Small-scale field experiments accurately scale up to predict density dependence in reef fish populations at large scales

Mark A. Steele*†‡ and Graham E. Forrester†§

*Marine Science Institute, University of California, Santa Barbara, CA 93106; and §Department of Natural Resources Science, University of Rhode Island, Kingston, RI 02881

Field experiments provide rigorous tests of ecological hypotheses but are usually limited to small spatial scales. It is thus unclear whether these findings extrapolate to larger scales relevant to conservation and management. We show that the results of experiments detecting density-dependent mortality of reef fish on small habitat patches scale up to have similar effects on much larger entire reefs that are the size of small marine reserves and approach the scale at which some reef fisheries operate. We suggest that accurate scaling is due to the type of species inter-action causing local density dependence and the fact that localized events can be aggregated to describe larger-scale interactions with minimal distortion. Careful extrapolation from small-scale experi-ments identifying species interactions and their effects should improve our ability to predict the outcomes of alternative man-agement strategies for coral reef fishes and their habitats.

spatial scaling

F ield experiments provide direct and compelling tests of ecological hypotheses and yield important insights into the nature of species interactions. Despite their scientific rigor, logistics typically constrain field experiments to plots no more than a few square meters in area (1, 2). Conservation and resource management generally occur in areas that are orders of magnitude larger than most experimental plots, so it is vital to determine whether the results of field experiments apply at larger spatial domains. Using small-scale field experiments, we tested empirically whether density dependence detected in reef fishes scales up to exert similar effects over larger areas. We chose to study this topic because density-dependent feedback in population growth determines the long-term stability of popu-lations and their response to exogenous perturbations (3). Defining the dynamical effects of density dependence and identifying its underlying biological causes are, therefore, of both theoretical and practical importance.

Manipulations of population density provide the most direct, rigorous, tests for density dependence. Coral reef fishes are excellent subjects for these tests because they are easily observed and manipulated *in situ*. Density manipulations often reveal strong density-dependent mortality of reef fishes, usually of recently settled juveniles (settlement occurs when planktonic larvae take up permanent residence on a reef) (4, 5). Recent cross-factored manipulations of both population density and putative biological causes of density dependence are particularly informative and have successfully identified the competitive and predator–prey interactions responsible for density-dependent mortality (6–11). Despite their scientific rigor, these experi-ments have all been performed on tiny patches of habitat (<10 m^2 in area), so whether their results can inform decisions about conservation and fisheries management is questionable. We tested whether density-dependent mortality detected on small habitat patches scales up to have equivalent effects on entire reefs (thousands of m^2 in area). Extrapolating to entire reefs of this size is of practical interest because they match the size of

smaller marine sanctuaries and approach the scale at which reef fisheries operate.

We studied the bridled goby (*Coryphopterus glaucofraenum*), a small site-attached fish common throughout the wider Carib-bean. Bridled gobies occupy reefs where sand and coral are interspersed because they feed on invertebrates in the sand but seek refuge from larger predatory fishes in crevices at the base of rock and coral. Field experiments show that bridled gobies suffer strong density-dependent mortality on small habitat patches (12). Additional experiments show that this density dependence occurs because, as they become crowded, gobies experience a shortage of the crevices they use as refuges and so become increasingly susceptible to predation (7, 11). Many other reef fishes use structural features of reefs as refuges, and increased predation due to limited shelter may be a common source of density-dependent mortality in reef fishes (10, 11, 13).

Methods

Density Dependence on Entire Reefs. We performed a large-scale study of goby populations over 5 years (1998–2001 and 2003) on five entire reefs spread over 25 km on the Great Bahama Bank near Lee Stocking Island, Bahamas (Fig. 2, which is published as supporting information on the PNAS web site). Each reef contained 3,000–15,000 m^2 of habitat suitable for gobies, a mix of stony corals, gorgonians, sponges, limestone rock, and sand. As is true of most reef fishes, larval gobies settle to reefs nightly throughout a long reproductive season (June through September for bridled gobies), and many die within days of arrival. Accurate estimates of settlement thus require daily monitoring of newly settled fish, which has been prohibitively time-consuming over large areas. To overcome this problem, we developed methods allowing us to monitor settlement throughout the reproductive season at our five sites (14). Further details of methods used to estimate settlement are in the *Supporting Text*, which is published as supporting information on the PNAS web site. To test for density dependence, we tested whether mortality of gobies settling during summer was related to the density of settlers averaged over the entire summer. The actual density experi-enced by settlers at a site depends on when during the summer they settle and how long they survive, but this index of density provides a simple time-averaged measure of the initial density of a year-class.

Estimating goby mortality after settlement was simplified by the isolation of the five reefs. Each was >100 m from any other suitable habitat and, because gobies do not move among reefs this isolated after settlement, we could infer that any goby disappearing from a reef had died. Mortality estimates also were facilitated by the gobies' short lifespan and the availability of

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preverified methods for aging this species. Gobies become reproductively mature roughly 3 months after settlement, at about 25 mm in length. Few adults survive from one summer to the next, and this species is effectively an annual. Therefore, we estimated mortality from the date of settlement until late October, the time when each generation reaches its peak adult abundance. Divers counted gobies on the reefs in late October and estimated their body lengths visually. Length estimates were converted to estimates of age, which were used to determine which of the fish present in October had settled during the preceding summer. Mortality was calculated by using the weekly summer counts of settlers and the October count of survivors, assuming that the probability of mortality after settlement was constant and identical for all settlers at a given site in a given year. Further details of methods used to estimate mortality are published in *Supporting Text*.

Because density dependence in bridled gobies is caused by a shortage of refuges, divers estimated the fraction of substratum covered by live and dead coral and small rocks, which, as we showed in ref. 11, is an index of the density of refuges. Further details of methods used to estimate refuge density are published in *Supporting Text*.

Density Dependence on Small Habitat Patches. We also compared the strength of spatially density-dependent mortality on entire reefs to the strength of spatial density dependence measured on small habitat patches. Four separate small-scale studies were used for this comparison. The first two studies were manipulations of goby density on small patch reefs near Guana Island, in the British Virgin Islands. Details of the first manipulation were published in ref. 12, and the second manipulation used nearly identical methods. The two remaining small-scale studies were done during summer and fall 1997 at two of our Bahamian reefs (Rainbow and Windsock). These studies were observational and tested for a correlation between settler density and mortality in the first week after settlement on small habitat patches. Further details of the methods used in the small-scale Bahamian studies are published in *Supporting Text*.

Results and Discussion

Accurate Scaling-Up of Spatial Density Dependence. We first tested for density dependence in space on entire reefs (mortality related to differences in density among sites), because past local-scale experiments on reef fishes all tested for spatial density dependence (4, 5). We used an analysis of covariance model that included terms for effects of settler density (a covariate), differences among years (a categorical factor), and the interaction between the two to test whether mortality was spatially density-dependent. The strength of density-dependent mortality, measured as the slope of the relationship between mortality and settler density, did not change appreciably among years ($F_{4,15} = 0.72$, $P = 0.59$). With this interaction term removed from the model, mortality was shown to differ significantly among years ($F_{1,15} = 4.3$, $P = 0.02$). Most notably, however, mortality on entire reefs increased progressively with settler density ($F_{1,19} = 63.9$, $P < 0.0001$), indicating that spatial density dependence in bridled gobies was detectable on entire reefs (Fig. 1A). Not only was spatial density dependence observable at small and large scales, its strength (measured as the slope of a linear regression relating population density to instantaneous per-capita mortality) was similar at small and large spatial scales. Regression slopes from our study of five entire Bahamian reefs fell within the range of slopes measured in four separate studies on small habitat patches, despite differences in scope and methods among the studies (Table 1).

Temporal Density Dependence on Entire Reefs. We also tested for density dependence over time (mortality related to differences
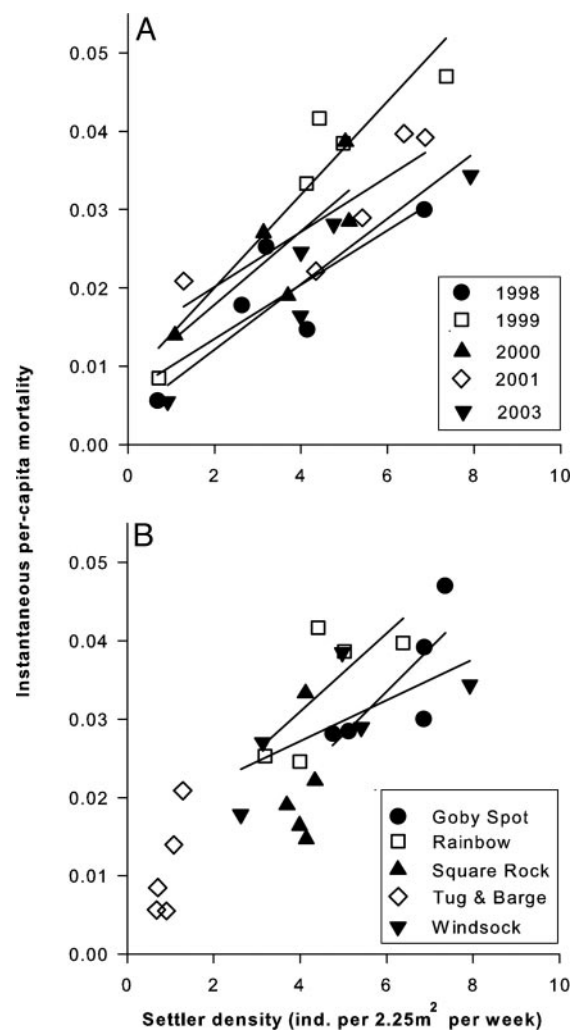
Fig. 1. Density-dependent mortality of bridled gobies on entire reefs. Data grouped by site reveal spatial density dependence (*A*), whereas data grouped by year show temporal density dependence (*B*). Regression lines are fit by using analysis of covariance and, in *B*, are omitted for two sites showing little interannual variation in settler density.

in density over time at a single reef). The distinction between spatial and temporal density dependence is important because one does not necessarily lead to the other, and only temporal density dependence can stabilize populations or facilitate their recovery from near extirpation (15). To test whether mortality was temporally density-dependent, we used an analysis of covariance model including terms for effects of settler density (a covariate) and differences among years (a categorical factor), and their interaction. Only the three reefs at which settlement varied appreciably among years (Goby Spot, Rainbow, and Windsock) were included in the analysis, although the results were qualitatively similar if the remaining two reefs were included. The slope of the relationship between mortality and settler density did not differ among reefs ($F_{2,6} = 0.61$, $P = 0.566$) and, after removal of this interaction term, there was no detectable variation in mortality among reefs ($F_{2,11} = 1.14$, $P = 0.354$). Bridled goby mortality was, however, higher in years when the density of settlers was highest ($F_{1,11} = 10.1$, $P = 0.009$) and so was temporally density-dependent (Fig. 1B).

Hypotheses for Accurate Scaling. Why does density dependence scale up in bridled gobies? Theoretical considerations suggest

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Table 1. The strength of spatially density-dependent mortality is similar at small and large spatial scales

Mean reef size, m²	Year	Location and type of study	Focal age group for mortality estimate	No. of reefs or patches	B (±SE)
Entire reefs					
6,200	1998	Bahamas, observational	Settlers to adults	5	0.0035 (±0.0013)
6,200	1999	Bahamas, observational	Settlers to adults	5	0.0060 (±0.0011)
6,200	2000	Bahamas, observational	Settlers to adults	5	0.0047 (±0.0019)
6,200	2001	Bahamas, observational	Settlers to adults	5	0.0035 (±0.0011)
6,200	2003	Bahamas, observational	Settlers to adults	5	0.0042 (±0.0009)
Small habitat patches					
8.4	1994	British Virgin Islands manipulation	Sub-adults and adults	16	0.0035 (±0.0010)
8.5	1995	British Virgin Islands, manipulation	Adults	8	0.0023 (±0.0005)
2.25	1997	Bahamas, observational	Settlers	10	0.0038 (±0.0059)
2.25	1997	Bahamas, observational	Settlers	5	0.0060 (±0.0098)

The strength of density dependence is measured as the slope (B) of a linear regression relating population density (mean number per 2.25 m²) to per-capita instantaneous mortality.

that density dependence should not scale up in situations where density dependence within small habitat patches interacts with spatial heterogeneity in density (16). Localized heterogeneity in fish density and habitat is obvious on coral reefs, and fish populations on entire reefs are well described as a collection of local patches. Distortion in density-dependent relationships will occur when aggregating the constituent local patches fails to describe the properties of the entire population (16). The degree of distortion, however, depends on the pattern of local heterogeneity in density, the functional form of the local relationship between density and mortality, and other details of demography at small scales. A simulation model tailored specifically to the demography of bridled gobies suggests that aggregation error should be minimal in this species and is thus in agreement with our empirical findings (17).

A second factor critical to the scaling of density dependence is its underlying cause at the local scale (18, 19). Local density dependence in bridled gobies is caused by a shortage of refuges from predation, and so the strength of density dependence at small scales is sensitive to changes in the local availability of refuges. The nature of refuge use in bridled gobies suggests that vulnerability to predation may be roughly approximated simply as the ratio of mean goby density to mean refuge density (11). We do not know whether density dependence has the same cause on entire reefs, but this is the most parsimonious explanation for our findings. Differences among reefs in our index of refuge density (15–33%; Table 2) were slight, compared with those needed to alter the strength of spatial density dependence on small habitat patches (1–58%, ref. 11). To test whether refuge density influenced the strength of spatial density dependence, terms for the effect of refuge density and all of its possible interactions were added to the original

analysis of covariance model. Although overall goby mortality was slightly higher on reefs where refuges were sparse, refuge availability did not appreciably alter the slope of spatial relationships between settler density and mortality ($P > 0.2$ for all interaction terms). Limited aggregation error and perhaps the relative homogeneity of refuge density among entire reefs may thus explain why density dependence in bridled goby mortality scaled up accurately.

Data on mortality at equivalent small and large spatial scales are available for only one other species of reef fish, the lemon damsel (*Pomacentrus moluccensis*). Small-scale experiments confirm that juvenile lemon damsels occupying small habitat patches suffer density-dependent mortality (13) within days of settlement (20). In contrast, a large-scale study on the lemon damsel showed that adult abundance on entire reefs increased in direct proportion to the prior density of older juveniles, indicating that mortality of older juveniles and adults was effectively density-independent (21). The large-scale study, although impressive and unparalleled in scope, was not designed to measure mortality in the first days or weeks after settlement, and therefore it cannot be used to ascertain whether density dependence detected in young juvenile lemon damsels scales up.

Implications for Conservation and Management. The fact that we can extrapolate from experiments on bridled gobies is encouraging because it suggests that small-scale manipulations may be used to inform fisheries management. Analyses of large-scale survey and catch data show that temporally density-dependent mortality is common in commercially harvested demersal (bottom-oriented) fishes but usually occurs only in small juveniles (22). Despite its importance for the stability of these populations under harvesting and other anthropogenic perturbations, we know little about the underlying interactions responsible for temporal density dependence at the juvenile stage. Although the bridled goby is not exploited by humans and is distinguished from many exploited species by its small adult size, limited home range, and short life cycle, there are hints that small juveniles of some harvested species are vulnerable to predators and use structural habitat features in ways reminiscent of bridled gobies (22, 23). Identifying the type of species interaction responsible for density dependence may help devise effective management strategies for specific stocks (24). Different strategies are suggested, for example, if density dependence among juveniles is caused by a shortage of habitat that provides shelter from predators than if it results

Table 2. Differences among five reefs in the availability of refuges for gobies

Reef	% hard substratum
Goby Spot	15.0 (7.0–23.0)
Rainbow	19.4 (14.1–24.6)
Square Rock	30.2 (21.8–38.5)
Tug and Barge	33.1 (18.9–47.1)
Windsock	21.0 (17.1–24.8)

Shown are means (with upper and lower 95% confidence intervals) of the percentage of the bottom covered by hard substratum (rock, coral, and rubble), which is an index of the density of refuges for gobies.

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from competition for food. Focused experimentation at local scales should allow us to better define the causes of density dependence in juveniles of harvested species, and our results illustrate that careful extrapolation of the results to larger spatial domains is possible.

Our results also demonstrate that density-dependent mortality occurs at spatial and temporal scales relevant to fisheries and marine reserves on coral reefs. No-take reserves are rapidly gaining favor as a tool for conservation and fisheries management. Fishing usually targets adults of larger species and so, once fishing is halted, adult populations of these species often build quickly within reserves (25). Long-term benefits to the fishery are anticipated once the offspring produced by these protected brood stocks begin subsidizing populations outside the reserve. The adults of many harvested species are generalist piscivores that prey on a variety of smaller fishes, and they are often the agents of density-dependent mortality in those smaller fishes. As adult populations of piscivores build within reserves, the increase in density-dependent predation that they inflict may fall partly on their own juveniles and so may offset some of the anticipated benefits of protection from harvesting. Increased density-dependent predation on unexploited species like bridled gobies also could have unexpected community-wide influences (26). More mechanistic studies on how fished and unfished species respond to building population densities are thus needed to evaluate the long-term success of marine reserves.

1. Wiens, J. A. (1989) *Funct. Ecol.* **3,** 383–397.
2. Kareiva, P. & Anderson, M. (1988) in *Community Ecology*, ed. Hastings, A. (Springer, Berlin), pp. 35–50.
3. Cappuccino, N. & Price, P. W. (1995) *Population Dynamics: New Approaches and Synthesis* (Academic, San Diego).
4. Hixon, M. A. & Webster, M. S. (2002) in *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*, ed. Sale, P. F. (Academic, San Diego), pp. 303–325.
5. Osenberg, C. W., St. Mary, C. M., Schmitt, R. J., Holbrook, S. J., Chesson, P. & Byrne, B. (2002) *Ecol. Lett.* **5,** 715–721.
6. Hixon, M. A. & Carr, M. H. (1997) *Science* **277,** 946–949.
7. Forrester, G. E. & Steele, M. A. (2000) *Ecology* **81,** 2416–2427.
8. Anderson, T. W. (2001) *Ecology* **82,** 245–257.
9. Carr, M. H., Anderson, T. M. & Hixon, M. A. (2002) *Proc. Natl. Acad. Sci. USA* **99,** 11241–11245.
10. Holbrook, S. J. & Schmitt, R. J. (2002) *Ecology* **83,** 2855–2868.
11. Forrester, G. E. & Steele, M. A. (2004) *Ecology* **85,** 1332–1342.
12. Forrester, G. E. (1995) *Oecologia* **103,** 275–282.
13. Beukers, J. S. & Jones, G. P. (1998) *Oecologia* **114,** 50–59.
14. Steele, M. A. & Forrester, G. E. (2002) *Ecology* **83,** 1076–1091.
15. Murdoch, W. W. (1994) *Ecology* **75,** 271–287.
16. Rastetter, E. B., King, A. W., Cosby, B. J., Hornberger, G. M., O'Neill, R. V. & Hobbie, J. E. (1992) *Ecol. Applic.* **2,** 55–70.
17. Forrester, G. E., Vance, R. R. & Steele, M. A. (2002) in *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*, ed. Sale, P. F. (Academic, San Diego), pp. 275–301.
18. Durrett, R. & Levin, S. (1994) *Theor. Popul. Biol.* **46,** 363–394.
19. Chesson, P. (1998) *Aust. J. Ecol.* **23,** 209–215.
20. Brunton, B. J. & Booth, D. J. (2003) *Oecologia* **137,** 377–384.
21. Doherty, P. J. & Fowler, A. J. (1994) *Science* **263,** 935–939.
22. Myers, R. A. & Cadigan N. G. (1993) *Can. J. Fish. Aquat. Sci.* **50,** 1576–1590.
23. Bailey, K. (1994) *Neth. J. Sea Res.* **32,** 175–189.
24. Mangel, M. & Levin, P. S. (2005) *Philos. Trans. R. Soc. London B* **360,** 95–105.
25. Halpern, B. S. & Warner, R. R. (2002) *Ecol. Lett.* **5,** 361–366.
26. Sanchez-Lizaso, J. L., Goni, R., Renones, O., Garcia-Charton, J. A., Galzin, R., Bayle, J. T., Sanchez-Jerez, P., Perez-Ruzafa, A. & Ramos, A. A. (2000) *Environ. Conserv.* **27,** 144–158.

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