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Bellwood, David R., Goatley, Christopher H.R., Khan, Joanna A., and Tebbett, Sterling B. (2016) *Site fidelity and homing in juvenile rabbitfishes (Siganidae)*. Coral Reefs, 35 (4) pp. 1151-1155.

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<http://dx.doi.org/10.1007/s00338%2D016%2D1466%2D4>

1 **Site fidelity and homing in juvenile rabbitfishes (Siganidae)**

2 **David R. Bellwood, Christopher H.R. Goatley, Joanna A. Khan and Sterling B. Tebbett**

3
4 *College of Marine and Environmental Science and ARC Centre of Excellence for Coral Reef*
5 *Studies, James Cook University, Townsville, QLD 4811.*

6
7 **Abstract**

8 The behaviour of juvenile fishes is critical in establishing the link between recruitment and
9 subsequent adult populations. If juvenile fishes move, they can respond to variation in local
10 conditions before adult home ranges are established. Alternatively, if juveniles establish fixed
11 home ranges at settlement, their decisions may determine future population densities at small
12 spatial scales. Field observations and translocations revealed that juvenile rabbitfishes
13 (*Siganus corallinus* and *S. doliatus*) have small home ranges and strong homing abilities,
14 (covering 6m in an hour or 36 m within 24 hours). Only four of 22 individuals failed to
15 return; all were transferred up-current, suggesting that olfaction is important in homing.
16 Small home ranges and strong homing tendencies in juvenile herbivores suggests that
17 decisions made by recruits will impact the spatial extent of both adult fishes and the
18 functional roles they deliver within ecosystems.

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21 Introduction

22 There is increasing evidence that herbivorous fishes play important roles in coral reef
23 ecosystems and that they may be critical for supporting coral reef resilience (Bellwood et al.
24 2004; Nyström et al. 2008). However, it is becoming clear that the capacity of fishes to
25 deliver essential ecological services, such as herbivory, is dependent upon their movement
26 patterns (e.g. Marshall et al. 2011; Welsh and Bellwood 2012a, 2012b; Nash et al. 2014).
27 Most herbivorous reef fishes are strongly site attached, usually with small home ranges
28 (Mumby and Wabnitz 2002). Even in schooling species, individuals join and leave schools in
29 a ‘Mexican wave’ as the school passes through their home-range (Welsh and Bellwood
30 2012b). Although some herbivorous fishes move in response to changing environmental
31 conditions (Ceccarelli et al. 2006; Nash et al. 2012), this movement is often limited. In the
32 vast majority of cases, resident herbivores remain strongly site attached (Mumby and
33 Wabnitz 2002; Marshall et al. 2011; Welsh and Bellwood 2014, 2015).

34 This strong site fidelity may drive spatial heterogeneity in realised ecosystem
35 functions on reefs (Welsh and Bellwood 2012a), with critical ecosystem functions, such as
36 herbivory, being heavily dependent on the extent and nature of home ranging behaviour of
37 functionally important species. How these home ranges are established, is of crucial
38 importance. If home ranges develop over an extended period (as in the Apogonidae; Finn
39 and Kingsford 1996), local resilience may be enhanced, as young fishes move to areas where
40 they are needed. Alternatively, site fidelity may occur at settlement and remain throughout
41 life. Although the majority of home range studies on herbivorous reef fishes have been
42 conducted on adults (e.g. Nash et al. 2014; Welsh and Bellwood 2014), some juveniles do
43 show home range fidelity, at least over the short term (Bellwood and Choat 1989). If home
44 ranging behaviour does develop early, patterns of recruitment and mortality may directly
45 affect the functional abilities of local herbivore communities. This spatial variation will, as a
46 consequence, determine the resilience of reef systems and their ability to respond to localised
47 perturbations.

48 The key question is: when do herbivorous reef fishes first establish a sense of place,
49 and how strong is this attachment? In answering this question we aimed to reveal the extent
50 of site attachment and homing ability in juvenile rabbitfishes during the first few weeks
51 following recruitment.

52

53 Materials and methods

54 This study was conducted in February 2015, at Lizard Island, on the northern Great
55 Barrier Reef. Three separate rubble sites were examined along a contiguous length of reef; A
56 and B were 6 m apart and site C 32 m away from B (linear distances; Fig. 1); following the
57 reef margin distances were 7.2 m and 43.5 m respectively. The sites were 2–4 m deep, and
58 characterised by coral rubble (broken *Acropora*) on a sandy substratum. These rubble beds
59 were the focal habitat for juvenile rabbitfishes (densities 0.5–4 ind. m⁻²).

60 Rabbitfish were collected using dilute clove oil and returned to the lab for tagging.
61 Fish were measured, tagged with elastomer tags, photographed (Fig. 2), and kept in 40 L
62 flow-through aquaria overnight. All fish recovered and fed within 1 hour. We tagged 40 fish
63 (30 *Siganus corallinus* and 10 *S. doliatus*) from 27–58 mm total length; the 27 mm
64 individuals appeared to have recently recruited. Tagged fish were released at their capture
65 sites (Fig. 2b). The sites were photographed, and a scale map constructed with key locations
66 identified. After 24 hours, eleven fishes (9 *S. corallinus* and 2 *S. doliatus*) were selected and
67 their home ranges quantified (ESM). Each individual was followed for 30-min periods (max.
68 2 per day), recording its location every 15 s. The locations were transferred to the scale map
69 and the area of the polygon calculated; observations were repeated until the area increased by
70 no more than 10 % (most asymptoted in 5–8 observations).

71 All tagged fishes were recollected, plus 3 extra (collected and tagged) to completely
72 clear the sites so that translocated fishes were introduced to sites suitable for occupation but
73 without resident rabbitfishes. All tagged fishes were then translocated to a different site.
74 Fishes were sealed in a plastic bag to block olfactory cues, placed inside an opaque bucket
75 with a lid to block visual cues, then transferred by diver to the new sites. Fishes from site A
76 were moved to B or C, fishes from B were moved to A, and those from C moved to A (to
77 maintain original site densities; Table 1). All transfers were on one day between 09:00 and
78 11:00 hrs: half were released immediately and half held for 24 h in 33 cm cube cages of 5
79 mm steel mesh before release. On the following four days, four divers searched each site,
80 recording the location and identity of tagged fishes.

81 82 **Results and Discussion**

83 For reef fishes, the juvenile phase is a period of critical transitions and it is during this
84 time that reef associations are likely to be most labile, as diet and home ranges change rapidly
85 and when all habitats represent new locations. This may therefore be a period of considerable
86 flexibility. This was not the case in rabbitfishes. In the first few days to weeks after
87 recruitment all fishes had small home ranges and a strong sense of ‘home’, with an ability to
88 navigate home over distances equivalent to over 600 body lengths or 23 times their average
89 home range diameter.

90 The mean home range for the six *S. corallinus* was $1.76 \pm 0.26 \text{ m}^2$ (three specimens
91 disappeared before their home range asymptoted), the two *S. doliatus* $2.45 \pm 0.91 \text{ m}^2$. There
92 was no effect of fish size on home range area ($R^2 = 0.005$, $p = 0.87$). Although preliminary,
93 these home ranges are typical given the fishes’ body size (Nash et al. 2014) and are
94 comparable to other small herbivorous fishes such as parrotfishes (Welsh et al. 2013). The
95 strength of the homing behaviour was, however, unexpected. Homing behaviour has been
96 reported in adult fishes, including serranids (Kaunda-Arara and Rose 2004), tripterygiids
97 (Thompson 1983) and apogonids (Rueger et al. 2014), but such early development of strong
98 homing behaviour has not been reported previously in juvenile herbivorous reef fishes. The
99 homing behaviour was remarkable in that fishes were released in demonstrably suitable
100 habitats with no occupants; movement was not a result of conspecific territoriality. Caging
101 for 24 hours (Table 1) may have helped fishes to settle, but it had no effect on the results.
102 Fishes returned to their original sites regardless of the suitability of the transfer location.

103 Of the 40 fish tagged, 12 were lost, equating to a daily mortality rate of approximately
104 2.5 %. This mortality rate is relatively low compared to similarly sized reef fishes (2 - 25 %;
105 (Almany and Webster 2006; Depczynski and Bellwood 2006), suggesting that tagging and
106 movement had only a limited effect on survivorship and that the drive to return was not
107 driven by exceptionally high predation risks in unfamiliar locations. This is supported by the
108 100 % survival of individuals relocated to site C.

109 Of 22 translocated fishes, 18 returned to their home sites (Table 1); 90 % within 24 h,
110 and at least 4 within 1 h (2 *S. corallinus* and 2 *S. doliatus*). With two exceptions, all returning
111 fish remained at their original site for at least 72 h, most in the vicinity of their original home
112 ranges. Of the two exceptions, one disappeared, presumably due to predation, the other
113 briefly returned to the transfer site. With this one exception, all homing fishes remained at
114 their original home sites throughout the study. The main exception to the pattern of rapid and
115 permanent homing was the 4 specimens transferred from A to C: all remained at site C for the
116 duration of the experiment.

117 The failure of these few fish to return may give an indication of the cues involved.
118 Fishes moving from A to B, or vice versa, often made the 6 m move in less than one hour.
119 The speed and bi-directional movement suggest that vision was likely to be the primary cue.
120 Those returning from A to C arrived in less than 24 hours, reflecting the greater distance (at

121 least 36 m, or 43.5m following the reef). The lack of returns from site C to A is interesting.
122 Two possibilities arise. Site C may be more desirable than A and the fish chose not to return.
123 However, there is no evidence to support this; initial densities were comparable at all sites,
124 and all other fishes returned rapidly. Alternatively, fishes at C may have wanted to return but
125 were unable to identify the appropriate direction. Site C is upstream and out of visual range
126 of site A. If fishes were homing by olfaction this up-current position may have prevented
127 their return (auditory cues would operate in both directions and do not appear to be important
128 at this scale). All returning fishes were either spatially close to their home (using vision), or
129 downstream (using olfaction); there is no evidence to suggest that auditory cues were used.
130 The most parsimonious explanation is that like many other fishes (e.g. Gerlach et al. 2007),
131 juvenile rabbitfishes used olfaction to navigate back to their home sites once beyond visual
132 range.

133 The extreme levels of site attachment suggest that there will be long-term
134 consequences of this behaviour, with local recruitment, and subsequent mortality shaping the
135 local distribution and abundance of adult rabbitfish. This may shape local variation in their
136 delivery of ecosystem functions (Brandl and Bellwood 2013a, 2013b). Increasing evidence
137 suggests that important functions on coral reefs are delivered by small suites of species
138 (Mouillot et al. 2014), and that the intensity of these functions is highly variable over small
139 spatial scales (Welsh and Bellwood 2012a). This variability may arise from the placement of
140 home ranges; a result of decisions made at settlement years or decades earlier. Such links
141 have been suggested in coral-dwelling fishes, such as damselfishes (Sweatman 1988) and
142 gobies (Munday et al. 1997), but similar factors may also affect roving herbivores such as *S.*
143 *corallinus* and *S. doliatus* where home ranges in juveniles are likely to expand steadily,
144 leading to adults with strong site attachments in the same areas (Brandl and Bellwood 2013a;
145 Welsh et al. 2013)

146 The key question was: when do juvenile herbivorous reef fishes first establish a sense
147 of place, and how strong is this attachment? The answer appears to be that rabbitfishes
148 develop strong attachments to home ranges soon after settlement. The population structure
149 and functional capacity of a reef at scales of 10s to 100s of metres may therefore depend on
150 decisions made by small juveniles at the time of settlement. It is often assumed that 'roving
151 herbivores' are capable of delivering their ecosystem services over large expanses of reef.
152 Recent research suggests that this ability is often constrained by home ranging behaviour
153 (Welsh and Bellwood 2015). Our study suggests that this desire to stay at home is already in
154 place from their earliest moments on the reef.

155 **Acknowledgements**

156 We thank S Gordon and Lizard Island Research Station staff for field support. Funded by the
157 Australian Research Council.

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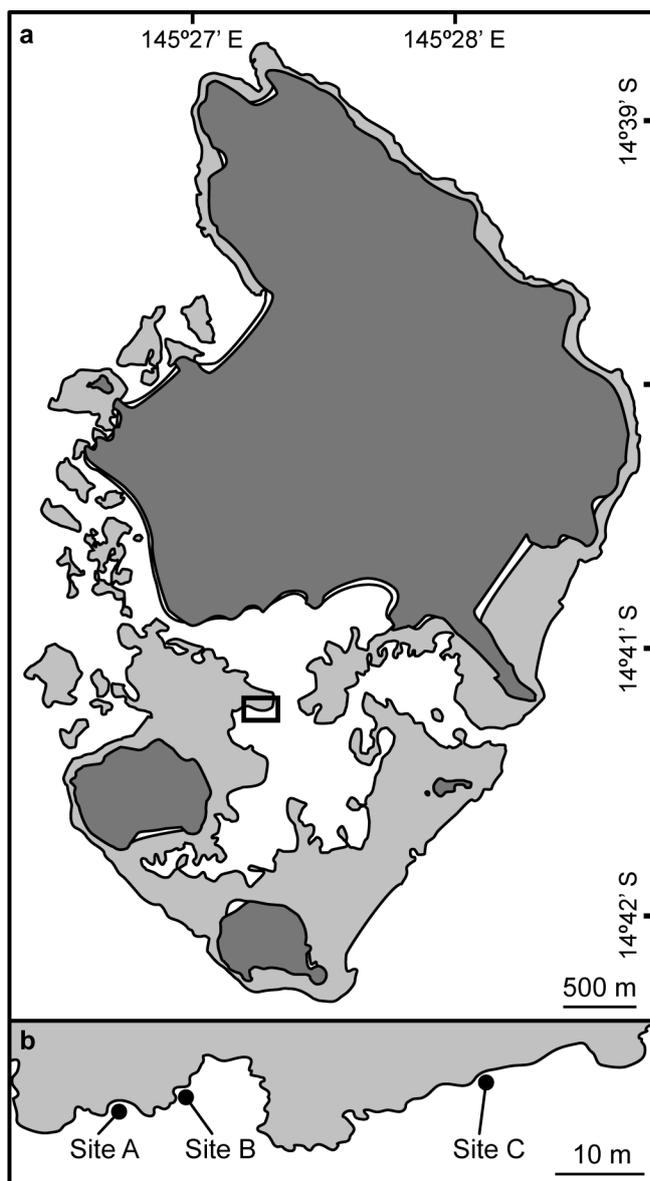
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218 **Table and Figure Legends**

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224 **Fig. 1. a** Map of Lizard Island, with box delineating the location of the study site. **b** detailed
225 map of the study site.

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Fig. 2. **a** Individual *Siganus corallinus* immediately post tagging (#18; TL 30 mm; scale bar 10mm) and **b** an individual *S. corallinus* after release and homing (#8; TL 29.5 mm).

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241 **Table 1.** Results of the translocation and homing experiment. The standard length (SL) of
 242 each translocated rabbitfish is presented in mm. Fishes were collected from one site and
 243 translocated to a release site (Fig. 1); half were held in a cage for 24 hours prior to release.
 244 The movement of each fish in the following four days is presented, noting whether they
 245 homed (in bold type) and the time taken.

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Species	SL	Collected -Released	Cage	Movement	Homed	Time
<i>S. corallinus</i>	28	A-B	No	B→A	Yes	<24 h
	30	A-B	No	B→A	Yes	<24 h
	33	A-B	No	B→A	Yes	<24 h
	28	A-B	Yes	B→A	Yes	<1 h
	50	A-B	Yes	B→A	Yes	<24 h
	29	A-B	Yes	B→A	Yes	<24 h
	28	B-A	No	A→B	Yes	<24 h
	26	B-A	Yes	A→B	Yes	<1 h
	54	C-A	No	A→C	Yes	<24 h
	52	C-A	No	A→C	Yes	<48 h
	35	C-A	No	A→C	Yes	<48 h
	27	C-A	Yes	A→C	Yes	<24 h
	46	C-A	Yes	A→C	Yes	<24 h
	51	C-A	Yes	A→C	Yes	<24 h
	45	A-C	No	none	No	
	30	A-C	Yes	none	No	
32	A-C	Yes	none	No		
<i>S. doliatus</i>	35	A-B	Yes	B→A	Yes	<1 h
	40	A-B	No	B→A	Yes	<24 h
	30	B-A	Yes	A→B	Yes	<1 h
	58	C-A	Yes	A→C	Yes	<24 h
	31	A-C	No	none	No	