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LASER WORDS	JFB	jfb_13043	B	Dispatch: June 6, 2016	Journal: JFB	CE: Geethapriya V.
	Journal Name	Manuscript No.		Author Received:	No of pages: 6	TS: priya.s

Journal of Fish Biology (2016) **0**, 0–0

doi:10.1111/jfb.13043, available online at wileyonlinelibrary.com

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BRIEF COMMUNICATION

Ability to home in small site-attached coral reef fishes

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(Received 1 December 2015, Accepted 20 April 2016)

The ability of two common, site-attached coral-reef fishes to return to their home corals after displacement was investigated in a series of field experiments at One Tree Island, southern Great Barrier Reef. The humbug *Dascyllus aruanus* was displaced up to 250 m, with 42% of individuals returning home, irrespective of body size, displacement, direction (up or across currents) and route complexity, while for the lemon damselfish *Pomacentrus moluccensis* 35% of individuals returned overall, with 33% from the greatest displacement, 100 m along a reef edge. Given that the home range of both species is <1 m², over their 10+ year life span, the mechanisms and motivations for such homing ability are unclear but it may allow resilience if fishes are displaced by storm events, allowing rapid return to home corals.

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Key words: body size; coral-reef fish movement; *Dascyllus aruanus*; habitat complexity; homing; *Pomacentrus moluccensis*.

Movement is a key demographic parameter used to describe and model dynamics of natural populations. For coral-reef fishes, dispersal of pelagic larvae drives large scale distribution patterns in space and time (recruitment limitation: Doherty, 1981), however these patterns are modified by post-settlement growth, mortality, reproduction and movement (Forrester, 1990; Booth, 1995). Small-scale post-settlement movement patterns of site-attached coral reef fishes are poorly understood. In some taxa, such as cardinalfishes, nocturnal foraging forays from reef bases can extend 100s of metres, and such species are able to navigate home when displaced experimentally up to 2 km (Marnane, 2000). Larger reef fishes long been known to possess strong abilities to home (Ogden & Buckman, 1979). Most small reef fishes, however, are highly site-attached with very small home ranges and when displaced have only limited ability to return to home [*e.g. Gobiodon histrio* (Valenciennes 1837), only 20% returned from 4 m: Wall & Herler (2009)]. Intertidal rockpool species may have strong homing ability, for example over 50% of fishes displaced up to 30 m returned to home pools within 42 days (White & Brown, 2013). Shima *et al.* (2012) showed ontogenetic differences in homing abilities in a temperate reef species, the common triplefin *Forsterygion*

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1 *lapillum* Hardy 1989, with overall 30% of *F. lapillum* displaced over 200 m returning
2 home, mostly larger adults.

3 In this study, the homing abilities of two common reef damselfishes, the humbug
4 *Dascyllus aruanus* (L. 1758) and the lemon damsel *Pomacentrus moluccensis* Bleeker
5 1853, were investigated by displacements of individuals to distances up to two orders of
6 magnitude greater than their presumed home range, and assessing the influence of body
7 size, habitat complexity and direction of displacement on the homing response. *Dascyl-*
8 *lus aruanus* and *P. moluccensis* are common and well-studied damselfishes on the Great
9 Barrier Reef and are widely distributed in the Indo-Pacific region. *Dascyllus aruanus*
10 lives in tight-knit groups of up to 20 individuals on small live branching corals and has
11 a very limited home range (Sale, 1971; Forrester, 1990; D.J. Booth pers. obs.). Larger
12 individuals are competitively dominant and may venture several metres among corals,
13 while smaller *D. aruanus* generally stay closer to the coral while foraging. *Pomacen-*
14 *trus moluccensis* also prefer small branching coral heads (Booth & Beretta, 2004) but
15 are more common along the edges of discrete reefs, in contrast to *D. aruanus*, which
16 is common on corals across the flat inter-reef bottom (Sale, 1971). New recruits of
17 *P. moluccensis* remain in close proximity to corals while larger and older individuals
18 may have a larger home range, up to 2 m from a home coral (D.J. Booth, unpubl. data),
19 and so would not be predicted to possess any strong ability to navigate beyond sever-
20 al metres. Sometimes these small *P. moluccensis* are seen singly occupying marginal
21 habitat, possibly displaced due to storm events. Whether individuals were more likely
22 to home from up-current v. down-current locations was also tested, to indicate whether
23 water-borne chemical cues may be involved. While these small site-attached reef fishes
24 rarely venture from coral shelter, such displacements may occur during times of strong
25 wave action and high turbidity. Lewis (1997) noted that 29% of *P. moluccensis* and 77%
26 of *D. aruanus* that arrived at experimental patch reefs were post-settlement, indicating
27 that both species are capable of across-sand movement, but their return to home corals
28 was not tested. Whether homing was facilitated by the substratum while the individual
29 was in transit was also tested. A more complex route (more live hard substratum) may
30 either enhance homing (less open sand to cross, so lower predation) or inhibit it (more
31 aggressive fishes to encounter).

32 The experimental area was located in One Tree Island Lagoon on the southern Great
33 Barrier Reef (23° 30' S; 152° 06' E). For *D. aruanus*, an experimental site was selected
34 on sandy bottom in the lagoon in c. 0.5 m water depth. Individual branching corals
35 (mostly *Pocillopora damicornis* or *Acropora* spp.) were scattered across this sand area,
36 about one third of which were occupied by groups of *D. aruanus*. In July 2011, 10 indi-
37 vidual corals, supporting no *D. aruanus*, were tagged at each of the following distances:
38 10, 25, 50, 100 and 250 m ($n = 50$ corals total) from the origin, a 1 × 1 m natural matrix
39 of fine-branching *Acropora* sp. surrounded by several metres of bare sand. Corals at
40 each distance were separated radially as much as possible (*i.e.* 10 corals each spread
41 by c. 35°). All individuals were captured by a snorkeller from the origin, spraying a
42 clove oil mixture (1:4 clove oil:ethanol solution) and netting the anaesthetised fishes.
43 Fishes were measured (total length, L_T , and standard length, L_S) then individually
44 tagged while anaesthetised using Visible Implant Elastomer (VIE: Bruyndoncx *et al.*,
45 2002; www.nmt.us/products/vie/vie.shtml). Each *D. aruanus* was randomly assigned
46 to a displacement distance ($n = 10$ individuals total at each displacement distance) and
47 carefully relocated singly in sea water in Ziploc bags in opaque buckets (*i.e.* there were
48 no visual or chemical cues on displacement). Individuals were observed on release (just

1 before dusk, when any aggression by resident fishes is minimal: Booth & Beretta, 2004)
2 and behaviours (*e.g.* aggression, movement and feeding) were recorded for 10 min.
3 Twice per day, for the following week, careful searches were made for tagged indi-
4 viduals up to 300 m from the origin. If found, they were identified and their location
5 (GPS) and behaviour were recorded. Four individuals (25–60 mm L_T) were captured
6 as above but replaced on the origin coral matrix as a control to check for movement
7 over the study period. Habitat complexity was assessed along the direct route from each
8 tagged coral to the origin. A belt transect 2 m wide was swum and the number of small
9 suitable coral heads *en route* counted as an index of habitat availability as stepping
10 stones.

11 For *P. moluccensis*, the experiment was conducted along a continuous reef edge.
12 Individuals were captured in the same way by a snorkeller with clove oil from a single
13 matrix of branching corals (*Porites* sp.) on the reef edge in One Tree Lagoon, measured
14 (L_T and L_S) and individually tagged using VIE. Each individual was assigned to one
15 displacement distance (25, 50 or 100 m) in one of two directions from the central coral
16 matrix, and carefully relocated singly in sea water in a Ziploc bag in an opaque bucket
17 on the reef edge. The reef edge was *c.* 2 m in height and it was possible to allocate six
18 fish to each distance, separated by at least 2 m. Along-reef homing at distances over
19 100 m was not tested since larger reefs were not available for testing. Individuals were
20 observed on release (just before dusk) for 10 min and notes made on behaviours, such as
21 aggression, movement and feeding, as for *D. aruanus*. Four individuals (25–55 mm L_T)
22 were captured as above but replaced on the origin coral matrix to check for movement
23 over the study period.

24 Binary logistic regression (SPSS Ver. 20; [www-01.ibm.com/software/au/analytics](http://www-01.ibm.com/software/au/analytics/spss)
25 /spss) was used to examine the relationship between independent variables [continu-
26 ous: fish size, habitat complexity (number of corals per metre); categorical: distance,
27 direction (*D. aruanus*: in quadrants of 0–90°, *etc.*), for *P. moluccensis*: along reef edge
28 in one direction *v.* another] and the response variable (arrived home, yes or no, within
29 1 week). Individuals of both species were observed immediately after release to seek
30 shelter deep within coral branches, with only a few ($n = 3$ for *D. aruanus*, $n = 3$ for *P.*
31 *moluccensis*) attacked by residents (these were encouraged back onto the coral until set-
32 tled). Surprisingly, 42% of displaced *D. aruanus* and 35% of *P. moluccensis* returned
33 to their original location within 1 week, most arriving within 24 h after release. Ten
34 per cent were found elsewhere for *D. aruanus* and 15% for *P. moluccensis*, taking
35 up residence on a range of small coral heads with and without residents, while 48%
36 disappeared for *D. aruanus* and 50% for *P. moluccensis*. For *D. aruanus* there was
37 no significant difference in proportion of displaced individuals homing among dis-
38 placement distances (up to 250 m), direction, body size (28–68 mm L_T) or among path
39 complexities (binary logistic regression, Table I, $P > 0.05$). Control fishes ($n = 4$ fish
40 for both species) did not move away during the experimental duration, reinforcing that
41 handling was unlikely to be a cause of disappearance.
42

43 For *P. moluccensis*, homing was related to both body size (larger individuals were
44 more likely to return home; Fig. 1 and Table I; binary regression, Wald statistic = 7.80,
45 d.f. = 3, $P < 0.05$) and less likely with greater displacement distances (Fig. 1 and
46 Table I; binary regression, Wald statistic = 6.45, d.f. = 3, $P < 0.05$). No clear mech-
47 anism for low rates of homing by *P. moluccensis* displaced the intermediate (50 m)
48 distance was seen.

TABLE I. Binary regression models for homing in two species of coral reef fish

Source	<i>B</i>	S.E.	Wald	d.f.	<i>P</i> -value	Exp(<i>B</i>)
(a) <i>Dascyllus aruanus</i>						
Body size	0.008	0.018	0.193	1	0.660	1.008
Distance			1.673	3	0.643	0.994
Complexity			0.395	2	0.821	1.009
Direction			3.968	3	0.265	0.464
Constant	0.560	1.485	0.142	1	0.706	0.893
(b) <i>Pomacentrus moluccensis</i>						
Body size			7.801	3	0.048	
Distance			6.452	2	0.040	
Direction	0.726	0.740	0.964	1	0.326	2.067
Constant	0.320	0.737	0.189	1	0.664	0.726

The direction of displacement (up- v. down-current) was not significant, $P < 0.05$, which suggests that long distance chemical cues such as sun compass, polarized light, olfaction and sound (Sweatman, 1988; Huijbers *et al.*, 2012) may not be used. Homing success dropped with distance displaced, which may reflect the loss of cues or more likely that when a greater distance along the reef edge is travelled, the individual encounters more aggressive residents. Displaced fishes were sometimes chased by residents including a wide variety of small conspecifics and heterospecifics. For *P. moluccensis*, larger individuals were overall more likely to home, possibly given the lower levels of aggression towards them, or reduced sensory abilities of younger and smaller individuals (Lecchini *et al.*, 2007).

Unexpectedly for *D. aruanus*, individuals displaced the furthest, 250 m, were just as likely to return home, and smaller individuals were not less likely to return home, despite the known strong size-based dominance hierarchies in this species (Forrester, 1990). Mann *et al.* (2014) investigated *D. aruanus* movement between habitats in aquaria and concluded that individuals use ‘stable’ information such as conspecific

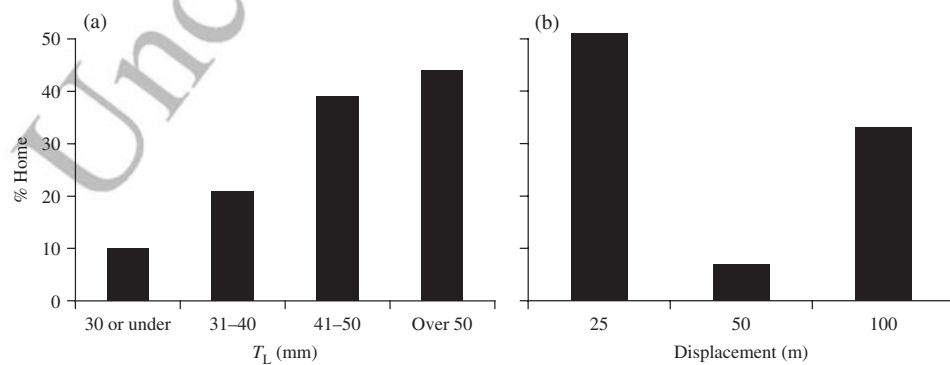


FIG. 1. Percentage of displaced *Pomacentrus moluccensis* ($n = 60$ total) returning home and (a) total length (L_T) and (b) displacement distance ($n = 12$).

1 group size as cues to move to new habitat, and loss of group members in the field may
2 prompt individuals to undertake larger journeys than are normally observed.

3 Reef fishes possess impressive abilities to home once displaced, with distances of
4 over 2 km (Marnane, 2000). These abilities were interpreted as adaptive for foraging
5 forays in more mobile reef fish species. This is the first documentation of homing
6 at 100 m+ scales of coral reef fishes that are not known to normally venture beyond
7 several metres from their home coral. So why does this behaviour exist and by what
8 mechanisms? Cues used for navigation are unknown but the lack of significance of
9 direction home and path complexity suggests that odour and chemosensory cues are not
10 primarily responsible. Path complexity, while not significant, was measured in a very
11 basic manner and this parameter could usefully incorporate a measure of coral clump-
12 ing or fish residency (aggression towards homing fishes) *en route* in future. Possibly,
13 the behaviour occurs as a remnant of a previously-adaptive response, or is occasionally
14 useful if the individual is displaced by storm events. If the latter, it may enhance the
15 resilience of these fish species. Both species studied here are from the family Poma-
16 centridae (damsel-fishes) so a next step would be to examine homing ability across a
17 range of sedentary reef-fish families.

18 Many thanks for field support to H. Beck and the UTS Coral Reef Ecosystems classes, and to
19 One Tree Island Research Station. I thank anonymous reviewers for their useful suggestions.
20

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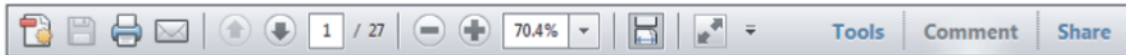
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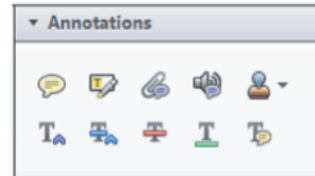
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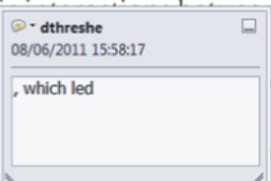


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there is no room for extra profits as mark-ups are zero and the number of firms (n) is not determined by market size. Blanchard and Kiyotaki (1987), in a model of perfect competition in general equilibrium, show that the structure of aggregate demand and supply in the classical framework assuming monopolistic competition is determined by an exogenous number of firms.

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dynamic responses of mark-ups to cost changes. The VAR evidence suggests that the structure of the sector is an important determinant of the level, are exogenous variables. (M henceforth) we open the black b



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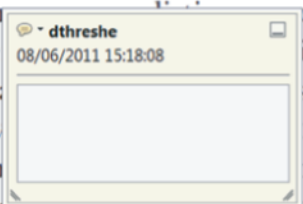


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and supply shocks. Most of the time, the number of firms is determined by market size. Blanchard and Kiyotaki (1987), in a model of perfect competition in general equilibrium, show that the structure of the sector is an important determinant of the level, are exogenous variables. (M henceforth) we open the black b



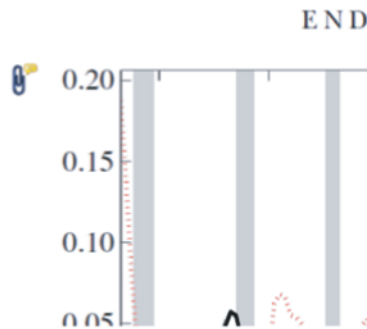
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
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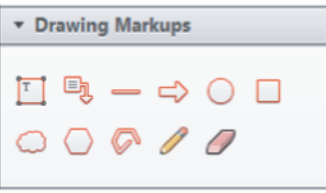
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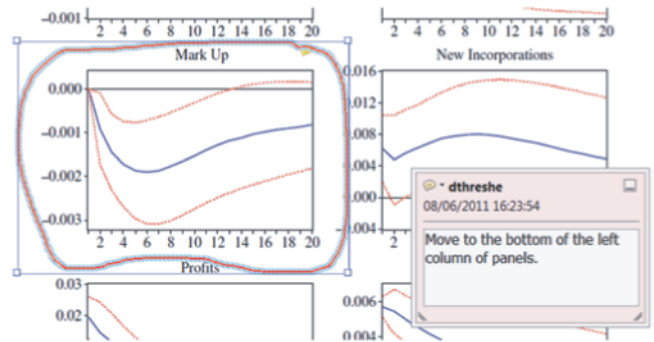


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