

Comment on “Chemically mediated behavior of recruiting corals and fishes: A tipping point that may limit reef recovery”

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Abstract

Dixon *et al.*¹ report that coral larvae navigate towards chemical cues associated with healthy reefs and avoid cues from degraded reefs. However, the swimming capabilities of coral larvae and well-established patterns of recruitment and reef hydrodynamics indicate that coral larvae will not be able to use these cues to recruit to healthy reefs.

Main Text

Dixon *et al.* (1) present a series of experiments suggesting that coral larvae can distinguish between chemical cues associated with healthy and degraded reefs, and subsequently imply that coral larvae will use these cues to navigate to healthy reefs. However, many of their results are contrary to our current understanding of coral larval swimming capabilities and

well-established patterns of recruitment in the field. In addition, the flow structure in their flume is likely to be more dynamic than suggested, making choice experiments with coral larval difficult to interpret.

In a first set of flume experiments, larvae of three species of *Acropora* overwhelming preferred to spend time in water collected from areas of reefs protected from fishing when compared to water collected from areas lacking protection. However, coral larvae are very slow swimmers and based on previously published work are unlikely to be able to maintain their position in the flume for the 5 min duration of the experiment. The reported flow speed of 4.2 mms^{-1} is greater than the mean of all average swimming speeds reported to date, even when larvae are assisted by gravity (i.e., swimming downwards; Fig. 1). The maximum horizontal swimming speed recorded for a coral larva is 3.45 mms^{-1} (Table 1), which is well below the minimum speed required to maintain position in the flume, let alone navigate between the two water bodies. The remarkable consistency of larval behavior in the flume (Fig. 1A; Dixon *et al.*) is highly unusual and suggests that a physical rather than behavioral mechanism is operating. Indeed, the flow structure in their flume is likely to be much more complicated than they describe due to the presence of a barrier initially separating the two water sources and the barrier's abrupt end at the beginning of the test section. It is highly unlikely that visual inspection of a dye plume would sufficiently characterize flow conditions experienced by such small larvae in this flume. Well established techniques such as particle image velocimetry, laser-Doppler velocimetry or planar laser-induced fluorescence (2) should have been used to verify that flow biases do not exist at the scale relevant to coral larvae.

The spatial pattern in the recruitment of corals to settlement tiles are also highly unusual for a reef system that has a high number of reefs in close proximity, such as Dixon *et al.* sites in Fiji. Their results imply a strong positive correlation between adult coral cover and recruitment to settlement tiles. Indeed, not a single recruit was found on tiles placed in

the non-protected reef areas where coral cover was uniformly low. In contrast, in a two year study of 33 reefs spanning the length of Great Barrier Reef there was no correlation between adult abundance and coral recruitment to settlement tiles (3). Furthermore, only one of the 132 sites (4 sites per reef and 8 tiles per site) had no recruits (3). The lack of an effect of algal clearance on juvenile recruitment to the substratum is also anomalous. In contrast, artificial exclusion of herbivores reduces rates of coral juvenile recruitment 3-fold, presumably due to dramatic increases in abundance of seaweeds in herbivore exclusion plots (4).

Even if coral larvae can distinguish between chemical cues associated with healthy and degraded reefs it is highly unlikely they will be able to use this information to navigate against ubiquitous tidal and other currents to preferred reefs for recruitment. Currents connecting reefs rarely fall below 100 mms^{-1} (5), which is almost two-orders of magnitude greater than typical coral larval swimming speeds (Table 1; Fig. 1). All existing measures indicate that coral larvae are very slow swimmers and therefore will behave as passive particles relative to inter-reef hydrodynamic regimes (6). Perfuming degraded reefs, as suggested by Dixon *et al.*, will not enhance recovery rather it will distract from the difficult task of reducing fishing effort and improving water quality.

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Table 1. Swimming speeds in mms^{-1} for hermatypic scleractinian coral larvae. n = number of larvae; SE = standard error; a = mean calculated as average of maximum and minimum value; b = mean calculated from larvae aged 2 to 7 days old.

Species	Swim direction	Min	Max	Mean	SE	n	Larvae length (mm)	Reference
<i>Heliogungia actinoformis</i>	horizontal	1.15	1.90	1.57	0.09	8	0.50	(7)
<i>Pocillopora damicornis</i> ^a	horizontal	1.67	1.88	1.78	na	na	1.00	(8)
<i>Pocillopora damicornis</i> ^b	horizontal	0.08	3.09	2.01	0.07	82	1.18	(9)
<i>Coelastrea aspera</i> ^a	horizontal	2.00	3.45	2.73	na	na	0.47	(10)
<i>Heliogungia actinoformis</i>	up	0.90	2.65	1.66	0.09	18	0.50	(7)
<i>Agaricia teunifolia</i>	up	1.04	3.16	2.10	0.20	28	na	(11)
<i>Galaxea horrescens</i>	up	1.32	3.33	2.41	0.15	20	2.30	(12)
<i>Pocillopora damicornis</i>	up	1.61	4.50	2.79	0.11	30	2.00	(13)
<i>Porties asteroides</i>	up	1.26	4.34	2.80	0.20	59	0.75	(11)
<i>Isopora bruggemanni</i>	up	1.10	4.55	2.86	0.24	20	2.50	(14)
<i>Seriatopora hystrix</i>	up	na	na	3.33	na	na	1.50	(15)
<i>Heliogungia actinoformis</i>	down	1.97	3.80	2.76	0.17	9	0.50	(7)
<i>Isopora bruggemanni</i>	down	2.56	5.56	3.55	0.18	20	2.50	(14)
<i>Agaricia teunifolia</i>	down	2.01	5.19	3.60	0.30	28	na	(11)
<i>Galaxea horrescens</i>	down	3.03	5.21	3.86	0.13	20	2.30	(12)
<i>Porties asteroides</i>	down	2.76	5.84	4.30	0.30	59	0.75	(11)
<i>Seriatopora hystrix</i>	down	na	na	4.44	na	na	1.50	(15)
<i>Pocillopora damicornis</i>	down	3.68	6.49	4.79	0.13	30	2.00	(13)

Figure 1. Coral larvae are notoriously slow swimmers. The minimum swimming speed required to hold position in the experimental flume used by Dixon *et al.* (4.2 mms^{-1} , red star) is more than twice the mean horizontal swimming speed of larvae in other studies. Mean swimming speeds were taken from 14 studies representing over 450 speed measurements (for references see Table 1. The raw data is available at coraltraits.org). An ANCOVA for log-transformed speed data against larvae size and swimming direction found only a significant effect of direction (after dropping size: $F_{2,15} = 13.72$, $p < 0.001$), where gravity-assisted swimming (downward) was significantly faster than other swimming directions (letters a and b denote significant differences at $\alpha = 0.05$, post-hoc Tukey's test).

