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

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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 interaction 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 experiments identifying species interactions and their effects should improve our ability to predict the outcomes of alternative management strategies for coral reef fishes and their habitats.

Spatial scaling

Field 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 populations 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 experiments have all been performed on tiny patches of habitat (<10 m² 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 m² 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 Caribbean. 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 (1998–2003) 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 m² 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 experienced 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 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 extinction (13). 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 reefs (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
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 hetero-
geneity 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, com-
pared 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 de-
dsigned 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 encour-
aging 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
can 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

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

<table>
<thead>
<tr>
<th>Location and type of study</th>
<th>Focal age group for mortality estimate</th>
<th>No. of reefs or patches</th>
<th>$B$ ($\pm$ SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Entire reefs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6,200 (1998 Bahamas)</td>
<td>Settlers to adults</td>
<td>5</td>
<td>0.0035 ($\pm$ 0.0013)</td>
</tr>
<tr>
<td>6,200 (1999 Bahamas)</td>
<td>Settlers to adults</td>
<td>5</td>
<td>0.0060 ($\pm$ 0.0011)</td>
</tr>
<tr>
<td>6,200 (2000 Bahamas)</td>
<td>Settlers to adults</td>
<td>5</td>
<td>0.0047 ($\pm$ 0.0019)</td>
</tr>
<tr>
<td>6,200 (2001 Bahamas)</td>
<td>Settlers to adults</td>
<td>5</td>
<td>0.0035 ($\pm$ 0.0011)</td>
</tr>
<tr>
<td>6,200 (2003 Bahamas)</td>
<td>Settlers to adults</td>
<td>5</td>
<td>0.0042 ($\pm$ 0.0009)</td>
</tr>
<tr>
<td>Small habitat patches</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8.4 (1994 British Virgin Islands)</td>
<td>Sub-adults and adults</td>
<td>16</td>
<td>0.0035 ($\pm$ 0.0010)</td>
</tr>
<tr>
<td>8.5 (1995 British Virgin Islands)</td>
<td>Adults</td>
<td>8</td>
<td>0.0023 ($\pm$ 0.0005)</td>
</tr>
<tr>
<td>2.25 (1997 Bahamas)</td>
<td>Settlers</td>
<td>10</td>
<td>0.0038 ($\pm$ 0.0059)</td>
</tr>
<tr>
<td>2.25 (1997 Bahamas)</td>
<td>Settlers</td>
<td>5</td>
<td>0.0060 ($\pm$ 0.0098)</td>
</tr>
</tbody>
</table>

The strength of density dependence is measured as the slope ($B$) of a linear regression relating population density (mean number per 2.25 m$^2$) to per-capita instantaneous mortality.

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

<table>
<thead>
<tr>
<th>Reef</th>
<th>% hard substratum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goby Spot</td>
<td>15.0 (7.0–23.0)</td>
</tr>
<tr>
<td>Rainbow</td>
<td>19.4 (14.1–24.6)</td>
</tr>
<tr>
<td>Square Rock</td>
<td>30.2 (21.8–38.5)</td>
</tr>
<tr>
<td>Tug and Barge</td>
<td>33.1 (18.9–47.1)</td>
</tr>
<tr>
<td>Windsock</td>
<td>21.0 (17.1–24.8)</td>
</tr>
</tbody>
</table>

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.
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 occur 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. 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.

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