Ice templates. (Left) Nacre-like layers after removal of ice dendrites from solidification of alumina suspension in water. [Adapted from (*12*)] **(Center)** Starburst voids after removal of naphthalene dendrites from solidification of alumina suspension in camphor-naphthalene, which do not provide a template for tough composites. **(Right)** Branching voids after removal of camphor dendrites from solidification of alumina suspension in camphor-naphthalene.

fibrous laminates (*11*) that were in fact much tougher ceramics. However, these were tedious to manufacture and limited in the suite of materials. On page 515 of this issue, Deville *et al.* report a better route, using simple freezing (*12*).

Deville *et al.* have shown how to replicate the nacre structure of shells using controlled freezing of mixtures of water and ceramic powder. The composites made by this route have remarkably improved mechanical properties. The researchers achieve this by combining conventional manufacturing approaches that are already part of the engineering toolkit. These are as follows: (i) fine powder processing, the mainstay of the ceramic industry; (ii) controlled solidification, the core capability for metal casting and the frozen-food industry; and (iii) freeze-drying, a routine technique in the chemical, food, and coffee industries. Their nacre-like composites start with a lamellar template assembled by ice crystals. Water freezes as lamellar dendrites (*13*), and the ice dendrites push the ceramic particles into the interdendritic regions, making layers on the same scale as the ice. After the ice is removed by freeze-drying, the ceramic keeps the shape of the interdendritic layers, forming a template for subsequent injection of tough metal or polymer. The choice of water is clever, as the lamellar ice dendrites make an excellent template for nacre (see the figure, left panel). Other media are not useful templates, forming starburst dendrites as with naphthalene (see the figure, middle panel) or branched dendrites as with camphor (see the figure, right panel).

The technology for controlling dendrites is commonly used in applications ranging from the improvement of exotic jet-engine alloys to creating a tastier texture in frozen desserts. With the scale and arrangement of dendrites determined by well-known physics, and pattern formation well understood, there are many opportunities to build on the ideas of templating composites with ice. The methods of Deville *et al.* promise a flexible strategy for combining what people can do in factories with design concepts inspired by biology.

References
1. A. A. Griffith, *Philos. Trans. R. Acad.* **A221**, 163 (1920).
2. B. Lawn, *Fracture of Brittle Solids* (Cambridge Univ. Press, Cambridge, UK, 1993).
3. D. Green, *An Introduction to the Mechanical Properties of Ceramics* (Cambridge Univ. Press, Cambridge, UK, 1998).
4. R. C. Garvie, R. H. Hannick, R. T. Pascoe, *Nature* **258**, 703 (1975).
5. A. H. Heuer, *J. Am. Ceram. Soc.* **70**, 689 (1987).
6. J. D. Curry, A. J. Kohn, *J. Mater. Sci.* **11**, 1615 (1976).
7. S. Kamat, X. Su, R. Ballarini, A. H.Heuer, *Nature* **405**, 1036 (2000).
8. G. Meyer, *Science* **310**, 1144 (2005).
9. Z. Tang, N. A. Kotov, S. Magonov, B. Ozturk, *Nat. Mater.* **2**, 413 (2003).
10. K. Kendall, N. M. Alford, J. D. Clegg, J. D. Birchall, *Nature* **339**, 130 (1989).
11. D. Kovar, B. H. King, R. W. Trice, J. W. Halloran, *J. Am. Ceram. Soc.* **80**, 2471 (1997).
12. S. Deville, E. Saiz, R. K. Nalla, A. P. Tomsia, *Science* **311**, 515 (2006).
13. S. W. Sofie, F. Dogan, *J. Am. Ceram. Soc.* **84**, 1459 (2001).

ECOLOGY

Staying Connected in a Turbulent World

The swimming behavior of fish larvae limits their dispersal among coral reef populations more than previously thought. This stands to affect the design of protected marine ecosystems.

Robert S. Steneck

Globally, coral reefs are endangered ecosystems that continually frustrate marine resource managers and policymakers charged with their protection and restoration. Sadly, we know much more about the frequency, intensity, and scale of coral reef degradation (*1*) than we do about the processes that drive their recovery (*2*). This is most noticeable among Caribbean coral reefs that have particularly low resilience in both resisting phase shifts to degraded states (*3*) and, once

degraded, in returning to their previous state (*4*). A study by Cowen *et al.* on page 522 in this issue (*5*) offers new insights into the spatial scale and rate of larval supply necessary to sustain Caribbean reef fish populations. Cowen *et al.* improved on past population "connectivity" models by developing a coupled biological-physical approach that integrates factors such as the duration of development and swimming behavior of larvae, together with a well-validated model of ocean currents. They determined that connectivity, or the nexuses among disjunct populations of reef fish, is more local and regionally more variable than previously thought. These simple but profound results

influence the scale at which coral reefs should be managed and identify regions that will likely be more resilient or more vulnerable to the effects of fishing. The results scale up to regional (ocean-basin scale) considerations of biogeography, genetic isolation, and invasions of nonnative species that apply to fish and potentially to other reef-dwelling organisms, including corals.
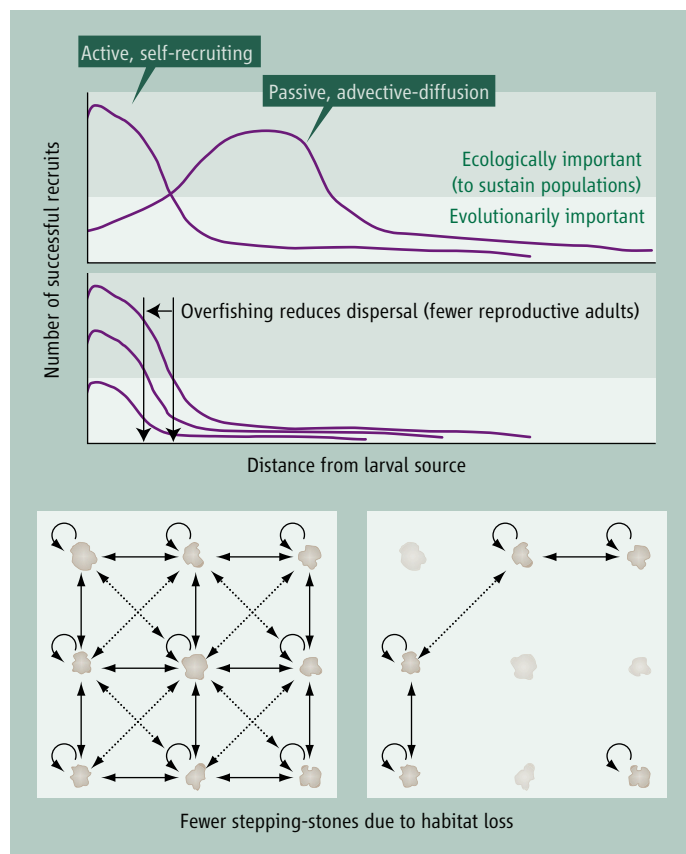
The model developed by Cowen *et al.* improves upon the work of Roberts (*6*), a highly influential paper on connectivity and the management of Caribbean coral reefs, that considered primarily passive transport of fish larvae via ocean currents in order to estimate

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the maximum range of larval connectivity among coral reefs. Roberts viewed many populations of marine organisms as being relatively open with substantial subsidies from distant upstream populations. In contrast, Cowen *et al.* have determined that larval transport via passive-diffusion cannot sustain reef fish at current levels unless there is substantial self-recruitment that results from the behavior of fish larvae themselves. The more realistic connectivity model of Cowen *et al.* provides the first robust estimates of the distance larvae will probably travel to successfully recruit to a specific reef [called the dispersal kernel (see the figure)]. Because a large portion of the larvae are recruiting at or near the reef where their eggs were hatched (that is, "self-recruiting" to the reef of larval origin) and because larval mortality will diminish the number of surviving larvae with time and distance from the larval source (7), the dispersal kernel will usually be greatest near the region where eggs were hatched and decline with distance. Conversely,

passive advective-diffusion models will result in larvae being transported, and thus their kernel dispersed, some distance away from their places of origin. The Cowen *et al.* model operates at several spatial scales and identifies distinct subregions within the Caribbean that have different levels of larval subsidies and self-recruitment. The finding that larval subsidies are very limited in some regions suggests that marine resource managers must directly manage their reefs on a local scale and not depend on substantial larval subsidies from distant upstream sources.

Another advantage of the Cowen *et al.* biological-physical model over past contributions is the specific spatial and organismal precautionary advice provided for marine resource managers. The authors determine that subsidies are more likely in some Caribbean regions such as the Bahamas than in others such as the Windward Islands and Mexico's Caribbean Yucatan coast, because many of the reefs in the latter regions

can, in turn, reduce larval abundance and thus shrink the dispersal kernel and effective connectivity distance (see the figure).

Although Cowen *et al.* focus on several common groups of reef fish with different larval durations and swimming behaviors, their conclusions apply to most occupants of coral reef ecosystems. Understanding what drives connectivity in these diverse ecosystems helps us to understand their resilience. For example, in recent decades, reefs suffered widespread coral mortality owing to diseases and thermally induced bleaching (1). However, recovery may be limited by the generally short dispersal kernels of most corals owing to their brief period of larval development while planktonic (12). Because some corals provide essential habitat for some reef fish (13), limited connectivity among corals may limit the recovery of dependent species of reef fish.

Reef management should integrate this new understanding of the geography of resilience. The Cowen *et al.* model predicts that some reefs might be more susceptible to the effects of overfishing than others elsewhere in the Caribbean. Similarly, different reef-dwelling organisms such as corals, fish, and lobsters have vastly different larval durations [that is, short (few days to weeks), medium (months), to very long (a year or more), respectively], which add to the challenge of managing these diverse ecosystems.

The growing movement toward ecosystem-based management (3, 14) and for networks of unfished or "no-take" fish reserves requires that they be spaced for connectivity. The approach illustrated by Cowen *et al.* should be broadly applicable because the inputs to their models—larval duration and behavior and the physical oceanography—apply to most organisms in most marine ecosystems. Finally, as these authors point out, their model suggests testable hypotheses with specific predictions that will allow the science of ecosystem-based management to move forward adaptively (2).

are beyond the dispersal kernel emanating from adjacent reefs. In effect, the discontinuous distribution of coral reefs provides a network of "stepping-stones" if reefs fall within the dispersal kernel of adjacent reefs (see the figure). However, as reef habitat and its associated reproductive fish populations decline (3, 8, 9), the distances between stepping-stones may increase to the point where they exceed the larval dispersal kernel, causing connectivity to decline (9).

The natural-history characteristics of fish species are also critical to their sustainability in a world increasingly influenced by human activities. Whereas short-lived fish may require regular recruitment to sustain their populations, longer lived species persist with periodic pulsed recruitment events. However, fishing pressure on reefs reduces both the population density and body size of harvested species (10, 11), which

Sustaining Caribbean reef fish populations. Shrinking larval dispersal kernels and connectivity due to (**top graphs**) increased proportion of self-recruiting larvae and declining abundance of reproductive populations, and (**bottom graphs**) diminished abundance of stepping-stones within the dispersal region for larvae. Horizontal shading in top graphs represent the ecologically important number of larval recruits necessary to sustain fish populations demographically, whereas the lower, unshaded portions represent the evolutionarily important number of larvae necessary to connect populations genetically. Arrowed lines in bottom denote connectivity among populations within or between adjacent reefs. Dotted arrowed lines represent limited or sporadic connectivity. [Modified from (9), copyright 2005, with permission from Elsevier]

References
1. J. Pandolfi *et al.*, *Science* **307**, 1725 (2005).
2. P. F. Sale *et al.*, *Trends Ecol. Evol.* **20**, 74 (2005).
3. D.R. Bellwood *et al.*, *Nature* **429**, 827 (2004).
4. J. C. Connell, *Coral Reefs* **16**, S101 (1997).
5. R. K. Cowen, C. B. Paris, A. Srinivasan, *Science* **311**, 522 (2006); published online 15 December 2005 (10.1126/science.1122039).
6. C. M. Roberts, *Science* **278**, 1454 (1997).
7. R. K. Cowen *et al.*, *Science* **287**, 857 (2000).
8. T. A. Gardner *et al.*, *Science* **301**, 958 (2003).
9. T. P. Hughes *et al.*, *Trends Ecol. Evol.* **20**, 380 (2005).
10. N. V. C. Polunin, C. M. Roberts, *Mar. Ecol. Prog. Ser.* **1000**, 167 (1993).
11. C. Birkeland, P. K. Dayton, *Trends Ecol. Evol.* **20**, 356 (2005).
12. P. W. Sammarco, J. C. Andrews *Science* **239**, 1422 (1988).
13. G. P. Jones *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **101**, 8251 (2004).
14. E. K. Pikitch *et al.*, *Science* **305**, 346 (2004).