unpubl. data). These incongruent observations may indicate that there are separate schools of fish occupying distinct habitats, or that the fish that occupy the patch reefs move across greater distances than those implied by the size of the halos and video observations.

Ningaloo Reef hosts a high diversity and abundance of herbivorous fish (Vergés *et al.* 2011; Downie *et al.* 2013) and, of the few species that specialise in eating brown algae, the grey drummer *Kyphosus bigibbus* is among the most abundant (R. D. Pillans and R. C. Babcock, unpubl. data). *K. bigibbus* is a large species found on rocky and coral reefs, and is widespread in the tropical and subtropical Indo-west Pacific from South Africa to Australia and northern and southern Japan (Sakai 2003). Its diet consists primarily of brown algae, and diet composition is largely determined by the availability of algae in the surrounding habitat (Yatsuya *et al.* 2015). The species reaches a maximum size of 75-cm fork length (FL) and, along Ningaloo Reef, it is frequently observed in large schools of up to 200–400 individuals of similar size (50–65 cm FL). To further elucidate the role of this species in the resilience of tropical coral reefs, the aim of the present study was to investigate residency and movement patterns of *K. bigibbus* within the Ningaloo Reef, Western Australia. Specifically we aimed to: (1) investigate whether individuals tagged around patch reefs were resident or nomadic, and determine whether resident fish moved at scales greater than those implied by tethering experiments and algal biomass adjacent to these patch reefs; (2) estimate the home range of resident animals and compare home range estimates

with other herbivorous coral reef fish; (3) investigate the effects of tide, time of day and season on home range and maximum linear distance (MLD) moved between receivers; (4) investigate the degree of overlap between fish tagged on adjacent patch reefs; (5) investigate the degree of schooling among individuals; and (6) investigate the relative importance of available habitat.

Materials and methods

Acoustic monitoring system

An array of acoustic receivers was located within and adjacent to the Mangrove Bay Sanctuary Zone in the Ningaloo Marine Park (695 ha). The array extended from ~1-m water depth near the shoreline to ~50-m water depth beyond the reef slope (Fig. 1). Receivers were spaced 200–800 m apart and detection ranges generally did not overlap (for a detailed description, see Pillans *et al.* 2014). The array encompassed multiple habitats, including mangrove-lined shores, limestone pavement, patch reefs dominated by *Porites* spp., extensive shallow coral reefs dominated by *Acropora* spp., sand and rock dominated by macroalgae (predominantly *Sargassum* spp. and other fuclean algae) within the lagoon. A near-continuous fringing reef creates a barrier to movement out of the lagoon at low tide and during times of high swell, but an adjacent reef pass provides direct access for fish to deeper reef slope waters. Several large *Porites*-dominated patch reefs are present within ~1 km of the reef pass (for a detailed description, see Downie *et al.* 2013). The reef slope consists of coral-dominated spur-and-groove habitat and limestone reef interspersed with sand. Beyond 35-m depth, the substratum is predominantly sandy sediment with occasional low relief limestone reef.

The Mangrove Bay array consisted of 50 acoustic receivers (VR2 and VR2W; VEMCO) from December 2007 to May 2008, and 60 acoustic receivers from May 2008 to May 2010 (see Pillans *et al.* 2014). In addition to the Mangrove Bay array, there were three cross-shelf lines of acoustic receivers extending from the reef slope (~12 m) to the 200-m isobath located along the Ningaloo Reef (<http://animaltracking.aodn.org.au>, accessed 8 December 2016; Fig. 1). Individual *K. bigibbus*, ranging in size from 49 to 66 cm TL, were internally tagged with VEMCO coded transmitters (tags; either V13-1H, V13-1L or V16-4H transmitters). The pulse rate of transmitters was either 60 or 180 s and battery life varied from 450 to 820 days. Range tests were conducted with the V9, V13 and V16 tags with power outputs encompassing the range used on grey drummer. Power output had little effect on detection range during testing and Pillans *et al.* (2014) demonstrated that tag type and power output (encompassing the range used on grey drummer) had negligible effects on movement parameters of spangled emperor tracked within the same array of receivers. Each successfully decoded pulse train was recorded as a single detection in the memory of the individual VR2 as the transmitter's identification number, date and time. Receivers were downloaded every 3–4 months throughout the study, and the batteries were changed at least every 6 months.

Capture and tagging

Capture and tagging of fish was conducted under CSIRO Brisbane Animal Ethics Permit (Permit A2/07). Fish were captured on

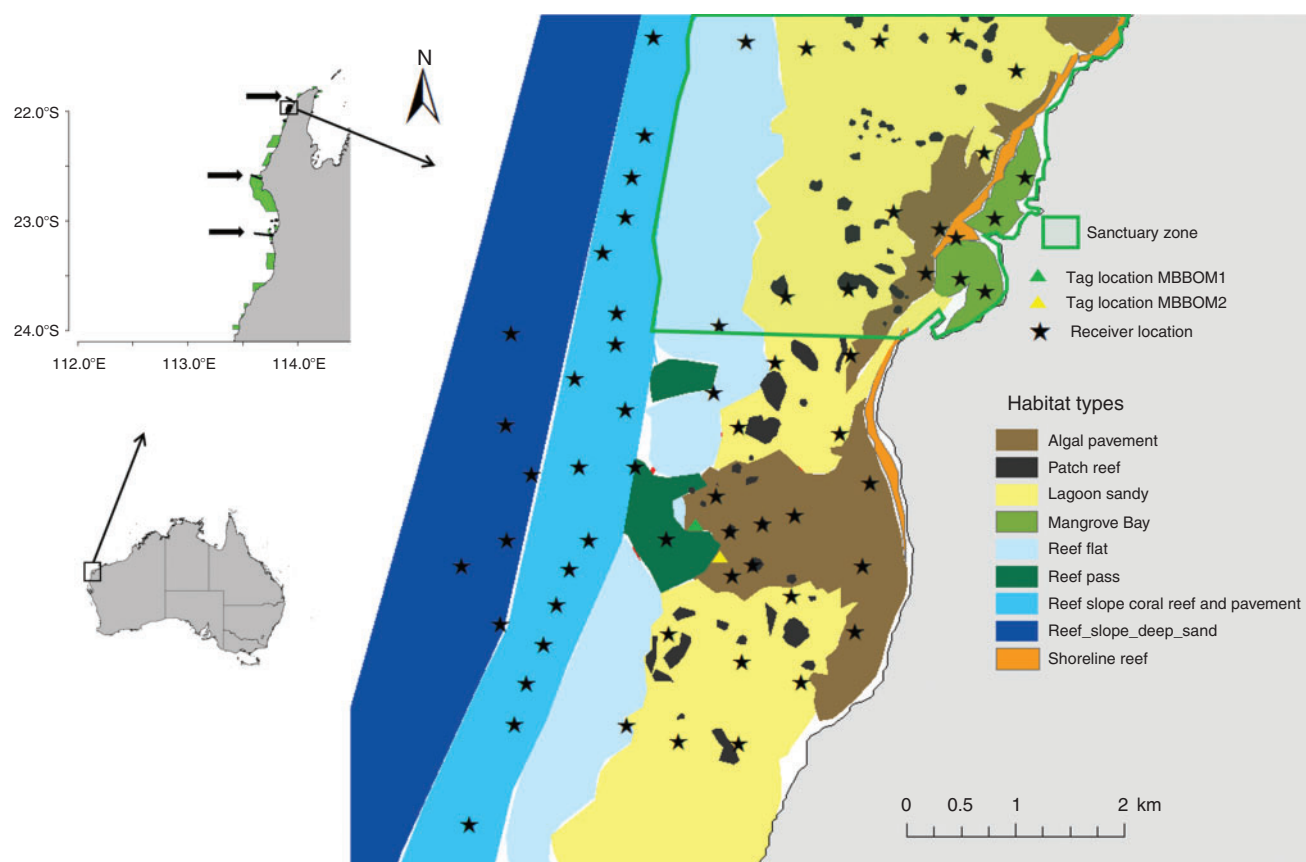


Fig. 1. Map showing Mangrove Bay array in relation to Australia and Ningaloo Marine Park Sanctuary Zones (green shading). All acoustic receivers are plotted as black dots, with the three cross shelf lines highlighted by arrows. The tag location of the two groups of fish is shown, with tag locations referring to the name of the receiver that fish were tagged at.

SCUBA using a 50-m-long barrier net with 44-mm stretched mesh between October 2008 and January 2009. Fish chosen for tagging were placed in a 120-L tub containing 30 mg L^{-1} of AQUI-S aquatic anaesthetic (Primo Aquaculture) in seawater. Fish remained in the tub until they reached Stage III anaesthesia (Iwama *et al.* 1989), at which time they were placed on their dorsal surface into a V-shaped piece of foam lined with plastic. After removing a few scales, a small incision was made slightly off the mid-line between the pelvic fins and anus. Transmitters that had been soaking in an antiseptic bath (povidone iodine and distilled water, 5:100) for at least 30 min were then inserted into the peritoneal cavity. Three dissolving sutures were used to close the wound. Following surgery, fish were measured and injected with a mass-dependent dose of Engemycin (MSD Animal Health; 100 mg mL^{-1} oxytetracycline) in the dorsal surface. Fish were allowed to recover in a 120-L tub filled with continuously replenished seawater. The average time from capture to completion of surgery was 6–7 min, whereas recovery times ranged from 15 to 30 min. Once fully recovered, fish were released at the site of capture.

Detection span and residency

For acoustic tags, the detection span of each tag was calculated as the date from first detection to last detection, whereas days

detected was the total number of days on which each individual was detected. The percentage of days detected was calculated by dividing detection span by days detected multiplied by 100. The residency index (RI) was calculated as the number of days an individual was detected at least once in the array as a proportion of the total number of days over which it was monitored.

Home range measures

Kernel distribution was calculated for nine individuals that were detected for more than 30 days. (B1-08-01 was excluded from the analysis because it appeared to have died, being detected for 10 months but only by one receiver at the tagging location). Area utilisation was estimated using the utilisation distribution (Van Winkle 1975), which is a probability density function that quantifies an individual's relative use of space (Kernohan *et al.* 2001); it quantifies the probability of an animal occurring at a location within its home range based on a set of relocation points (data obtained from receiver detections; White and Garrott 1990). Kernel utilisation distribution (KUD) has been widely used to investigate animal movements from acoustic telemetry of a range of species ranging from marine turtles (Makowski *et al.* 2006; MacDonald *et al.* 2012) to dugongs (Zeh *et al.* 2015) and fish (Pillans *et al.* 2014). The bandwidth (or smoothing parameter; h) can greatly affect the

shape and size of the kernel (Gitzen *et al.* 2006; Pillans *et al.* 2014). There is no single *a priori* method for determining the most appropriate bandwidth. Choice of bandwidth may vary depending on the study goals, sample size and patterns of space use by the study species (Worton 1989; Gitzen *et al.* 2006). In the present study, we set the bandwidth to 200 m ($h = 200$) based on range test data from stationary tags of varying power outputs within the array and compared this with the least-squares cross-validation function (h_{lsqv} ; Silverman 1986). This smoothing parameter ($h = 200$) provided the most realistic representation of space use, with h_{lsqv} tending to produce unrealistic multiple kernels that were fragmented and clustered around receivers, excluding important areas occupied by grey drummer. KUD (50 and 95%) was calculated using the *adehabitatHR* package (Calenge 2011) in R (R Foundation for Statistical Computing, Vienna, Austria).

The behaviour of individuals was characterised by the 50% (core area) and 95% (total area) KUDs, which were calculated for all months combined, as well as for each month–year combination in which an individual was detected. To determine the effects of tide on movement and habitat use, 50 and 95% KUDs of each individual and all individuals combined were calculated during a period spanning 1 h each side of high and low tide for each month–year combination for the entire monitoring period. High and low tide times were obtained from the Western Australian Department of Transport. Diel differences were investigated by comparing the degree of overlap in 50 and 95% KUDs for day and night using local time of sunrise and sunset. The utilisation distribution overlap index (UDOI; Fieberg and Kochanny 2005) was used to measure the degree of overlap between KUDs of individual fish, the degree of overlap between day and night and high and low tide. In addition, as an index of the daily spatial extent of linear movement, we calculated maximum linear dispersal (MLD) as the distance between the two most widely separated receivers that individuals were detected on during each day. Differences in MLD during the day and night, and between seasons, were also evaluated. Season was classified as summer (December–February), autumn (March–May), winter (June–August) and spring (September–November).

To investigate whether fish tagged at distinct patch reefs had overlapping home ranges, the UDOI for all individuals was compared. To investigate schooling behaviour, we calculated the coefficient of sociality (S_C ; Kenward *et al.* 1993) for pairs of fish to indicate the extent to which they stayed close to each other as they moved around. Sociality differs from home range overlap because it considers whether fish visit the same locations together rather than independently. The S_C for a pair of individuals is defined as follows:

$$S_C = (D_E - D_O) \div (D_E + D_O)$$

where D_O is the observed mean distance between the two individuals (m) and D_E is the expected mean distance between them (m). The observed mean distance is the mean distance between simultaneous detections of the two individuals. The expected mean distance is the mean distance between random pairs of detections of the two individuals. The S_C varies from -1 to 1 and values above and below 0 indicate cohesion and

avoidance respectively. For example, a value of 0.33 indicates that the average observed distance between two individuals is half that expected when they move independently. To calculate S_C , we required the locations of each pair of fish at a series of matching times; however, in the acoustic array data a single detection of a fish often included multiple locations (of the nearest receivers) and the detections of different fish were staggered in time. To create data suitable for calculating S_C , we calculated the average (receiver) location of the detections of each fish in each 20-min interval. The S_C was calculated for all pairs of the six fish that had detection spans of at least 1 year. To investigate cohesion during short- and long-term changes in habitat utilisation, we calculated the S_C on time intervals ranging from 1 day to the entire study period.

To determine habitat use of fish tagged at distinct patch reefs, habitat types were classified based on aerial imagery and a spatial habitat database collected over 10 years of extensive surveys. Habitat polygons were generated in Google Earth. The degree of overlap between the utilisation distribution (all months combined) and different habitat types was calculated as the proportion of the utilisation distribution corresponding with each habitat (i.e. probability density integrated over the area of each habitat). The total area of each habitat was calculated as the total area within a 1-km buffer of the extent of the acoustic array. Ivlev's electivity (E ; Ivlev 1961) was calculated using these proportions and areas as follows:

$$E = (r_i - p_i) \div (r_i + p_i)$$

where r_i is the relative use of habitat i in the study area (i.e. the proportion of the utilisation distribution corresponding to a particular habitat) and p_i is the proportion of the entire study area corresponding to that habitat.

Comparisons among times and individuals were made with the monthly KUD areas for the individual animals. Average KUD area or MLD over all individuals was calculated on the averages (over months) for the individuals. All averages are presented as the mean \pm s.e. unless stated otherwise. Significance tests for effects of day or night, season and tide were made with linear models of KUD area or MLD on the factor of interest. (The present-values were calculated by analysis of variance (ANOVA) of the nested models with and without the factor.) When the test was over all individuals, tag was included as a factor. For day or night and tide, time (month) was included as a factor (crossed with tag in tests over all individuals). Because tag is nested within tagging location, significance tests for the effects of tagging location were made with mixed-effects models of KUD area or MLD on the factor of interest and with a tag random effect. With mixed-effects models, the effect of a factor was determined to be significant if the 95% confidence interval (CI) of the effect did not include zero. Mixed-effects models were fitted with the *lme4* package in R (R Project for Statistical Computing, Vienna, Austria) and CIs were estimated with the *confint.merMod* function using the default (likelihood profile) option.

Results

Nineteen *K. bigibbus* ranging in size from 49 to 67 cm FL were captured and tagged adjacent to two isolated patch reefs

(MBBOM1 and MBBOM2) within the Mangrove Bay array (Fig. 1). These two patch reefs were located in ~4–6-m depth adjacent to the reef pass and were 360 m apart. Both patch reefs were dominated by large *Porites* spp. colonies (~4 m high and 10 m in diameter) and large schools (200–1000 fish) of *K. bigibbus* were observed throughout the year. The size and habitat available within and around patch reefs at MBBOM1 and MBBOM2 were very similar. The area adjacent to these patch reefs was dominated by algal reef (limestone pavement with varying algal biomass and overlying sand; Downie *et al.* 2013). In October 2008, six individuals were tagged at MBBOM1 and three were tagged at MBBOM2; in January 2009, four and six individuals were tagged at MBBOM1 and MBBOM2 respectively (Table 1). When fish were tagged in January 2009, all fish tagged in October 2008 were still being detected at or adjacent to their original tagging location.

Detection span and residency

The detection span and RI of tagged fish were in the range 1–569 days and 0.002–0.99, with fish tagged in October 2008 detected for significantly longer (detection span, days detected and RI) than fish tagged in January 2009. Fish tagged in the same month had similar detection spans, regardless of the patch reef at which they were captured. However, for fish tagged in October 2008, the average number of days fish were detected in the array was 426.3 ± 54.3 , which was significantly longer than for fish tagged in January 2009 (20.7 ± 13.7 days). Only one individual tagged in January 2009 (B1_09_01) was detected for more than 30 days. There was no apparent pattern in residence related to size, and the sex of individuals could not be determined externally or based on size.

Home range, linear dispersal and space use

For the nine individuals that were selected for statistical analysis (see 'Materials and methods'), the average (over individuals) 50 and 95% KUD areas were 0.27 ± 0.03 and 1.61 ± 0.30 km² respectively (Table 1). The average MLD of these long-term residents was 0.75 ± 0.09 km. The 50% KUD or core areas of individuals were centred on the patch reefs where they were captured with individuals most frequently detected on receivers adjacent to the tagging location (Fig. 2). Average KUD areas and MLD were generally larger for fish tagged at MBBOM1 than for those tagged at MBBOM2, but only significantly so for MLD. For fish tagged at MBBOM1 and MBBOM2, the 50% KUD area was 0.30 ± 0.05 and 0.230 ± 0.003 km² respectively, whereas the 95% KUD area was 1.89 ± 0.45 and 1.14 ± 0.04 km² respectively. The MLD of fish tagged at MBBOM1 was significantly larger than that of fish tagged at MBBOM2 (0.88 ± 0.10 v. 0.53 ± 0.08 km respectively; significance test: mixed-effects regression of MLD on tagging location with a tag random effect; MBBOM2 effect: -0.34 , 95% CI -0.62 , -0.07 (excludes zero); $n = 135$). Some individuals (B1_08_04, B1_08_05, B1_08_06) made less frequent movements to the reef slope via the reef pass, with these movements represented in the 95% KUDs (total area) of some fish (Fig. 2). Of the fish that departed the array within 30 days, six of eight were detected primarily from reef pass and reef slope habitats, as well as adjacent to the patch reefs where they were tagged.

Effects of tide, time of day and season

Average (over individuals) KUDs and MLDs were not significantly different between periods of high and low tide (significance tests: linear regression of each quantity on tide, tag, time (month) and tag–time interaction; high tide effects: 50% KUD area effect = 0.017, $t = 1.90$, d.f. = 133, $n = 269$, $P = 0.06$; 95% KUD area effect = 0.031, $t = 0.58$, d.f. = 133, $n = 269$, $P = 0.6$; MLD effect = 0.22, $t = 1.17$, d.f. = 130, $n = 266$, $P = 0.2$). There was a high degree of overlap, with UDOI ranging from 0.27 to 0.33 for long-term residents. Average (over individuals) 50 and 95% KUD areas and MLD were higher during the day than during the night (Table 2; Fig. 3). The day and night 50% KUD areas were 0.27 ± 0.03 and 0.24 ± 0.02 km² respectively, the 95% KUD areas were 1.59 ± 0.30 and 1.23 ± 0.12 km² respectively and the MLDs were 0.60 ± 0.09 and 0.26 ± 0.04 km respectively. These differences were all significant (significance tests: linear regression of each quantity on day or night, tag, time (month) and tag–time interaction; day effects: 50% KUD area effect = 0.039, $t = 3.60$, d.f. = 134, $n = 270$, $P < 0.001$; 95% KUD area effect = 0.371, $t = 4.74$, d.f. = 134, $n = 270$, $P < 0.001$; MLD effect = 0.32, $t = 10.34$, d.f. = 130, $n = 256$, $P < 0.001$). In the majority of tagged fish, average (over months) KUD areas were larger during the day than during the night. In cases where day area was significantly different to night area, day area was always larger than night areas in all (four cases for 50% KUDs and six cases for 95% KUDs; Table 2). The degrees of overlap between day and night 50 and 95% KUDs were 0.14–0.30 and 0.53–2.0 respectively (Table 2).

Monthly 50 and 95% KUDs were relatively stable, with no statistically significant pattern in size during the detection period (significance tests: linear regression of each of 50 and 95% KUD area on season and tag; ANOVA for addition of season: 50% KUD area $F_{3,124} = 1.65$, $n = 135$, $P = 0.2$; 95% KUD area $F_{3,124} = 1.15$, $n = 135$, $P = 0.3$). There was no significant difference in MLD between autumn and winter or between spring and summer; however, MLD was significantly higher in winter than in summer (0.94 ± 0.11 v. 0.61 ± 0.11 km respectively; significance test: linear regression of MLD on season and tag; ANOVA for addition of season; $F_{3,124} = 4.00$, $n = 135$, $P = 0.009$; summer–winter contrast effect = 0.28, $t = 3.265$, d.f. = 124, $n = 135$, $P = 0.0014$; other pairwise season comparisons not significant or (in one case) not significant after Bonferroni correction).

Home range overlap

For individuals that were tagged in October 2008 and detected on more than 30 days, the UDOIs of the two adjacent patch reefs were compared (Fig. 4). There was high overlap in the core area (50% KUD) among individuals tagged at MBBOM1, with an average UDOI of 0.26 ± 0.05 . Similarly, for individuals tagged at MBBOM2, average UDOI was 0.33 ± 0.07 . Individuals captured at MBBOM1 had very little overlap with those captured at MBBOM2, with average core area UDOI of 0.03 ± 0.03 . Only one fish tagged in February 2009 was detected on more than 30 days. This individual was tagged at MBBOM1 and had a higher degree of overlap with individuals tagged at this patch reef in October 2008 (average UDOI 0.24 ± 0.02) than with individuals tagged at the same location on the same day in

Table 1. Fish ID, fork length (FL), date tagged and name of closest receiver for 19 *Kyphosus bigibbus* tagged within the Mangrove Bay array
 The tag power output, minimum predicted range of the tag, average ping frequency, detection span, number of days each individual was detected and the percentage of days detected (detection span \div days detected since tagged \times 100) are also shown. RI, residence index; NA, not applicable; KUD, kernel utilisation distribution (given as the mean \pm s.e.)

ID	FL (cm)	Date tagged	Receiver name	Tag power output (dB)	Minimum predicted range of tag (m)	Average ping frequency (s)	Detection span	Number days detected	Percentage of days detected	RI	50% KUD	95% KUD
B1_08_01	57	16-Oct-08	MBBOM1	153	406	60	282	275	98	NA	NA	NA
B1_08_02	58	16-Oct-08	MBBOM1	153	406	60	576	568	99	0.984	0.180 \pm 0.002	0.87 \pm 0.04
B1_08_03	55	16-Oct-08	MBBOM1	153	406	60	572	569	99	0.986	0.190 \pm 0.002	0.89 \pm 0.02
B1_08_04	55	19-Oct-08	MBBOM1	153	406	60	180	134	74	0.232	0.310 \pm 0.05	2.05 \pm 0.38
B1_08_05	51	19-Oct-08	MBBOM1	153	406	60	572	444	78	0.769	0.38 \pm 0.05	2.40 \pm 0.27
B1_08_06	54	19-Oct-08	MBBOM1	147	282	60	572	490	86	0.849	0.42 \pm 0.05	3.22 \pm 0.24
B1_09_01	54	22-Jan-09	MBBOM1	147	282	60	473	137	29	0.285	0.32 \pm 0.05	1.79 \pm 0.31
B1_09_02	57	22-Jan-09	MBBOM1	147	282	60	4	4	100	0.008	NA	NA
B1_09_03	54	22-Jan-09	MBBOM1	147	282	60	17	7	41	0.015	NA	NA
B1_09_04	59	22-Jan-09	MBBOM1	150	351	180	11	11	100	0.023	NA	NA
B2_08_01	56	16-Oct-08	MBBOM2	153	406	60	573	567	99	0.983	0.23 \pm 0.01	1.07 \pm 0.06
B2_08_02	66	16-Oct-08	MBBOM2	153	406	60	577	569	99	0.986	0.24 \pm 0.01	1.14 \pm 0.08
B2_08_03	56	16-Oct-08	MBBOM2	153	406	60	224	221	99	0.383	0.22 \pm 0.035	1.19 \pm 0.25
B2_09_01	63	21-Jan-09	MBBOM2	147	282	60	6	3	50	0.006	NA	NA
B2_09_02	57	21-Jan-09	MBBOM2	147	282	60	1	1	100	0.002	NA	NA
B2_09_03	61	21-Jan-09	MBBOM2	147	282	60	93	12	13	0.025	NA	NA
B2_09_04	57	21-Jan-09	MBBOM2	147	282	60	12	8	67	0.017	NA	NA
B2_09_05	57	21-Jan-09	MBBOM2	147	282	60	320	17	5	0.035	NA	NA
B2_09_06	49	21-Jan-09	MBBOM2	147	282	60	213	7	3	0.015	NA	NA

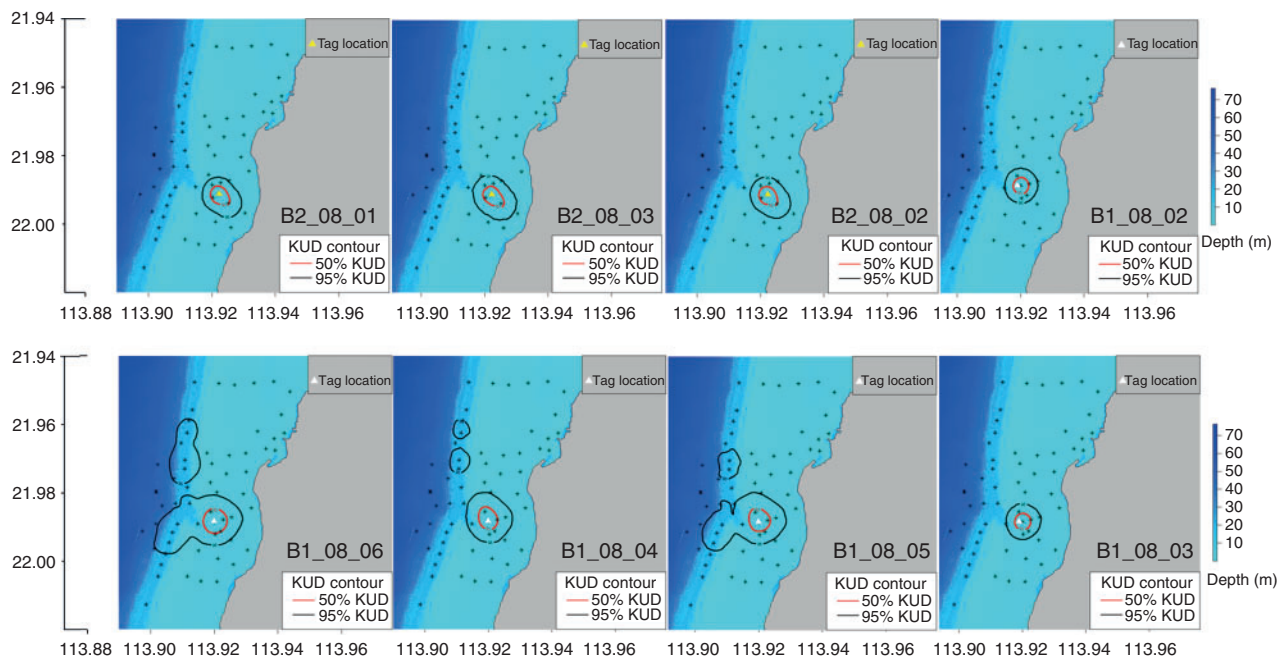


Fig. 2. Map showing tag location and 50 and 95% kernel utilisation distribution (KUD) contours of eight individual *Kyphosus bigibbus*. Tag ID code of each animal is shown in the top right-hand corner of each panel. Fish B2_08_01, B2_08_03 and B2_08_02 were tagged at MBBOM2 (see Fig. 1), whereas Fish B1_08_02, B1_08_06, B1_08_04, B1_08_05 and B1_08_03 were tagged at MBBOM2.

Table 2. Mean (\pm s.e.) of day and night 50 and 95% kernel utilisation distribution (KUD) area for individual fish detected on more than 30 days. Asterisks indicate significance of differences between day and night (from linear regressions of KUD area on day or night and time (month)): *, $P < 0.05$; **, $P < 0.01$. The overlap of day and night 50 and 95% KUD contours was determined using the utilisation distribution overlap index (UDOI)

Fish ID	50% KUD area		95% KUD area		UDOI	
	Day	Night	Day	Night	50% KUD	95% KUD
B2_08_01	0.23 \pm 0.01	0.24 \pm 0.01	1.02 \pm 0.04	1.13 \pm 0.10	0.19	1.06
B2_08_02	0.24 \pm 0.01	0.23 \pm 0.01	1.09 \pm 0.06	1.19 \pm 0.12	0.15	1.12
B2_08_03	0.19 \pm 0.01	0.26 \pm 0.04	1.02 \pm 0.17	1.41 \pm 0.30	0.23	0.41
B1_08_01	0.32 \pm 0.05	0.22 \pm 0.02	1.69 \pm 0.28	1.06 \pm 0.12*	0.14	1.06
B1_08_04	0.32 \pm 0.06	0.25 \pm 0.05	2.14 \pm 0.39	1.18 \pm 0.18*	0.24	0.53
B1_08_05	0.37 \pm 0.05	0.30 \pm 0.04*	2.24 \pm 0.25	1.77 \pm 0.19*	0.23	2.00
B1_08_06	0.44 \pm 0.05	0.27 \pm 0.03**	3.22 \pm 0.26	1.52 \pm 0.15**	0.15	1.66
B1_08_02	0.19 \pm 0.01	0.170 \pm 0.001**	1.04 \pm 0.08	0.78 \pm 0.01**	0.30	1.15
B1_08_03	0.190 \pm 0.003	0.180 \pm 0.001**	0.93 \pm 0.03	0.84 \pm 0.02*	0.30	1.84

February 2009 that departed the array within a few weeks (average UDOI 0.03 \pm 0.03).

Schooling behaviour

The average monthly S_C was low for all pairs of the six fish with detection spans of at least 1 year (Fig. 5). S_C was significantly positive for pairs of fish tagged at the same reef and near (and not significantly different from) zero for all pairs tagged at different reefs. The pair of fish with the strongest cohesion (B1_08_05 and B1_08_06; mean S_C = 0.24) was the pair with broad utilisation distributions that shifted around over the study period (Table 1). For this pair, S_C increased with the calculation time interval from 0.11 for 1 day to 0.29 for the whole dataset

(576 days; e.g. difference from 3 to 60 days, Wilcoxon rank sum test, S_C = 0.13, 0.24; n = 130, 10; W = 301; P = 0.004). This indicates that although the fish did not follow each other particularly closely (average distance apart 545 m), they tended to move to the same general areas as they used different parts of their home ranges over the period of the study.

Habitat overlap

Because individuals from the two patch reefs exhibited different habitat use, we compared Ivlev's E of individuals from these reefs. All individuals spent more time in algal pavement than expected from its proportional availability, with E values of individuals from both patch reefs more than 0.74 (Fig. 6). Fish

tagged at MBBOM1 had higher E scores for reef slope and reef pass areas dominated by coral and pavement. Fish tagged at MBBOM2 spent very little time in these habitats, but demonstrated an increased preference for patch reefs. Fish were very rarely recorded in bare sand within the lagoon, or in reef slope, shoreline pavement, Mangrove Bay and the reef flat.

Discussion

Herein we demonstrate the existence of both resident and nomadic individuals of *K. bigibbus*. This study provides the first estimates of movement and home range in *K. bigibbus* and strengthens our knowledge of the role of kyphosids as mobile herbivorous trophic links on coral reefs (cf. Welsh and Bellwood 2014). The home ranges of resident *K. bigibbus* were centred around the patch reefs at which individuals were captured, providing additional evidence that low algal biomass adjacent to these reefs (see Downie *et al.* 2013) is a result of high rates of herbivory. The lack of food resources around these heavily grazed areas presumably forces resident individuals to forage more widely around their home reef, with individuals detected up to 7.6 km away. Fish that departed shortly after tagging presumably forage more widely and can be classified as

transients, with these fish only detected within the array for up to 17 days after tagging. We also demonstrated strong partitioning of groups of fish tagged in large schools of conspecifics less than 400 m apart. This highlights the diversity and complexity of fish movements and the need for long-term studies that tag animals in a range of habitats and at different times of the year. The different size and shape of the home range in groups of fish tagged less than 400 m apart suggest that resident fish at adjacent patch reefs are potentially foraging in different areas, which increases the spatial scale and range of habitats over which this species exerts its functional role. This partitioning of habitat has important ecological consequences with regard to algal removal and reef resilience and highlights the need for spatial closures to encompass the range of habitats used by individuals within a population.

Short-term residents

Tagged fish exhibited multiple behaviours, with 47% of the fish tagged departing the array within 17 days, whereas the remaining fish were all detected over long periods. All the surviving fish tagged in October 2008 were detected for more than 130 days, whereas 9 of 10 fish tagged in January 2009 departed the array within 17 days. Although mortality or capture of the fish tagged in January 2009 cannot be ruled out, given that identical capture and tagging procedures were used the rapid departure of individuals tagged in January 2009 was attributed to transient fish leaving the area. Rapid departure of tagged fish from the capture site has been demonstrated for several herbivorous fish species (Meyer *et al.* 2010; Marshall *et al.* 2011; Garcia *et al.* 2014), as well as more broadly in coral reef fish (Garcia *et al.* 2015; Pillans *et al.* 2014). In several of these studies, individuals were subsequently recorded several kilometres away, with differences in site attachment attributed to behaviour. A plausible explanation for *K. bigibbus* tagged in January 2009 is that these individuals were part of schools of fish that were using the patch reefs as temporary refugia while undertaking more widespread movements. Indeed, one fish (B1_09_03) that departed after 7 days was detected 8 months after tagging by acoustic receivers 138 km south of where it was tagged, adding further support to the nomadic and more wide-ranging movement of individuals within the population. Similar

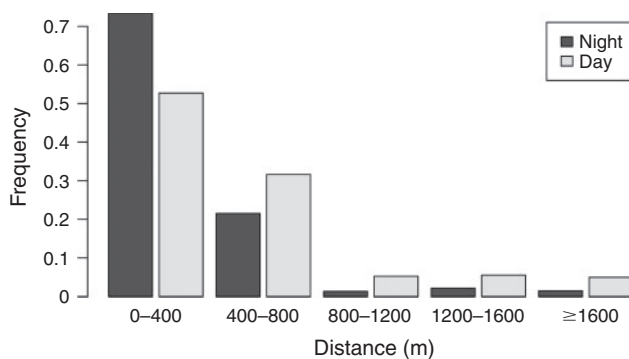


Fig. 3. Frequency of movements between the most distant receivers visited each day (maximum linear distance) for all long-term resident *Kyphosus bigibbus* during the day and night. Distance was measured as the distance between the two most widely separated receivers individuals were detected on each day.

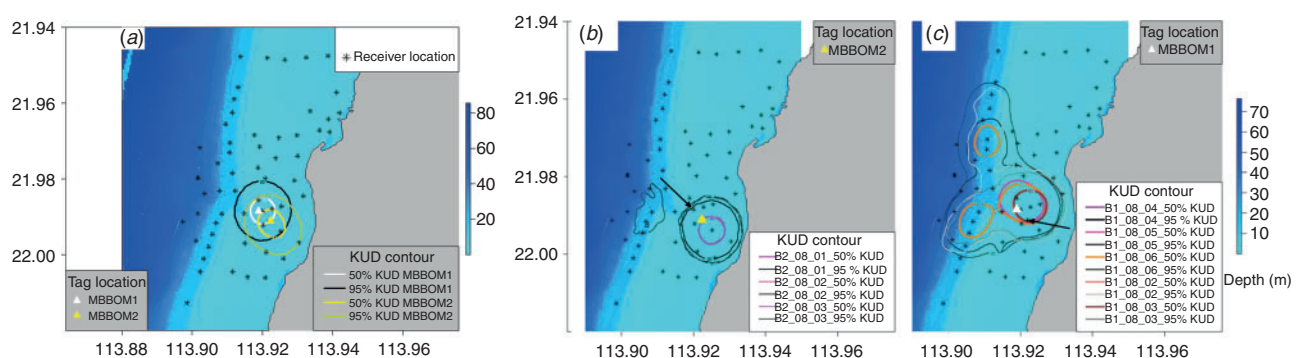


Fig. 4. Kernel utilisation distribution (KUD) contours of all long-term resident *Kyphosus bigibbus* tagged at MBBOM1 and MBBOM2 (see Fig. 1) respectively. (a) KUD contours from all detections for all fish combined. (b, c) KUD contours of all detections, excluding those at the site, of tagging for MBBOM1 (b) and MBBOM2 (c). Arrows indicate the location of the adjacent patch reef where other fish were tagged.

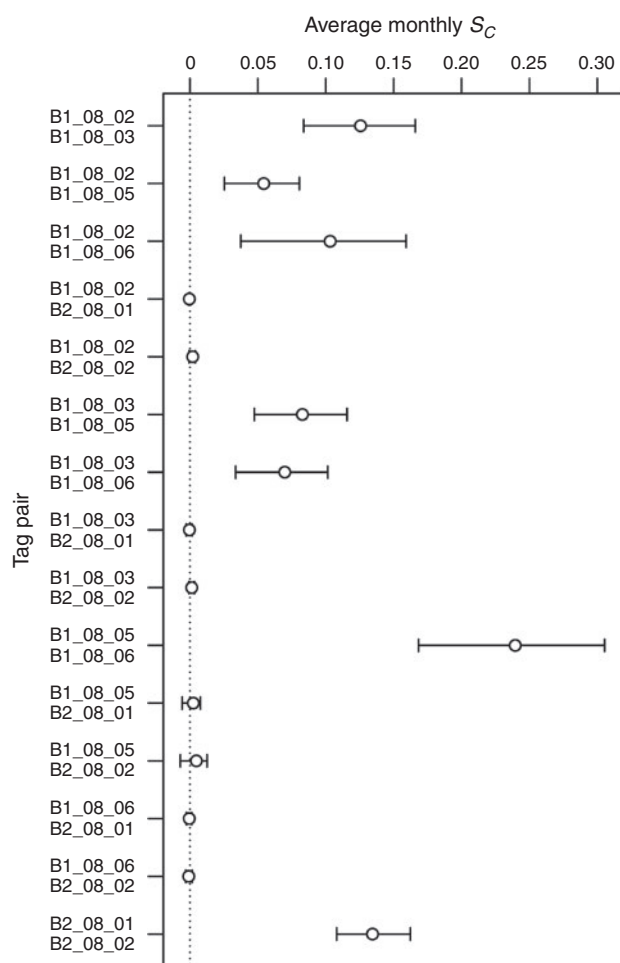


Fig. 5. Average monthly coefficient of sociality (S_C) for each pair of the six fish with the longest detection spans. The error bars indicate 95% bootstrap confidence intervals.

long-distance movements by some individuals, high site fidelity and small home ranges in others have been recorded in the herbivorous *Girella tricuspidata* (Gray *et al.* 2012; Ferguson *et al.* 2013). As more long-term research into fish movements is conducted, there is increasing evidence of this behaviour (see Attwood and Bennett 1994; Egli and Babcock 2004; Parsons *et al.* 2011; Koeck *et al.* 2013; Pillans *et al.* 2014).

Home range of long-term residents

Long-term residents were detected for up to 569 days, and although individuals were detected up to 7.4 km away from the patch reefs where they were tagged, home range was centred around these patch reefs with a core area of $0.27 \pm 0.03 \text{ km}^2$. These estimates of core area home range were larger than those reported for other kyphosids, such as *Kyphosus vaigiensis* (50% KUD = 0.16 km^2) on the Great Barrier Reef (Welsh and Bellwood 2014) and for *Kyphosus sectatrix* (total home range 0.03 km^2) in the West Indies (Eristhee and Oxenford 2001). However, our home range area is possibly an overestimate because this area (equivalent radius 0.29 km^2) is too small to be resolved accurately by our receiver array (receiver spacing generally $0.35\text{--}0.5 \text{ km}$). With our choice of smoothing parameter (200 m), the smallest possible area is 0.17 km^2 (when all detections are by one receiver). The lower estimates of home range in *K. vaigiensis* may represent species-specific differences, but the arrangement of receivers along a linear depth contour ($\sim 5 \text{ m}$) on a narrow reef slope with no receivers in deep water off the slope or in the narrow lagoon inshore (Welsh and Bellwood 2014) may have resulted in smaller home range estimates in *K. vaigiensis*. Compared with other tropical herbivorous fish species studied to date, the home range of *K. bigibbus* was significantly larger, with estimates in surgeonfish (Meyer and Holland 2005; Marshall *et al.* 2011) and parrotfish (Welsh and Bellwood 2012a, 2012b; Howard *et al.* 2013) ranging from 0.001 to 0.13 km^2 .

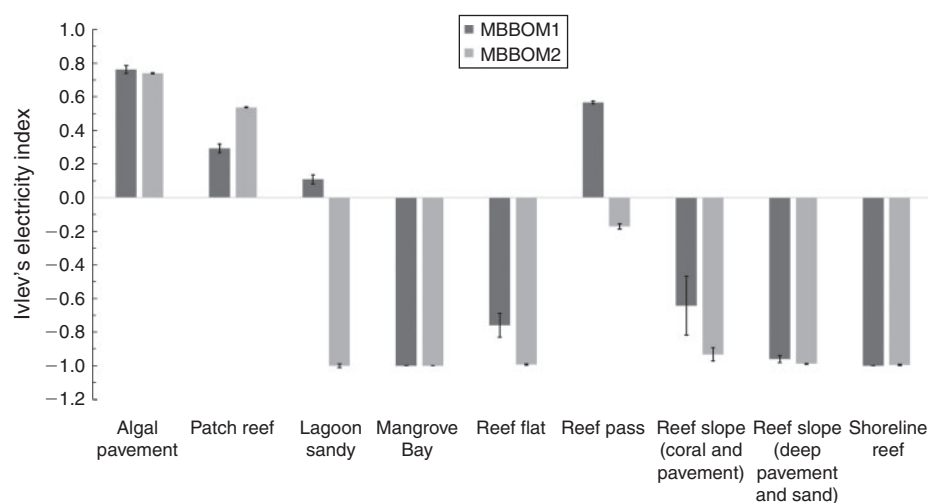


Fig. 6. Mean (\pm s.e.) habitat selection (Ivlev's 1961 electivity index) of long-resident *Kyphosus bigibbus* tagged at MBBOM1 and MBBOM2 (for locations, see Fig. 1).

Direct comparisons between studies can be confounded by array design (number of receivers and area or habitat covered by receivers), as well as the length of time animals were monitored (e.g. Stocks *et al.* 2015). However, it is clear that *K. bigibbus* tagged on patch reefs within the Ningaloo Reef have the largest reported home ranges of herbivorous fish species studied to date. Additional research that investigates the home range and linear dispersal of *K. bigibbus* tagged within aggregations on the reef slope as well as the reef flat are required to determine the effects of habitat on the size and shape of home range and dispersal patterns. *K. sectatrix* tagged in two different habitats exhibited marked differences in the linear extent and shape of their home ranges, which was attributed to the availability of habitat adjacent to the areas where fish were tagged (Eristhee and Oxenford 2001). *K. sectatrix* tagged along a narrow reef slope covered a linear distance of up to ~800 m, whereas fish tagged on fringing reef had home range covering a linear distance of up to ~300 m. The long, narrow home range and small, circular home range at the two areas resulted in similar home range areas. In the case of *K. bigibbus*, despite the similarity in habitat at the two patch reefs, differences in the size and shape of home range were apparent. Our results illustrate that resident *K. bigibbus* regularly travelled up to 1 km away from the home reef on a daily basis, with individuals tagged at MBBOM1 regularly being recorded up to 3.5 km from their home reef. These linear movements combined with larger home ranges in this species support the role of *K. bigibbus* as a mobile herbivorous trophic link (cf. Welsh and Bellwood 2014).

Despite the presence of persistent schools of grey drummer around patch reefs as well as the high degree of home range overlap between long-term residents tagged at the same patch reef, there was no evidence that individuals were consistently detected together when they were detected by receivers away from their home reef. The average monthly coefficient of cohesion was significantly positive, but low, for all pairs of fish tagged at a common reef. The pair of fish with the highest cohesion was the pair that ranged most widely (partly because increased movement makes cohesion easier to detect). Cohesion for this pair increased with the calculation time interval, indicating that although the pair did not forage particularly close together, they tended to move to the same general areas as they used different parts of their home ranges over the study period. The apparent lack of schooling behaviour during movements away from the home reef was unexpected given the high degree of overlap in the home range of conspecifics tagged at the same patch reefs and infrequent but near simultaneous detections of groups of up to four fish at receivers 10 km away from home reefs. Thus, although some individuals appear to form persistent schools around their home reefs, the timing of movement away from the home reef appears to be affected by individual behaviour and not group behaviour. Although the timing of movements away from the home reef varied among individuals, the distance and direction of movement away from home reefs was largely similar, resulting in the use of different habitats at the same time (when away from home reefs) but the same habitat use over time.

Ecological implications of movement

The two patch reefs where *K. bigibbus* were tagged have been identified previously as areas of high *K. bigibbus* density, and

have a high density of other browsing herbivorous fish (Downie *et al.* 2013). Circular halos around these patch reefs were visible from aerial images and were due to very low algal biomass compared with areas more than 120 m away. These halos were attributed to intensive grazing by herbivorous fish that resulted in a strong density gradient of algae on the pavement away from the home reef (as per Downie *et al.* 2013). Downie *et al.* (2013) used remote cameras and a 24-h tethered algae experiment to investigate grazing rates at 0, 30, 60, 90 and 120 m away from these patch reefs and demonstrated that grazing, in terms of both numbers of bites and reduction of tethered algae, was highest within 60 m but negligible at 90–120 m, with no bites taken from tethered algae more than 90 m away (where the biomass of macroalgae communities began to dominate substrate cover). Using data from individuals tagged at these same patch reefs, we have demonstrated that *K. bigibbus* tagged on the same patch reefs forage over considerably larger distances than original grazing experiments and visual observations suggested, with fish regularly detected up to 3 km away from patch reefs. These data highlight the importance of large mobile herbivores in maintaining coral–algal balance adjacent to their home reef and up to several kilometres away. The use of acoustic telemetry to investigate the range and scale of movements of herbivorous fish are providing a valuable insight into the ecological functionality of coral reefs (Welsh and Bellwood 2012b, 2014) and highlight the complexity of movement patterns of roving herbivorous fish.

Intraspecific differences in behaviour

Fish tagged at adjacent patch reefs were detected on different parts of the array. Fish tagged at MBBOM2 primarily used the area to the east of their home reef, whereas fish tagged at MBBOM1 primarily foraged to the west of their home reef. Even in the absence of detailed movement data, variation in individual movement and behavioural differences not related to sex, size or age class have long been acknowledged from a wide range of taxa (Bolnick *et al.* 2003). Heterogeneity in cores area used by generalist predatory fish species not attributed to ontogenetic shifts has been demonstrated in the sea bream *Diplodus sargus*, with this species exhibiting differing diurnal patterns depending on the habitat individuals occupy (Koeck *et al.* 2013; Di Lorenzo *et al.* 2016). Evidence of groups of individuals occupying different areas has also been demonstrated in tropical Lutjanids (Hammerschlag-Peyer and Layman 2010), temperate Sparids (Egli and Babcock 2004) and freshwater Esocidae (Kobler *et al.* 2009).

The schooling behaviour and use of distinct areas by groups of *K. bigibbus* tagged less than 400 m apart is one of the more extreme cases of heterogeneity in habitat use in the fish movement literature. The similarity in habitat available to the two groups of fish suggests that individual and schooling behaviour around their home reef, rather than habitat, were responsible for these differences. That groups of schooling fish in close proximity to one another exhibit such little overlap in core and total home range has important ecological ramifications with regard to coral reef resilience because the two groups are responsible for the large-scale removal of algae in largely non-overlapping areas, with one group foraging to the west of

their home reef and the other to the east. Although both groups showed positive selection of algal pavement and patch reefs, differences between the groups with regard to reef pass and coral- and pavement-dominated reef slope suggest the two schools exert their functional roles in differing habitats.

Area-specific differences in rates of algal removal by herbivorous fish as a result of schooling behaviour can have important functional implications (Welsh and Bellwood 2012b; Michael *et al.* 2013). For example, *K. bigibbus* within schools of conspecifics took more bites than single fish, resulting in significantly higher feeding intensity (Michael *et al.* 2013). Similarly, *Scarus rivulatus* in schools of fish took twice as many bites as single fish (Welsh and Bellwood 2012b). Despite similar benefits in forming schools (Robertson *et al.* 1976; Lukoschek and McCormick 2000), the schooling behaviour of *S. rivulatus* was different to that observed in *K. bigibbus* in the present study. Individual *S. rivulatus* had limited fidelity to the schools they were tagged in, with individuals from one school mixing with individuals from another school as long as the home range of the schools overlapped. Individual *S. rivulatus* were also equally likely to be solitary (Welsh and Bellwood 2012b). In *K. bigibbus*, limited home range overlap occurred despite the home range of groups of individuals being significantly larger than the distance between the two home reefs. Furthermore, individuals within schools were detected together at their home reefs for up to 3 years, suggesting that schools can persist for multiple years with a stable home range. Schooling behaviour in *K. bigibbus* appears to increase the importance of this species functional role in algal removal by facilitating increased browsing rates, as well as increasing the spatial extent of browsing, with different schools feeding in different areas despite the proximity of their home reefs. Although we did not investigate the diet of fish, comparisons of gut content from fish captured at adjacent patch reefs are required to determine the degree to which differences in habitat use result in dietary differences that would lead to further intraspecific heterogeneity in herbivore functionality on coral reefs.

Schooling behaviour can disproportionately affect a species functional role when populations are overharvested, with rate of foraging potentially exhibiting a non-linear rather than linear decline (Welsh and Bellwood 2012b). Furthermore, given the restricted movement patterns of individuals from adjacent patch reefs, it is uncertain whether a reduced browser biomass would be compensated for by individuals from adjacent patch reefs. The ecological importance of large roving herbivores that exhibit an increasing array of complex behaviours that we are only beginning to understand highlights the need to encompass large areas within marine protected areas to ensure that not only is the range of habitats that individuals occupy protected, but also that the range of behaviours that individuals within groups of fish exhibit is adequately protected to ensure the maintenance of functional processes. Although Kyphosid species are not targeted by fisheries in Australia, elsewhere they are a valuable resource (Sakai 2003). The removal of animals from specific habitats or home reefs is therefore likely to have a disproportionate effect on local reef resilience given the apparent school-specific home range exhibited by *K. bigibbus*.

Although the overall frequency of movements of resident *K. bigibbus* away from their home reef was relatively small, a

seasonal pattern was observed, with fish more likely to move further away from their home reef in winter than in summer. This was also reflected in home-range estimates with core area in autumn and winter larger than in spring and summer. The increased frequency of long-distance movement may be related to availability of preferred food, with the biomass of some important species being significantly lower in the cooler months (Fulton *et al.* 2014). Fulton *et al.* (2014) demonstrated that the biomass of canopy-forming algae within the Ningaloo lagoon showed strong seasonal fluctuations that were attributed to temperature. Total biomass of algae in summer was nearly twice that in winter. Summer biomass was dominated by *Sargassum* spp., whereas understorey species *Dictyopteris*, *Lobophora* and *Dictyota* reached peak biomass in winter (Fulton *et al.* 2014).

Diet of *K. bigibbus* in south-west Japan (Yatsuya *et al.* 2015) included many of the genera that were abundant at the patch reefs where fish were tagged (Downie *et al.* 2013), with Yatsuya *et al.* (2015) demonstrating marked seasonal changes in the diet of *K. bigibbus* that predominantly mirrored the abundance of macroalgae at their study site. The low density of algal biomass adjacent to the patch reefs where fish were tagged, combined with the high density of fish and the ability of Kyphosids to remove large quantities of algae in short time periods (Cvitanovic and Bellwood 2009; Downie *et al.* 2013; Michael *et al.* 2013), presumably results in fish having to move away from the shelter of these home reefs in order to obtain enough food. However, despite the existence of areas of high macroalgal density to the east-north-east of home reefs, fish were not detected in this area. The presence of structurally complex habitat has been linked with grazing intensity (McCook 1997), with the risk to predation increasing away from structure. Observations of schools of *K. bigibbus* adjacent to structurally complex habitat in the lagoon and on the reef slope, together with home range centres of resident fish around patch reefs, support this. In the present study we have demonstrated that the potential grazing footprint of a species is likely to be affected by the availability of shelter and the spacing of home reefs, variability in the movement patterns of individuals and in the schooling behaviour of groups of fish at particular patch reefs.

Given the close association with the patch reef where individuals were tagged, it was expected that fish may return to these patch reefs at night and forage more widely during the day; however, although this pattern was observed in most individuals, it was not consistent across all animals. The lack of a consistent difference between day and night core and total KUD areas, as well considerable overlap in day and night KUDs, suggest that daily nocturnal sheltering at the home reef did not occur in all individuals and did not result in large differences in the size of day and night home range measures. However, for all individuals where differences in area were apparent, daytime KUD area was larger than night-time area and detections at the home reef were highest at night. Similarly, estimates of daily dispersal away from the home reef showed that animals were more likely to be detected up to 1000 m away from their home reef during the day, with the majority of night detections at or close to the home reef. Several studies on herbivorous fish have demonstrated individual variation in the degree of nocturnal movements (Meyer and Holland 2005; Welsh and Bellwood 2014; Stocks *et al.* 2015) and an overall pattern of increased

diurnal movement. It is unknown whether detection of fish away from their home reef during the night represents nocturnal foraging or was due to individuals sheltering in the numerous caves and crevices along the reef slope following diurnal foraging in these areas. Large schools of grey drummer were repeatedly observed in structurally complex areas on the reef slope during UVC transects, suggesting that schools of *K. bigibbus* also have home range centres on the reef slope. The detection frequency of moored acoustic tags has been shown to be reduced at night (Payne *et al.* 2010), suggesting that the ability to interpret diurnal behaviour could be compromised by both animal behaviour (sheltering at night) and background noise (reducing tag detection range at night). However, given that home range measures (as opposed to activity patterns investigated by Payne *et al.* 2010) were not markedly affected by the total number of detections, it is unlikely that changes in diurnal detectability would affect the home range measures used in the present study. Furthermore, using moored acoustic tags in a coral reef environment, Welsh and Bellwood (2012a) found no diurnal pattern in detection frequency.

Conclusion

The present study contributes to the increasing body of literature on the variability and complexity of relationships between herbivorous fish and algal consumption on coral reefs. The coral–algal balance and ability of coral reefs to recover from algal dominance has been attributed to browsing by herbivorous fish (McCook 1997; Hughes *et al.* 2007; Burkepile and Hay 2010). Grazing rates and subsequent algal biomass have been shown to vary over a range of spatial and temporal scales, with these differences attributed to the availability of shelter for grazing fish (McCook 1997; Vergés *et al.* 2011; Downie *et al.* 2013), small-scale variability in the species responsible for macroalgal removal (Cvitanovic and Bellwood 2009), species-specific food preferences and grazing intensity (Bellwood and Choat 1990; Choat 1991; Pillans *et al.* 2004), feeding behaviour of individuals and schools of fish (Michael *et al.* 2013) and differences in the movement patterns of species (Marshall *et al.* 2011; Welsh and Bellwood 2014; present study). Herein we provide evidence of different habitat use and movement patterns of groups of the same species tagged only a few hundred metres apart, adding further evidence that variability in intraspecific foraging behaviour and movement can have implications on the foraging footprint of a single species, effectively increasing the species foraging area. The overall contribution to herbivory, and therefore maintenance of functional process, is increased by schooling through increased feeding rates, as well as expanded spatial extent of non-overlapping home range in schools of fish.

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