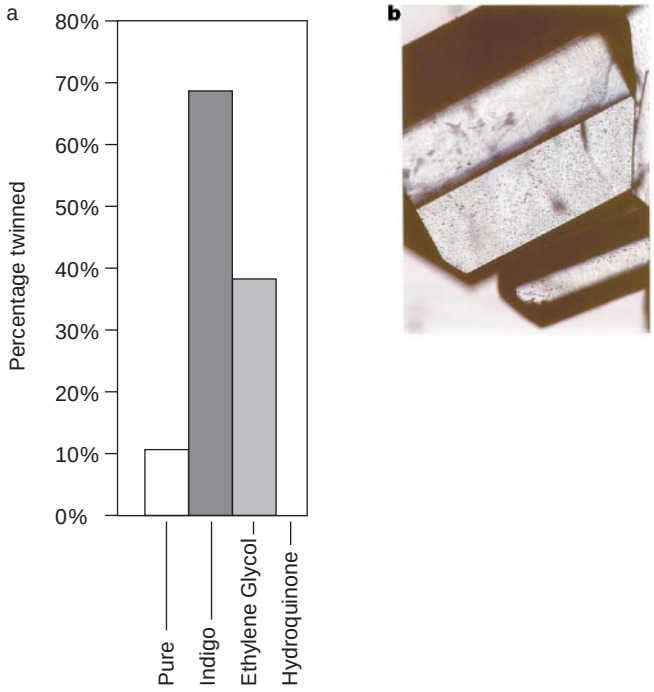

Figure 4 Production of twinned saccharin crystals. **a**, A comparison of the frequency of twinning in pure and doped solutions for crystals grown at 25 °C and a supersaturation of 0.4 in unstirred vessels. **b**, Micrograph of a twinned saccharin crystal grown from an indigo-doped saccharin solution, showing blue colouration at the interface.

After crystallization, crystals were removed and the percentage of twinned crystals determined by manual counting. The number of crystals counted varied between experiments, but was always between 100 and 200. The histogram in Fig. 4a summarizes these results: in pure solutions, 10% of crystals grow as twins; in the presence of ethylene glycol, 40% grow as twins; while in solutions containing indigo, almost 70% of the crystals are twinned. These data are in line with our expectations. In addition, we show in Fig. 4b an optical micrograph of a detail of the twin interface for a crystal grown in the presence of indigo. The blue colouration verifies that this molecule is indeed concentrated at the interface. In complete contrast, the addition of hydroquinone was found to yield no twins at all, again confirming our expectations.

The success of this study shows that our understanding of intermolecular interactions and interfacial processes can be applied successfully to the solid–solid interface. It suggests a general strategy for designing adhesive molecules to span and stabilize such interfaces, utilizing a combination of molecular dimensions and specific intermolecular interactions. We note that we were only able to demonstrate this success because we had previously developed a molecular model of the interfacial region—without this, such engineering would be relegated to randomized trials and serendipitous successes. Fortunately, such information is rapidly becoming routinely available, not only through the increased power and sophistication of molecular modelling, but also using state-of-the-art structural techniques such as scanning probe microscopy, microscopic spectroscopy and glancing-angle X-ray diffraction[12]. □

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1. Maoz, R., Matlis, S., Dimasi, E., Ocko, B. M. & Sagiv, J. Self-replicating amphiphilic monolayers. *Nature* **384,** 150–153 (1996).
2. Hatzor, A. *et al.* Coordination-controlled self-assembled multilayers on gold. *J. Am. Chem. Soc.* **120,** 13469–13477 (1998).
3. Weissbuch, I., Popvitz-Biro, R., Leiserowitz, L. & Lahav, M. in *The Lock and Key Principle* (ed. Behr, J. P.) 173–246 (Wiley & Sons, Chichester, 1994).
4. Docherty, R. & Roberts, K. J. Modelling the morphology of molecular crystals. *J. Cryst. Growth* **88,** 159–168 (1988).
5. Gavazotti, A. & Fillipini, G. Polymorphic forms of organic crystals at room conditions: thermodynamic and structural implications. *J. Am. Chem. Soc.* **117,** 12299–12305 (1995).
6. Docherty, R. & Jones, W. in *Organic Molecular Solids—Properties and Applications* (ed. Jones, W.) Ch. 5 (CRC Press, London, 1997).
7. Davey, R. J., Blagden, N., Potts, G. D. & Docherty, R. Polymorphism in molecular crystals: stabilization of a metastable form by conformational mimicry. *J. Am. Chem. Soc.* **119,** 1767–1772 (1997).
8. Davey, R. J., Maginn, S. J. & Polywka, L. in *Advances in Industrial Crystallisation* 150–165 (Butterworth-Heineman, Oxford, 1991).
9. Lieberman, H. F., Williams, L., Davey, R. J. & Pritchard, R. G. Molecular configuration at the solid-solid interface: twinning in saccharin crystals. *J. Am. Chem. Soc.* **120,** 686–691 (1998).
10. Williams-Seton, L., Davey, R. J. & Liebermann, H. F. Solution chemistry and twinning in saccharin crystals: a combined probe for the structure and functionality of the crystal-fluid interface. *J. Am. Chem. Soc.* **121,** 4563–4567 (1999).
11. Cerius^2 version 2.0 (Molecular Simulations Inc., Cambridge, UK, 1998).
12. Gidalevitz, D. *et al. Angew. Chem. Int. Edn Engl.* **36,** 955–959 (1997).

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Larval retention and recruitment in an island population of a coral-reef fish

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For close to a century, recruitment of larvae to a local population has been widely accepted as a primary determinant of marine population dynamics[1,2]. However, progress in elucidating the causes of recruitment variability has been greatly impeded by our ignorance of the sources of recruits. Although it is often assumed that recruitment is independent of local reproduction[3–6], there is increasing circumstantial evidence that physical[7,8] and behavioural[9,10] mechanisms could facilitate larval retention near source populations. To develop a direct method for reconstructing the dispersal history of recruiting larvae, we put forward the hypothesis that differences in nutrient and trace-element concentrations between coastal and open oceans could result in quantifiable differences in growth rate and elemental composition between larvae developing in coastal waters (locally retained) and larvae developing in open ocean waters (produced in distant locations). Using this method, we show that recruitment to an island population of a widely distributed coral-reef fish may often result from local retention on leeward reefs. This result has implications for fisheries management and marine reserve design, because rates of dispersal between marine populations—and thus recruitment to exploited populations—could be much lower than currently assumed.

Our approach is based on the following two predictions. (1) Coastal environments are the most productive regions of the world's oceans[11], where local nutrient inputs can enhance food resources for developing fish larvae[12,13]. Thus, larvae retained in coastal water masses should grow faster, and settle at larger sizes, than larvae dispersing through nutrient-depleted oceanic waters. (2) Along coastal margins, concentrations of many particle-reactive trace elements are significantly higher than in the open ocean[14]. Thus, larvae developing in coastal environments should have elevated trace-element concentrations in their tissues compared with oceanic larvae if these elements are absorbed from sea water and permanently incorporated into the larvae. We used otoliths—crystalline structures in the inner ear of teleost fishes—as recorders of growth history and trace-element environmental signatures because they are formed at birth, new layers of calcium carbonate

are deposited daily as discernible growth bands[15], and elements from the surrounding sea water can substitute for calcium and become permanently incorporated into the otolith[16,17]. In addition, otolith trace-element signatures have recently been used to identify stocks[17] and nursery habitats[18,19] for several temperate fishes.

The focal species for this study was the bluehead wrasse, *Thalassoma bifasciatum*, an abundant Caribbean coral-reef fish with a long planktonic larval duration (~45 days). Past research on St Croix, US Virgin Islands (northeastern Caribbean Sea, 17° 45′ N, 64° 35′ W) has detected consistent recruitment patterns[20]. On the windward shore of St Croix, recruitment was highest on the eastern (up-current) end and decreased towards the western end of the island. Along the leeward shore, recruitment was lowest at the eastern end and increased to highest recruit densities at the westward (down-current) end of the island. We put forward the hypothesis that physical oceanographic processes were responsible for the patterns of recruitment along the two shores. Windward reefs may receive recruits primarily from larvae dispersing from nearby up-current source populations (possibly Saba, St Martin, or other islands of the lesser Antilles, from where passively drifting larvae could reach St Croix in as little as 7–14 days; ref. 21) whereas leeward reefs may receive recruits retained within coastal waters in the lee of the island. Regions of weak converging currents as well as wake eddies have been detected along the leeward coast of St Croix[22], and may also facilitate larval retention near other islands[23,24]. Thus the importance of larval dispersal versus local retention to patterns of recruitment may vary across windward and leeward reefs.

In order to determine the sources of recruits to St Croix, we compared larval growth histories and otolith trace-element composition (see Methods) of newly settled individuals among three locations: an up-current site on the windward shore (Jack's Bay) and two down-current sites on the leeward shore (Northstar and Butler Bay) during the summer and autumn of 1992. For this analysis, we selected individuals that recruited during five periods: three summer periods (June–August) when average recruitment was more than five times greater at the leeward sites relative to the windward site, and two autumn periods (September and October) when average recruitment levels were lower and similar among the leeward and windward shores (1.1 and 0.9 fish per m^2, respectively)[20]. We found significant differences in both growth history and otolith trace-element signatures among larval populations of bluehead wrasse recruiting to each site as well as among recruitment periods (Table 1), indicating that recruiting larvae experienced different environmental histories both within recruitment periods as well as among recruitment periods.

Differences among recruitment periods resulted from the clustering of both larval growth history and otolith trace-element signatures along a retention–dispersal gradient as indicated by canonical discriminant analysis (Fig. 1; see Methods). In support of our hypotheses, larvae with positive canonical factor 1 (CF1) scores were large, fast-growing individuals with otoliths enriched in trace elements (that is, retention characteristics) whereas larvae with negative CF1 scores were small, slow-growing individuals whose otoliths had low trace-element concentrations (that is, dispersal characteristics).

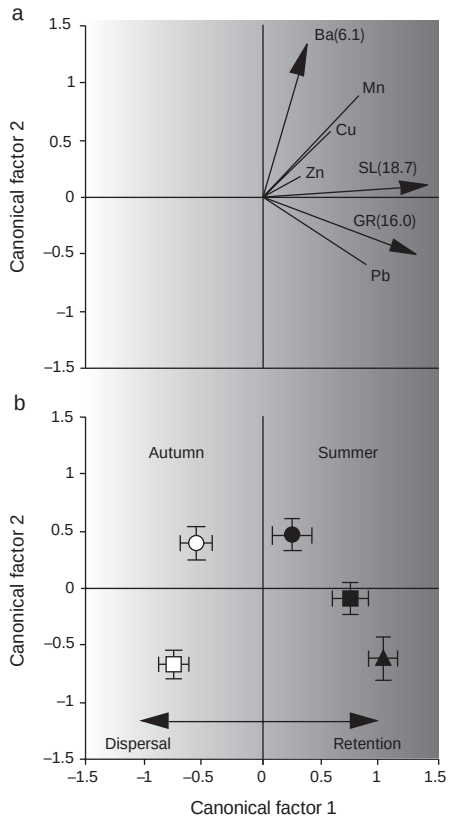

Figure 1 Results of the canonical discriminant analysis of larval source population signatures. Along the canonical factor 1 axis, predominantly elevated growth rates, larval size, and trace-element concentrations (retention signature) occur in larvae recruiting in summer relative to larvae recruiting in autumn. **a**, Vector plot depicting the strength and direction of the correlations between the dependent variables and the first two canonical factors[30]. Vectors with arrows indicate endpoints beyond the scale of the figure (values in parentheses). **b**, Centroids (means) for each recruitment period. Bars = ± 1 s.e. See Table 1 legend for key to chemical symbols, and growth-rate and fish-size abbreviations. Filled circles, June; filled squares, July; filled triangles, August; open circles, September; open squares, October.

High proportions of larvae settling during the summer months were characterized by retention signatures (positive CF1 scores) in contrast to larvae settling in the autumn, which were characterized by dispersal signatures (negative CF1 scores). During the summer recruitment periods, there were strong differences among sites in the CF1 scores (Table 1), with 89% of the leeward-shore recruits with retention signatures compared to only 32% of the windward-shore recruits with such signatures. The variation in the prevalence of larvae with retention signatures had important repercussions for the intensity of recruitment to St Croix (Fig. 2a–c). Using the CF1 score (from Fig. 1) as an index of the intensity of local retention (positive values represent high retention and negative values represent low retention/high dispersal), we discovered pronounced differences between the leeward sites and the windward site in the relative importance of local retention of larvae to recruitment. At both leeward reefs (Butler Bay and Northstar, Fig. 2a, b), recruitment levels were positively correlated with CF1, indicating that the heavy summer recruitment events followed periods when large numbers of larvae tended to be locally retained (larvae had both high growth rates and high otolith trace-element concentrations).

Table 1 Comparisons of larval source population signatures among sites and among monthly recruitment events

Effect	MANOVA Pillai trace	Dependent variables (ANOVAs) Mn	Cu	Zn	Ba	Pb	GR	SL
Site	4.77‡	3.02*	3.73*	0.36	8.46†	1.65	2.38	3.88*
Month	6.22‡	3.18*	3.78†	2.04	8.45†	3.26*	18.76†	20.73†

Symbols used: Mn, manganese; Cu, copper; Zn, zinc; Ba, barium; Pb, lead; GR, somatic growth rate; SL, adjusted standard length. Trace-element concentrations were log transformed to conform to assumptions of the statistical tests. The MANOVA results indicate that significant overall differences existed among sites (first row) and months (second row). Significant ANOVA tests identify the important variables in the MANOVA models. Shown are *F*-ratios for tests based on differences in larval growth histories and otolith elemental composition among sites and months. Not shown are the pairwise multivariate comparisons (Hotelling's T^2) among sites and months; all were significant at the appropriate Bonferonni adjusted significance level except for the July versus August comparison. Hotelling's T^2 comparisons among sites within season (summer versus autumn) indicated that significant differences occurred among sites in summer (June and July) but not in autumn (September and October). The untransformed means (ranges) for elements (in $\mu mol\,mol^{-1}$ Ca) were: Mn, 3.83 (1.19–29.38); Cu, 15.74 (4.11–59.98); Zn, 32.81 (4.46–126.77); Ba, 3.70 (2.05–8.22); Pb, 1.95 (1.06–6.95), and for growth histories: GR, 0.23 (0.18–0.28) $mm\,d^{-1}$; SL, 12.05 (9.95–13.9) mm.
*$p \leq 0.05$, †$p \leq 0.007$ (Bonferonni adjusted $\alpha = 0.05/7$), ‡$p \leq 0.001$.

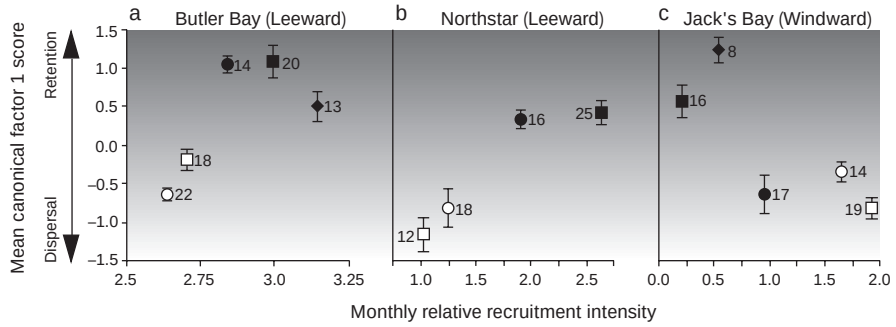

Figure 2 Relationship between larval retention and the intensity of recruitment. These data are evidence for high recruitment levels of bluehead wrasse, *Thalassoma bifasciatum*, coinciding with periods of greater larval retention (positive CF1 score) at leeward sites (**a**, **b**) in contrast to a windward site (**c**) when high recruitment levels occurred during periods dominated by dispersing larvae (negative CF1 score). Shown are the mean monthly CF1 scores and relative recruitment intensity for each site (bars show ± 1 s.e., see Fig. 1 for monthly symbol definitions). Relative recruitment is defined as [site average monthly recruit density (no. of fish per m^2)]/[island average monthly recruit density (no. of fish per m^2)]. Values adjacent to symbols are sample sizes (note: no data were available for the August Northstar recruit collection due to poor sample preservation). Under the assumption that each larva is an independent recorder of environmental conditions, the relationship between CF1 and recruitment intensity was strong and significant at all sites (Butler Bay, $r = 0.462$, $p < 0.001$; Northstar, $r = 0.546$, $p < 0.001$; Jack's Bay, $r = -0.476$, $p < 0.001$). A more conservative approach, using monthly mean CF1 values for each site, yields stronger Pearson product-moment correlation coefficients but these are not significant due to small sample size (Butler Bay, $r = 0.686$, $p = 0.201$; Northstar, $r = 0.922$, $p = 0.078$; Jack's Bay, $r = -0.784$, $p = 0.116$). Mean CF1 and recruitment were significantly correlated when data from the two leeward sites were pooled ($r = 0.752$, $p = 0.019$).

In contrast, recruitment levels at Jack's Bay (Fig. 2c) were inversely correlated with CF1, indicating that the elevated windward recruitment events in the autumn were related to larval transport through offshore water (larvae had both low larval growth rates and low otolith trace-element concentrations). In addition, the presence of positive CF1 scores during low summer recruitment events at Jack's Bay indicates that a small proportion of retention-signature larvae can settle to windward reefs.

Our findings suggest that recruitment to island populations, in particular to leeward reefs, may often result from the retention of locally spawned larvae. Local retention, compared with dispersal through oceanic waters, may be the more pervasive and adaptive larval dispersal strategy for many coastal marine organisms with planktonic larvae, given the more favourable environmental conditions for larval growth and survival and the higher probability of encountering suitable adult habitat at the end of larval development.

For bluehead wrasse populations on St Croix, recruitment is not simply a result of settlement from a common larval source. Instead, larvae settling to windward and leeward reefs spent significant amounts of time in different environments, indicating that processes affecting larval dispersal not only operate at intermediate spatial scales (>100 km; between-island dispersal) but also at much smaller spatial scales (<10 km; within-island dispersal). Temporal differences in larval growth rates and otolith trace-element signatures among recruitment periods indicate that reefs probably receive a mixture of locally retained and dispersing larvae over time. However, variation in recruitment intensity indicates that most of the recruits to a site may come from a primary source: locally retained larval populations for leeward reefs, and dispersing larval populations for windward reefs. Given the high rate of settlement on leeward reefs (>70% of the annual recruitment to St Croix), these findings suggest that a significant proportion of recruitment to St Croix results from the retention of locally produced larvae. While 'retention signatures' could occur in larvae produced on other islands that disperse quickly and spend the majority of larval development accumulating in coastal waters before settlement, we tested for such an effect by estimating the minimum number of days a larva would need to spend in coastal waters to produce the high otolith trace-metal concentrations observed in this study (see Methods: analysis of retention signatures). On the basis of these conservative estimates, a minimum of 50% of the recruits with retention signatures (positive CF1 scores) had spent their entire larval life in coastal waters.

The results we report here have implications for evaluating the efficacy of marine reserves, as reserve location may strongly determine the extent to which reserves can function to protect self-sustaining populations or enhance fisheries by supplying recruits to exploited populations. □

Methods

Larval growth rate and size

For all recruits ($n = 232$), we used standard length (SL in mm) and planktonic larval duration determined from otolith increment counts to calculate average somatic growth rates (mm d^{-1}). To remove post-settlement (PS) effects on growth, SL was regressed against PS age (number of increments after the settlement mark), and the residuals of the model were used in subsequent analyses (mean PS age (range): 3 (0–7) days).

Otolith trace-element analyses

On the basis of previous research[25,26] and the coastal water chemistry of St Croix[27], we chose the following elements for otolith analyses: manganese, copper, zinc, barium and lead. Both sagittal otoliths from each recruit were: (1) crushed and immersed for 72 h in a 5% NaOCl solution to remove organic contaminants, (2) rinsed three times at 80 °C in 18 MΩ water to remove residual NaOCl, (3) transferred to acid-leached vials and (4) dissolved to ~1 mM Ca to reduce matrix suppression effects. We measured element concentrations on a VG Plasma Quad 2+ Inductively-coupled plasma mass spectrometer using a combination of internal standardization and external calibration techniques. Measurement error was <5% relative standard deviation for all elements. We standardized concentrations to molar calcium concentration to remove the effects of variable sample loss during sample cleaning. Since differences in otolith elemental signatures between larvae developing in water masses with different trace-element concentrations could be confounded by somatic growth rate (or temperature)[28], otolith precipitation rate[29], or post-settlement otolith growth, we tested for such effects on otolith elemental composition of bluehead wrasse recruits. Results of multiple analysis of covariance (MANCOVA) and subsequent univariate analysis of covariance (ANCOVA) tests for the five trace elements analysed produced nonsignificant effects ($p > 0.05$) for all three covariates.

Canonical discriminant analysis

We used canonical discriminant analysis (CDA) to determine which dependent variables in the multiple analysis of variance (MANOVA) model were most important for separating groups. For our model, months were maximally separated by weighting more heavily the otolith concentrations of barium, manganese, copper and lead, and both growth rate and standard length of each larva in the calculation of the canonical factors. In addition, these variables (Ba, Mn, Cu, Pb, GR and SL) were all positively correlated with canonical factor 1 (which explained 53% of the between-group variance), indicating that differences between months were consistent for all variables. That is, larvae with elevated otolith trace-element concentrations were also larger and grew faster. Additional complexity in the differences among recruitment periods was revealed by CF2 (which explained an additional 31% of the between-group variance). Along this axis, recruits showed strong differences in barium concentrations among months. This probably reflects the temporal cycling of barium which has a nutrient-type distribution[14]. Measurements of the monthly average barium concentration in sea water around St Croix in 1997 (S.E.S., unpublished data) show a strong correlation with CF2 ($r = 0.974$),

suggesting that the additional complexity in the data captured in CF2 reflects this temporal variability in barium.

Analysis of retention signatures

We estimated the minimum number of days a larva must spend in coastal waters in order to recruit with a retention signature. This calculation was based on the following: (1) A maximum 3-fold difference in seawater lead concentration between St Croix coastal and oceanic waters measured in 1997 and a Pb/Ca = 0.8 μmol mol^{-1} concentration ratio in otoliths of reef fish larvae collected from oceanic waters in 1997 (S.E.S., unpublished data) as well as in otoliths from bluehead wrasse recruits with dispersal signatures collected in 1992, and (2) the assumption that trace elements are incorporated into otoliths in proportion to seawater concentrations. First, we calculated the percentage of the total otolith mass contained within each day of growth for a larva that spent 45 days in the plankton (average age at settlement for a bluehead wrasse larva). For each day spent in oceanic waters, the fraction of the otolith that grew incorporated 0.8 μmol Pb per mol Ca. For each day spent in coastal water, the fraction of the otolith that grew incorporated 2.4 μmol Pb per mol Ca. Assuming that days spent in oceanic waters occur before movement into coastal waters, we then calculated lead concentrations for larvae which spent zero days up to 45 days in coastal waters (the whole larval life). Finally, we compared the distribution of predicted lead concentrations to the distribution of observed lead concentrations. On the basis of this comparison, during the high summer recruitment pulses to leeward reefs, more than 50% of the larvae with retention signatures spent their entire larval duration in coastal waters.

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1. Hjort, J. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer* **20,** 1–228 (1914).
2. Doherty, P. J. & Williams, D. McB. The replenishment of coral reef fish populations. *Oceanogr. Mar. Biol. Annu. Rev.* **26,** 487–551 (1988).
3. Sale, P. F. in *The Ecology of Fishes on Coral Reefs* (ed. Sale, P. F.) 564–598 (Academic, San Diego, 1991).
4. Caley, M. J. *et al.* Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* **27,** 477–500 (1996).
5. Roughgarden, J., Iwasa, Y. & Baxter, C. Demographic theory for an open marine population with space-limited recruitment. *Ecology* **66,** 54–67 (1985).
6. Warner, R. R. & Hughes, T. P. in *Proc. 6th Int. Coral Reef Symp.* (eds Choat, J. H. *et al.*) Vol. 1 149–155 (Coral Reef Symposium Executive Committee, Townsville, 1988).
7. Sammarco, P. W. & Andrews, J. C. Localized dispersal and recruitment in Great Barrier Reef corals: the helix experiment. *Science* **239,** 1422–1424 (1988).
8. Wolanski, E. & Hamner, W. Topographically-controlled fronts in the ocean, and their influence on the distribution of organisms. *Science* **241,** 177–181 (1988).
9. Neilson, J. D. & Perry, R. I. Diel vertical migrations of marine fishes: an obligate or facultative process? *Adv. Mar. Biol.* **26,** 115–168 (1990).
10. Stobutzki, I. C. & Bellwood, D. R. Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Mar. Ecol. Prog. Ser.* **149,** 35–41 (1997).
11. Denman, K. L. & Powell, T. M. Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanogr. Mar. Biol. Annu. Rev.* **22,** 125–168 (1984).
12. Heywood, J., Barton, E. D. & Simpson, J. H. The effects of flow disturbance by an oceanic island. *J. Mar. Res.* **48,** 55–73 (1990).
13. Rissik, D., Suthers, I. M. & Taggart, C. T. Enhanced zooplankton abundance in the lee of an isolated reef in the south Coral Sea: the role of flow disturbance. *J. Plankton Res.* **19,** 1347–1368 (1997).
14. Bruland, K. W. in *Chemical Oceanography* Vol. 8 (eds Riley, J. P. & Chester, R.) 157–220 (Academic, San Diego, 1983).
15. Campana, S. E. & Neilson, J. D. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.* **42,** 1014–1032 (1985).
16. Mugiya, Y., Hakomori, T. & Hatsutori, K. Trace metal incorporation into otoliths and scales in the goldfish, *Carassius auratus*. *Comp. Biochem. Physiol. C* **99,** 327–331 (1991).
17. Campana, S. E., Gagné, J. A. & McLaren, J. W. Elemental fingerprinting of fish otoliths using ID-ICPMS. *Mar. Ecol. Prog. Ser.* **122,** 115–120 (1995).
18. Gillanders, B. M. & Kingsford, M. J. Elements in otoliths may elucidate the contribution of estuarine recruitment to sustaining coastal reef populations of a temperate reef fish. *Mar. Ecol. Prog. Ser.* **141,** 13–20 (1996).
19. Thorrold, S. R., Jones, C. M. & Campana, S. E. Response of otolith microchemistry to environmental variations experienced by larval and juvenile Atlantic croaker (*Micropogonias undulatus*). *Limnol. Oceanogr.* **42,** 102–111 (1997).
20. Caselle, J. E. & Warner, R. R. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* **77,** 2488–2504 (1996).
21. Gordon, A. L. Circulation of the Caribbean Sea. *J. Geophys. Res.* **72,** 6207–6223 (1967).
22. Corredor, J. E., Morell, J. & Mendez, A. Dissolved nitrogen, phytoplankton biomass and island mass effects in the northeastern Caribbean Sea. *Carib. J. Sci.* **20,** 129–132 (1984).
23. Boehlert, G. W., Watson, W. & Sun, L. C. Horizontal and vertical distributions of larval fishes around an isolated oceanic island in the tropical Pacific. *Deep-Sea Res.* **39,** 439–466 (1992).
24. Cowen, R. K. & Castro, L. R. Relation of coral reef fish larval distributions to island scale circulation around Barbados, West Indies. *Bull. Mar. Sci.* **54,** 228–244 (1994).
25. Shen, G. T. & Boyle, E. A. Determination of lead, cadmium, and other trace metals in annually-banded corals. *Chem. Geol.* **67,** 47–62 (1988).
26. Lea, D. W., Shen, G. T. & Boyle, E. A. Coralline barium records temporal variability in equatorial Pacific upwelling. *Nature* **340,** 373–376 (1989).
27. U.S. Environmental Protection Agency *U.S. Virgin Islands Ambient Monitoring Survey Sept. 15–23, 1992* (Environ. Services Div. Region 2, Edison, NJ, 1995).
28. Hoff, G. R. & Fuiman, L. A. Morphometry and composition of red drum otoliths: changes associated with temperature, somatic growth rate, and age. *Comp. Biochem. Physiol. A* **106,** 209–219 (1993).
29. Morse, J. W. & Bender, M. L. Partition coefficients in calcite: examination of factors influencing the validity of experimental results and their application to natural systems. *Chem. Geol.* **82,** 265–277 (1990).
30. Overall, J. E. & Klett, C. J. *Applied Multivariate Analysis* (McGraw-Hill, New York, 1972).

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Self-recruitment in a coral reef fish population

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The question of how far the larvae of marine organisms disperse is fundamental to an understanding of their population dynamics[1–3], the management of exploited species[4,5] and the conservation of marine biodiversity[6,7]. It is generally assumed that larvae disperse away from their natal population so that local populations operate as 'open' systems, driven by recruitment of larvae from other sub-populations[8]. However, this assumption has never been critically tested. Here we show for the first time that juveniles from a coral reef fish population can return to their natal reef. We marked otoliths (ear bones) of over 10 million developing embryos of the damselfish, *Pomacentrus amboinensis*, at Lizard Island (Great Barrier Reef). Subsequently, from an examination of 5,000 juveniles settling at the same location, we found 15 marked individuals. On the basis of an estimate of the proportion of embryos marked (0.5–2%), as many as 15–60% of juveniles may be returning to their natal population (self-recruitment). We challenge the assumption that long-distance dispersal is the norm for reef fish populations.

The majority of marine organisms (~70%) have a so-called 'dispersive' planktonic larval stage in their early life history before recruiting into adult habitat[9]. However, just how far these juveniles normally travel from their natal area is an unanswered question in marine biology[10,11]. The potential for dispersal by ocean currents is so great that self-recruitment within local populations has been considered extremely unlikely. However, over the last few years information has been accumulating that suggests a degree of self-recruitment. This includes the unexpected genetic subdivision of some marine populations[12,13], the persistence of endemic species with pelagic larvae on small isolated islands[14], the persistence of new populations established from marine introductions[15], the persistence of populations with no upcurrent source[16] and new information on the behaviour of larvae in the vicinity of reefs[17–19]. However, none of this information can provide direct and irrefutable evidence for the existence and importance of self-recruitment as a mechanism for population maintenance. Here we test for the first time whether any juveniles of a marine fish species return to their parent population, if they do, we assess the proportion of the population that is self-recruiting.

The only way to unequivocally answer these questions is to mark larvae so that they can be traced from their origin to their ultimate destination. Mark/recapture techniques to assess larval dispersal have not been attempted in the marine environment. We developed a technique of marking the otoliths of developing embryos of the small coral reef damselfish, *Pomacentrus amboinensis*, a common species on the northern Great Barrier Reef. It allows them to be marked en masse in their natural habitat, and to hatch and disperse