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Population regulation by post-settlement mortality in two temperate reef fishes

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Abstract Input of individuals dispersing into open populations can be highly variable, yet the consequences of such variation for subsequent population densities are not well understood. I explored the influence of variable input ("supply") on subsequent densities of juveniles and adults in open local populations of two temperate reef fishes, the bluebanded goby (*Lythrypnus dalli*) and the blackeye goby (*Coryphopterus nicholsii*). Variable recruitment was simulated by stocking a natural range of densities of young fishes on replicate patch reefs. Density and mortality of the stocked cohorts were followed over time, until the fishes reached maturity. Over the first day of the experiments, mortality of both species was significantly density-dependent; however, there was still a very strong relationship between density on day 1 and density on day 0 (i.e., simulated recruitment was still an excellent predictor of population density). At this point in the study, the main effects of density-dependent mortality were to reduce mean densities and variation about the mean. Over the period from the start of the experiments until the time when maturity was reached by each species (about 1 and 3 months for *Lythrypnus* and *Coryphopterus*, respectively), mortality was strongly density-dependent. Such strong density-dependent mortality virtually eliminated any linear relationship between adult density and "recruit" density. However, for both species, the relationship between these two variables was well fit by an asymptotic curve, with the asymptotic density of adults equal to *c.* 3/m^2 for *Coryphopterus*, and *c.* 10/m^2 for *Lythrypnus*. Natural recruitment (via settlement of larvae) to the reefs over the period of the study (9 months) was above the asymptotic densities of adults for the two species, even though the study did not encompass the periods of peak annual recruitment of either species. This suggests that adult populations of these two gobies may often be limited, and regulated, by post-settlement processes, rather than by input of settlers. Other studies have shown that mortality of the two species is density-independent, or only weakly density-dependent, on reefs from which predators have been excluded. Hence, it appears that predators cause density-dependent mortality in these fishes.

Key words Open populations · Density dependence · Population regulation · Recruitment limitation · Reef fishes

Introduction

The size of any population is set by the rates of input and loss of individuals. Input may come from births or immigration, and loss is caused by death and emigration. For many organisms with complex life cycles that include a widely dispersed stage and a more sedentary stage (i.e., many aquatic and terrestrial plants, many insects, most marine invertebrates, and most demersal marine fishes), input to local populations of the sedentary stage(s) comes mainly from immigration of the dispersive stage and not from local reproduction (Doherty and Williams 1988; Sale 1990). These sorts of local populations are considered to be "open" (*sensu* Caswell 1978). At some sufficiently large spatial scales, all organisms will have closed populations, but understanding the determinants of abundance at spatial scales where populations are open is particularly important because relevant environmental factors (e.g., habitat structure, density of predators and competitors) vary and influence populations at these scales (e.g., Holbrook et al. 1990; Levin 1993; Carr 1994; Robertson 1996; Connell 1996). Moreover, research programs are often logistically constrained to work at these smaller scales, and it is at these scales that populations commonly are managed.

For open populations, there is little consensus on the relative importance of input via the dispersive stage ver-

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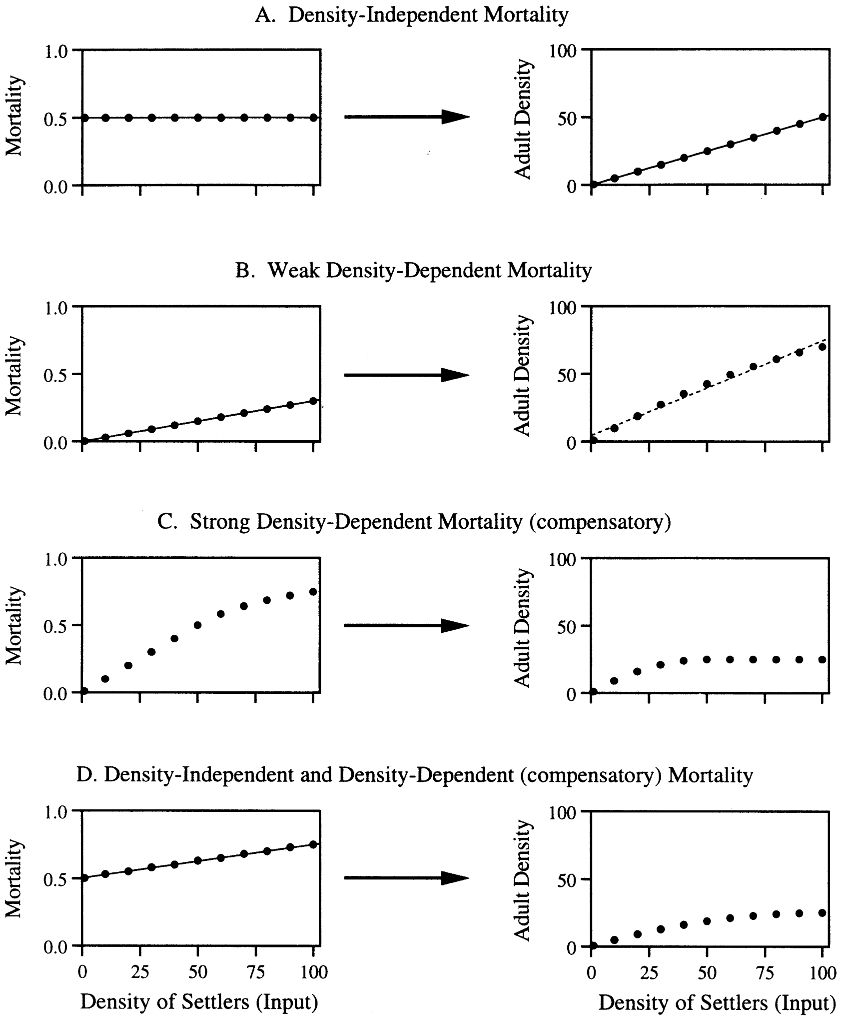

Fig. 1 **A–D** Effects of four different mortality regimes on the relationship between density of adults (or any later, sedentary stage) and density of settlers (input). The consequences of mortality in known cohorts of settlers are shown. In *left-hand panels,* mortality is per capita (=m). Adult density was calculated as the density of settlers (S)×(1 –m); values for mortality are shown in the *left-hand graphs*. The four cases illustrate **A** density-independent, constant (non-stochastic) mortality (m=0.5), **B** weak density-dependent, constant mortality (m=0.003×S), **C** compensatory density-dependent, constant mortality, and **D** both density-independent mortality and compensatory density-dependent mortality (m=0.5+0.0015×S). *Solid lines* indicate linear relationships between variables. To illustrate how difficult it would be to distinguish between a linear and a non-linear relationship between density of adults and density of settlers, the *broken line* in the *right-hand graph* in case **B** shows a linear fit to the non-linear relationship between adults and settlers

sus loss of sedentary individuals in setting patterns of population abundance. Input can vary tremendously in space and time (reviewed in Underwood and Denley 1984; Connell 1985; Doherty and Williams 1988; Mapstone and Fowler 1988; Underwood and Fairweather 1989; Sale 1990; Doherty 1991; Olafsson et al. 1994; Booth and Brosnan 1995), yet the consequences of such variation are not entirely clear. It has often been stated that variable input will be the main cause of variation in density among local populations when densities do not reach levels at which resources become limiting (e.g., Doherty 1983; Connell 1985; Victor 1986; Doherty and Williams 1988). This, however, is not necessarily true, because, even when resources are not limited, processes other than competition, e.g., predation, can cause density-dependent mortality (e.g., Holling 1959; Murdoch and Oaten 1975).

A lack of density dependence in the sedentary stage has been cited as a defining characteristic of a “recruitment-limited” (*sensu* Doherty 1981) system (Doherty 1983; Doherty and Williams 1988). Others (e.g., Victor 1986; Forrester 1990; Holm 1990; Caley et al. 1996) have noted that this requirement is too strict, because input (recruitment) will still limit (i.e., influence) population density when there is weak density-dependent mortality. Problems of interpretation have arisen when a strong linear relationship between population density and input is found (e.g., Sutherland 1990; Doherty and Fowler 1994a, b). This has rightly been interpreted as evidence of “recruitment limitation” (in the sense that input has been demonstrated to influence population density), but wrongly interpreted as demonstrating that post-dispersal mortality was density-independent. I illustrate this point with some simple simulations.

Figure 1A shows recruitment limitation in its purest sense: mortality is independent of input (density of settlers) and does not vary among populations; hence, there is a perfect linear relationship between density of adults produced from these settlers and density at settlement. However, weak density-dependent mortality will not eliminate a strong positive relationship between input and subsequent density of the cohort (Fig. 1B). Moreover, based on data from populations in nature, where there is virtually always some inherent variation (i.e., stochasticity), it is unlikely that a slightly non-linear, density-dependent, relationship between densities of adults and settlers (e.g., Fig. 1B) could be distinguished from a truly linear, density-independent, relationship (e.g., Fig. 1A). When there is weak density-dependent mortality, as in Fig. 1B, both input and subsequent mortality will play important roles in setting attributes of population density (Caley et al. 1996); specifically, both will influence mean densities and the range of variation about the mean. When density-dependent mortality is strong and compensatory (Fig. 1C and D), above a certain level, input will not influence population density. It has been argued that such high levels of input are rarely encountered in marine systems, so variation in input will almost always account for some of the variation in population density (Caley et al. 1996).

Most marine reef fishes live in open local populations, which receive input primarily via settlement of planktonic larvae (Doherty and Williams 1988). Although many studies have tested for density-dependent mortality in reef fishes (reviewed in Jones 1991; Booth and Brosnan 1995; Caley et al. 1996), only two recent studies have detected strong density-dependent mortality (Forrester 1995; Tupper and Boutilier 1995). The weight of the available evidence suggests that settlement in most reef fish populations is below a level that would induce compensatory mortality. Forrester (1995) suggested that the general failure to detect strong density-dependent mortality is a consequence of researchers conducting experimental tests over periods of time that are short relative to the life span of the test subjects (e.g., Doherty 1982, 1983; Jones 1987a, b, 1988; Forrester 1990; Booth 1995). He argued that experiments conducted on adults of short-lived species would be more likely to detect density-dependent effects on abundance. This assumes that density-dependent processes act most strongly on adults; yet mortality is often highest early in life (Victor 1986; Doherty and Sale 1985; Shulman and Ogden 1987; Booth 1991; Hixon 1991; Carr and Hixon 1995), so this period may be a likely time for density-dependent mortality to act – depending upon which processes induce any density dependence.

In this study, I manipulated densities of populations of young reef fishes to simulate variable input via recruitment of larvae and then followed the populations through time to adulthood. I tested for density-dependent mortality after different amounts of time had passed, to explore whether one life stage (juveniles or adults) was affected more strongly by density-dependent mortality. I also examined the extent to which variation in simulated recruitment predicted variation in juvenile and adult density, and the degree to which variation in simulated recruitment determined mean densities and the range of variability about the mean.

Materials and methods

Study system and natural history

I worked at Santa Catalina Island (33°27′N, 118°29′W; 33 km off the coast of southern California) with two fishes that are common residents of rocky reefs in southern California and northern Baja California (Miller and Lea 1976): *Lythrypnus dalli*, the bluebanded goby, and *Coryphopterus nicholsii*, the blackeye goby. *Lythrypnus* is a small [<50 mm standard length (SL)], brilliantly colored fish that can reach densities >100 individuals/m^2 in rocky, high-relief areas. While this species reaches its highest densities in areas with high relief (e.g., vertical rock walls), it is ubiquitous in all rocky areas at Santa Catalina Island. For shelter, *Lythrypnus* uses rocky crevices, as well as the spines of the sea urchin *Centrostephanus coronatus*. *Coryphopterus* is larger (up to 90 mm SL) and drab colored. It reaches its highest densities in areas where rocky reefs meet sand; on natural reefs, densities can approach 20 fish/m^2. *Coryphopterus* uses rocky crevices and undercuts for shelter. The majority of suitable habitat for both fishes is found on large (thousands of sqare meters), continuous rocky reefs, because small patch reefs are uncommon within the geographic range of the two species. However, wherever small isolated reefs (artificial or natural) are found, these two species are numerically dominant residents, which colonize these areas primarily by larval settlement (M. Steele, personal observations). On isolated 1-m^2 rock rubble reefs, both species can reach densities >60/m^2 via settlement of larvae (M. Steele, unpublished work).

Both gobies are primarily planktivorous, although *Coryphopterus* incorporates more benthic prey in its diet than does *Lythrypnus* (M. Steele, unpublished work). There does not appear to be any strong competition between the two species (Steele 1995). The two gobies vary greatly in their longevity: *Lythrypnus* is essentially an annual – most individuals perish within a year, and few, if any, live 2 years (Behrents 1983). *Coryphopterus* may live as long as 5 years (Wiley 1973). Based on size at maturity (*c.* 20 mm for *Lythrypnus*: Behrents 1983; St. Mary 1993; *c.* 45 mm for *Coryphopterus*: Wiley 1973) and known growth rates during summer and fall (Steele 1995), on average, *Lythrypnus* reach maturity within 1 month post-settlement, while *Coryphopterus* are mature within 2.5 months. Both species are territorial, although *Coryphopterus* much more so than *Lythrypnus* (Steele 1995). Males of both species guard demersal eggs laid in nests under rocks, in crevices, or in mollusk shells (Wiley 1973, 1976). After hatching, the larvae of both species spend 2–3 months in the plankton (M. Steele, unpublished work) before settling at 9–11 mm SL for *Lythrypnus* (Behrents 1987) and 15–29 mm SL for *Coryphopterus* (Wiley 1973; M. Steele, unpublished work). Settlement of *Coryphopterus* occurs, at low levels, year-round at Santa Catalina Island, with a peak in early summer (June–July) (M. Steele, personal observations). Settlement of *Lythrypnus* occurs late in May through January, peaking in July and August (Behrents 1987; M. Steele, personal observations). Larvae of both species settle to adult habitat and consume the same types of food as adults.

Predation, mainly by the serranid *Paralabrax clathratus*, which is the numerically dominant piscivore at Santa Catalina Island, plays an important role in determining the abundance of the gobies (Steele 1995, 1996, 1997). *Lythrypnus*, however, suffers greater risk of predation than *Coryphopterus* (M. Steele, unpublished work), probably by virtue of its smaller size, greater activity, and brighter coloration.

Methods

I initiated two experiments, on 26 and 27 August 1993, to test for density-dependent mortality in *Lythrypnus* and *Coryphopterus*, respectively. I used replicate 1-m^2 reefs constructed on the south side of Big Fisherman Cove, Santa Catalina Island, on a large expanse of sand at depths of 8–14 m (see Steele 1997, for further site description and a maps). Each replicate reef was separated from the next nearest reef by 10 m of bare sand. Sets of experimental reefs were separated from the only nearby natural reef by 20 m (*Coryphopterus* reefs) or 30 m (*Lythrypnus* reefs) of sand. With these distances separating reefs, successful emigration from experimental reefs to other experimental reefs or to the nearby natural reef, is rare (1.0 and 0.5% during 25-day-long experiments with *Lythrypnus* and *Coryphopterus*, respectively: Steele 1995). Hence, nearly every fish that disappears from a reef can reasonably be assumed to have died. In this study, I tested this assumption by making extensive searches for emigrants (which were marked) on other nearby reefs (experimental and natural).

I used a set of six replicate reefs to test for density-dependent mortality in *Coryphopterus* and a separate set of nine reefs for *Lythrypnus*. The sets of reefs were constructed in two rows parallel to one another and separated by 10 m of sand. For each species, a range of densities was stocked on the replicate reefs. Linear regressions of per capita mortality [=proportion of stocked fish that disappeared=(1 –number of fish remaining/number stocked)] on density stocked were used to test for density-dependent mortality. Because I was interested in positive density-dependent mortality as a mechanism for population regulation, I used one-tailed statistical tests, testing the null hypothesis that the slope of the relationship between mortality and density was ≤0. In these same regressions, I measured density-independent mortality as the *y*-intercept (see, e.g., Fig. 1D, where density-independent mortality=0.5). When the relationship between mortality and density is non-linear, the *y*-intercept may be a poor estimate of density-independent mortality, but, in this study, these relationships appeared to approximate a straight line quite well. To explore whether the extent to which mortality was density-dependent changed with time, I used regression analysis on mortality measured at different times after the experiments were initiated.

I used densities that fell within the range of densities encountered on natural reefs at Santa Catalina Island. Each reef was stocked with 5–67 *Lythrypnus*, and 1–15 *Coryphopterus*.. All of these fish were caught and handled in the same way, and for each species, all of the experimental reefs were stocked at the same time (within a *c.* 0.5-h period). In contrast to what is found in some other species (e.g., a damselfish: Jones 1990), after stocking over a thousand individuals of each goby species in various experiments, I have never observed a single case of spontaneous emigration at the time of reef stocking. To minimize differences in shelter availability, each reef was constructed of a standard size distribution of 64 rocks, 5–30 cm long, which were translocated from nearby natural reefs. The rocks were placed on a square of plastic mesh (19 mm mesh) to keep them from sinking into the sand bottom. I used *Lythrypnus* that were 13–22 mm SL and *Coryphopterus* that were 20–35 mm SL. Fish of this size have resided on reefs for <1 day to *c.* 40 days. Based on their size, a few of the larger *Lythrypnus* were probably mature, while none of the *Coryphopterus* were expected to be mature. The size distributions of fish stocked were similar among density levels and roughly average sized individuals were stocked on low density reefs. Since the species I worked with mature rapidly, I was able to follow cohorts that initially were mostly, or exclusively, composed of juveniles until they were composed entirely of adults. To help distinguish experimental fish from immigrants or larval recruits, every goby stocked on the reefs was given an acrylic paint tattoo on its anterior right dorsal surface (a batch mark). I initiated the experiments after the normal seasonal pulses of recruitment so that there would be few recruits to confuse with the stocked cohorts. As it turned out, this was fortunate because all of the gobies eventually lost their tattoos, some very rapidly (within a week in some cases). There was some natural recruitment during the periods over which I tested for density-dependent mortality (the first 37 days of the experiment for *Lythrypnus*, and the first 86 days for *Coryphopterus* – after these times I could no longer distinguish recruits from stocked fish). Had recruitment been intense and variable among density treatments during this period, my tests for density dependence could have been weakened because recruitment could have altered the patterns of density among treatments (i.e., high-density reefs could have become low-density reefs, relative to other reefs). This, in fact, did not occur: recruitment of both species was low and fairly even among reefs. At any census before maturity was reached (days 1–16 and 1–36 for *Lythrypnus* and *Coryphopterus*, respectively), the total density of the target species was significantly correlated with the density of stocked individuals remaining on the reefs (r>0.89, P<0.013, in every case).

Censuses were made nine times over the course of the experiments, fie times in the first 37 days, and four times thereafter, over 25- to 90-day intervals. After 9 months, all gobies present on the reefs were collected with hand-nets and quinaldine, an anesthetic. During each census, the number of tattooed fish, the number of recruits estimated to be less than 1 month old, and the total number of each species was recorded. Further, because it was obvious that the tattoos were fading, throughout the study I recorded the number of fish whose size or scars from the tattooing process indicated that they were part of the cohort originally stocked.

Results

Lythrypnus

Lythrypnus suffered density-dependent per capita mortality within one day after the start of the experiment (Table 1A). However, the relationship between mortality and density was much tighter (i.e., higher r^2) over the period from the start of the experiment until the time when sexual maturity was reached (day 37 – based both on expected growth rates and visually estimated sizes) (Table 1A, Fig. 2A). By this time, *Lythrypnus* on high density plots had suffered about twice as much mortality as fish on low density plots. Also, at this time, *c.* 46% of the *Lythrypnus* stocked had died of density-independent causes (density-independent mortality was measured as the *y*-intercept: Fig. 2A and Table 1A). Fish were not censused again until day 87, and by this time few marked fish remained (7 total). I suspect that more of the initial cohort remained but had lost their tattoos. Laboratory trials indicated that acrylic paint tattoos were usually lost within 3 months. From the day 87 census on, *Lythrypnus* that had lost their tattoos were no longer distinguishable by size from fish that had recruited shortly after the experiment was initiated, so I no longer tested for density-dependent mortality.

During the first 37 days, when the tattoos were still visible, searches for experimental fish that had successfully emigrated (meaning they left the reef they were

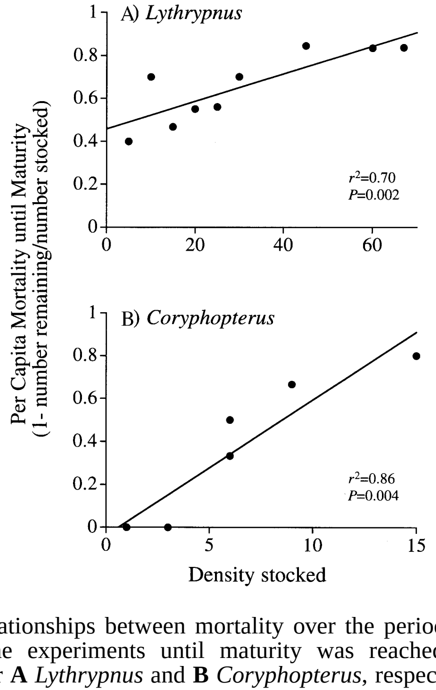

Fig. 2 Relationships between mortality over the period from the start of the experiments until maturity was reached (37 and 86 days for **A** *Lythrypnus* and **B** *Coryphopterus*, respectively) and initial density, for each species. Each *point* represents one reef

Table 1 Results of linear regression testing for density-dependent and density-independent mortality, with mortality measured at different times after the start of the two experiments

Days since start of experiment	Density-dependent		Density-independent		
	Slope of mortality vs. density (±1 SE)	*P* slope ≤	Density-independent mortality[a] (±1 SE)	*P* density-independent mortality ≤	r^2
A *Lythrypnus*					
1	0.006±0.0025	0.024	0.30±0.09	0.0075	0.45
4	0.006±0.0027	0.026	0.31±0.10	0.0085	0.44
10	0.003±0.0017	0.059	0.48±0.06	<0.0001	0.31
16	0.004±0.0017	0.024	0.47±0.06	0.0001	0.45
37[b]	0.006±0.0016	0.002	0.46±0.06	<0.0001	0.70
B *Coryphopterus*					
1–36[c]	0.038±0.010	0.010	–0.02±0.08	0.42	0.78
86[b]	0.063±0.013	0.004	–0.04±0.10	0.37	0.86

[a] Measured as the *y*-intercept of the linear relationship between mortality and initial density

[b] Beyond these dates, members of the cohorts initially stocked could no longer be distinguished from fish that recruited near the beginning of the experiments

[c] Densities of *Coryphopterus* did not change from day 1 to day 36

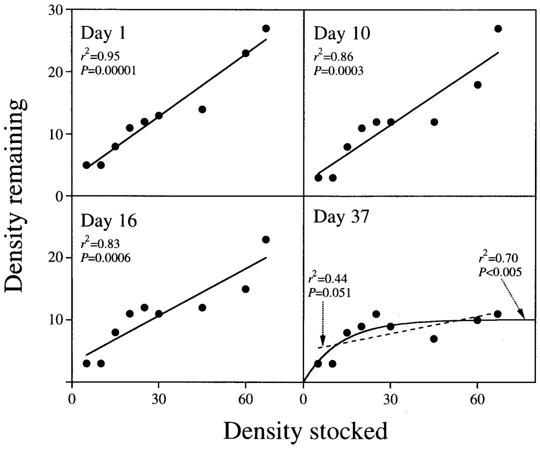

Fig. 3 Relationships between density of surviving *Lythrypnus* and initial density, at four different times after the start of the experiment. By day 37 all surviving fish were large enough to be sexually mature. Each *point* represents one reef

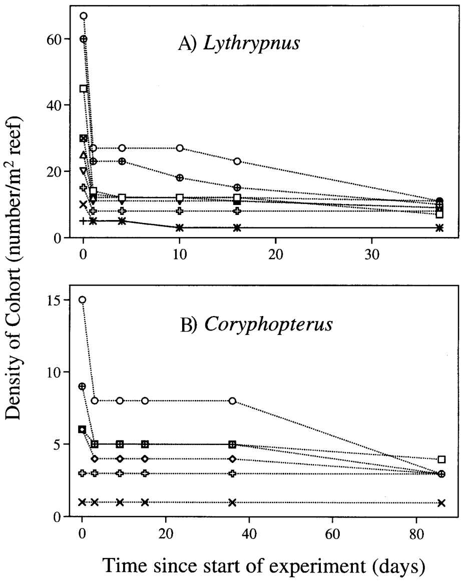

Fig. 4 **A, B** Changes in density of experimental cohorts of the two gobies over time. **A** shows changes in density of *Lythrypnus* on each of the 9 reefs over 37 days. **B** shows changes in density of *Coryphopterus* on each of the 6 reefs over 86 days. By the end of these two periods, based on their estimated sizes, all individuals were mature

stocked on and survived to make it to another reef) turned up no migrants. These searches were made on nearby experimental reefs (i.e., the "*Coryphopterus* reefs" 10 m away) and the large natural reef 30 m away. However, movement among reefs stocked with *Lythrypnus* could not be detected (except as an increase in numbers above what was stocked on a reef – which was never observed) since reef-specific tattoos were not given.

Over time, density-dependent mortality weakened the relationship between the density of *Lythrypnus* remaining on reefs and the initial "recruit" density (Fig. 3) and decreased the absolute and relative variation among reefs (Fig. 4A; CV on days 0, 1, and 37: 71, 58, and 39%) by causing densities to converge (Figs. 3 and 4). Nevertheless, after 37 days, there still remained a marginally significant linear relationship between the densities remaining on the reefs and the initial "recruit" densities (r^2=0.44, P=0.051; Fig. 3). An asymptotic relationship, however, explained much more of the variance in adult density (r^2=0.70, P<0.005; Fig. 3). Densities reached an asymptote at about 10 *Lythrypnus*/m². Since density-independent mortality eliminated about 46% of the "recruits" before they reached maturity, at "recruit" densities above *c.* 19/m², adult densities were not limited by recruitment.

Even after densities of the stocked cohorts converged (day 37) the total density of *Lythrypnus* (stocked fish+recruits) varied greatly temporally and spatially (Fig. 5A). An unexpected huge pulse of recruits prior to the November census (day 87) caused densities to increase sharply (Fig. 5A). Recruitment during this pulse was spatially variable, hence the range of density nearly encompassed that stocked on the reefs at the outset of the experiment, except that density on every reef was above the asymptotic density of adults (10/m²), and only two

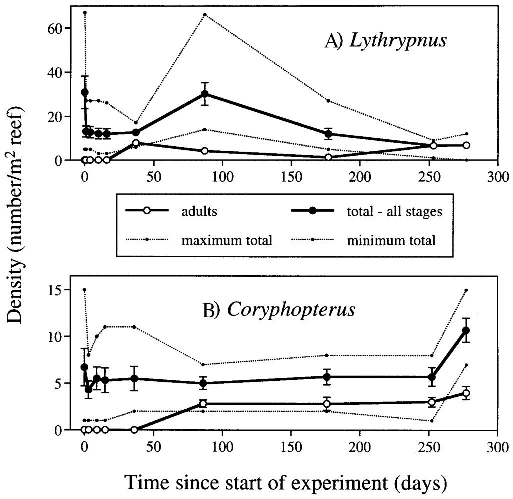

Fig. 5A, B Changes in density over the 9-month duration of the two experiments. Shown are the average densities (±1 SE) of adults (based on estimated sizes) and all stages combined; and the minimum and maximum densities on any reef at each census of all stages combined; n=9 and 6 reefs for **A** *Lythrypnus* and **B** *Coryphopterus*, respectively

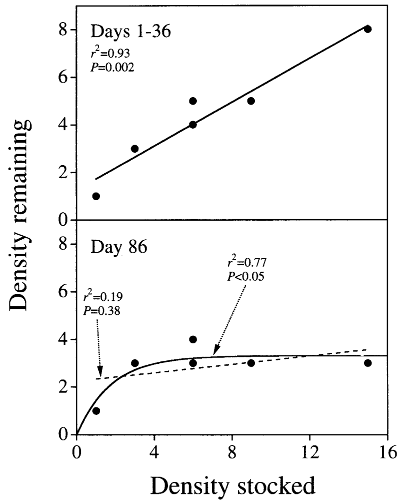

Fig. 6 Relationships between densities of surviving *Coryphopterus* and densities initially stocked. Based on their sizes, all stocked individuals had reached maturity by day 86. Each *point* represents one reef

reefs had densities lower than 20/m^2 (14 and 18/m^2). The density of *Lythrypnus* in November, after the pulse of recruitment, was a poor predictor of the density at the February census (90 days later): there was no relationship between the density on a reef in February and its density in November (linear regression, r^2=0.10, P=0.4, n=9). Either mortality or recruitment, or both, varied among reefs after the November census in a manner that destroyed the spatial pattern of abundance present in November, but I cannot distinguish between the two mechanisms. The per capita change in density over this period, however, was not significantly density-dependent {linear regression of per capita change in density [(density in February –density in November)/density in November]} on density in November: slope= –0.0078; r^2=0.18; P=0.26).

Over the 9 months of the experiment, recruitment averaged 26.1 recruits/reef (±3.8, SE), ranging from 12 to 50 recruits/reef. This measure of recruitment surely underestimates the actual numbers of settlers, since considerable mortality of newly settled fish likely occurred during the intervals between censuses. Nonetheless, recruitment was above the level required to produce the asymptotic density of adults (*c.* 19 recruits/reef) on all but two reefs (they had 12 and 17 recruits). At the end of the study, every *Lythrypnus* present on the reefs was mature – based on their sizes (they ranged from 24 to 41 mm). There was no relationship between the density of these adults and the total input to the reefs (the number of fish stocked+the number of recruits) over the 9 months of the study (linear regression, r^2=0.13, P=0.35, n=9). Likewise, on the reefs used in the experiment with *Coryphopterus*, which received an average of 16.8±2.8 *Lythrypnus* recruits (range 6–23), there was no relationship between the density of adult *Lythrypnus* at the end of the study (again, all *Lythrypnus* on these reefs were adults by this time) and recruitment over the 9 months of the study (r^2=0.15, P=0.45, n=6). At the end of the study, the maximum density of adult *Lythrypnus* on both sets of reefs was the same, 12/m^2 – very near the asymptotic density of adults in the experimental cohort (10/m^2).

Coryphopterus

Coryphopterus also experienced density-dependent mortality within a day after the start of the experiment (Table 1B). The numbers in these cohorts of fish did not change over the next 36 days, i.e., there was no mortality over this 35-day period. However, by day 86, the strength of the density-dependent mortality increased to the point where mortality of fish stocked at the highest densities was near 80%, while there was no mortality of fish at the two lowest densities (Fig. 2B). So, in contrast to *Lythrypnus*, there was no density-independent mortality of *Coryphopterus* (see y-intercept in Fig. 2B and Table 1B). But like *Lythrypnus*, I did not detect any cases of successful emigration by tattooed *Coryphopterus*. Moreover, since there was no density-independent mortality, migration from high- to low-density reefs would have been detectable as an increase in the density on low-density reefs to levels above that initially stocked: this was never observed.

Even though mortality was density-dependent near the start of the experiment (days 1–36; Table 1B), a strong relationship between survivor density and initial density existed during this period (Fig. 6). However, 86 days after the start of the experiment, no significant linear relationship remained between survivor density and initial density (r^2=0.19, P=0.38; Fig. 6), but an asymptotic relationship explained a significant proportion of the total variance (r^2=0.77, P<0.05; Fig. 6). Survivor density reached an asymptote at *c.* 3 *Coryphopterus*/m^2. As a consequence of the strong density-dependent mortality, densities converged by day 86 and variation among reefs decreased until this point (Fig. 4**b**; CV days 1–36 vs. day 87: 74 vs. 35%). Few of the surviving *Coryphopterus* were large enough to be mature 36 days after the experiment began, but by day 86 the 17 survivors were large enough to have reached maturity. When the reefs were censused at 176 days, every surviving fish had lost its tattoo and older recruits could no longer be distinguished from individuals in the stocked cohort, so no further examination of mortality could be made.

From the time the stocked cohort reached maturity (day 86 – November) until the end of the experiment (day 277 – 31 May), the density of adults (including recruits that had matured) remained quite constant on the reefs (Fig. 5B). The total density of *Coryphopterus* on the reefs was also fairly constant from November to early May, but after this time, a pulse of recruitment nearly doubled the number of fish per reef (Fig. 5B). In contrast to the pulse of *Lythrypnus* recruitment (day 87 – November), *Coryphopterus* recruiting in the May pulse (day 277) accumulated on the reefs in a fairly uniform manner, which did not increase spatial variation in total density (compare Fig. 5A with 5B).

On both sets of reefs, recruitment of *Coryphopterus* exceeded considerably the level required to produce the asymptotic density of adults. On the "*Coryphopterus* reefs," an average of 9.3± 1.1 (range 6–12; n=6) juveniles recruited, and on the "*Lythrypnus* reefs," recruitment averaged 14.4±1.6 (range 8–23; n=9) juveniles. On both sets of reefs, at the end of the study, densities of adults (fish ≥45 mm) were similar, and near the asymptotic density of 3.3 adults/reef: mean densities were 4.0±0.7 (range 1–6) and 2.8±0.6 (range 0–5) on "*Coryphopterus* reefs" and "*Lythrypnus* reefs," respectively. Moreover, the median densities of adults were identical on the two sets of reefs (4 fish/reef).

Discussion

The consequences of density dependence in open populations

Variable input into open populations may have important effects on subsequent patterns of abundance (reviewed in Underwood and Denley 1984; Doherty and Williams 1988; Mapstone and Fowler 1988; Underwood and Fairweather 1989; Sale 1990; Doherty 1991; Booth and Brosnan 1995; Caley et al. 1996). The consequences of variable input for subsequent patterns of abundance hinge upon the extent to which post-dispersal mortality alters patterns of input (Fig. 1). Both stochastically variable density-independent mortality and density-dependent mortality can weaken or eliminate the relationship between local population abundance and input (Warner and Hughes 1988). Critical questions are: how much do post-dispersal processes alter patterns of input?; or, approached at a different angle, how well do patterns of input predict subsequent patterns of abundance?

One way to assess the influence of variable input is to quantify the proportion of the total variance in abundance explained by a linear relationship between abundance and input (e.g., Sutherland 1990; Doherty and Fowler 1994a, b). This can be a very useful approach, because if a strong relationship exists between input and subsequent abundance, then the known relationship can be used to forecast population abundance at other times and places, based on observed levels of input. Such a scenario could be very helpful for managing species with open populations. However, for such a management approach to work, the relationship between input and subsequent abundance must not vary among times or places.

The existence of a significant linear relationship between input and subsequent abundance has sometimes been interpreted as evidence for density-independent post-dispersal mortality (e.g., Sutherland 1990; Doherty and Fowler 1994a, b). However, even a strong relationship between input and subsequent abundance does not rule out significant density-dependent mortality (as shown in Fig. 1B). Near the start of my experiments, I detected density-dependent mortality in both species, yet virtually all of the variation in density among reefs was predicted by the "recruitment" levels that I set (r^2=0.93 and 0.95; Figs. 3 and 6). In such cases, density-dependent mortality has not eliminated the input signal; rather, it has reduced the slope of the relationship between input and subsequent abundance, thus reducing mean population density and the range of variation about the mean. Only very strong density-dependent modification will eliminate completely a positive relationship between input and subsequent abundance (Holm 1990; Fig. 1C and D). Hence, the existence of an apparently linear relationship between input and subsequent abundance is not evidence for density-independent mortality. Density-dependent mortality can be identified by testing for a positive relationship between mortality and initial density (=input), or alternatively, for a slope <1 in a regression of $\log_{10}$(subsequent population density) on $\log_{10}$(input density) (Murdoch and Walde 1989).

Patterns of variable abundance among open populations can be set simultaneously by input, subsequent density-dependent mortality, and subsequent density-independent mortality (Warner and Hughes 1988; Caley et al. 1996). If there is no density-independent mortality and input to some local populations is below the level at which density-dependent mortality sets in (for brevity called K), and above K in others (e.g., Fig. 1B and C), then variation in density among populations and mean population density will be set by both input and subsequent density-dependent mortality. If constant density-independent mortality also occurs, it will increase the extent to which variation among populations is set by input, instead of subsequent density-dependent mortality, if it reduces densities below K in some populations that otherwise would have been above K. In fact, if density-independent mortality is severe enough, densities may be driven so low that no density-dependent mortality occurs [Victor (1986) called this "secondary recruitment limitation"]. In this case, variation in density among populations is set by solely by input, or by input and density-independent mortality, if this mortality is variable. If density-independent mortality varies among local populations, but does not reduce densities of all populations below K, then all three processes – input, density-dependent mortality, and density-independent mortality – will determine variation in density among populations and mean population density. This was probably the case for *Lythrypnus*, although I cannot tell whether the density-independent component, or the density-dependent component of mortality, or both, were variable. Surprisingly, there was no density-*independent* mortality in *Coryphopterus* over the first 3 months of the study.

By the time the surviving individuals had reached maturity, density-dependent mortality in *Lythrypnus* and *Coryphopterus* was strong enough to destroy nearly all evidence of simulated recruitment signals (i.e., linear relationships between the density of survivors and the initial densities of cohorts were very weak). This result would not be meaningful had I used densities well above those naturally encountered, but the densities I used were well within the range of natural densities of recruits. In fact, later in the study, natural input via settlement of larvae to the experimental reefs caused densities to reach maximal levels virtually identical to those established experimentally (see Fig. 5). Only at low densities of "recruits" (≤ *c.* 3 fish/m^2 and *c.* 19 fish/m^2 for *Coryphopterus* and *Lythrypnus*, respectively) did input (via simulated recruitment) limit population density of adults. At Santa Catalina Island, such low densities of recruits are commonly encountered at certain sites, and occasionally in most areas during certain years; but at other times (such as during this study) and in many places, recruit densities often exceed the levels above which additional recruits did not produce additional adults in this study (Behrents 1983; M. Steele, personal observations). This suggests that adult densities of these two gobies at Santa Catalina Island are commonly set both by supply of larvae and by density-dependent post-settlement mortality. This is probably the case for many benthic and demersal marine organisms (Connell 1985; Gaines and Roughgarden 1985; Warner and Hughes 1988; Menge 1991; Caley et al. 1996).

Density-dependent mortality in reef fishes

In a relatively recent review, Jones (1991) noted that a fairly large body of research had failed to detect strong density-dependent mortality in reef fishes. In the space of 2 years, three studies have experimentally detected such strong density-dependent post-settlement mortality (Forrester 1995; Tupper and Boutilier 1995; this study). Neither of the other two studies directly examined the consequences of density-dependent mortality for subsequent adult density, but in examining the values reported for mortality and density in those papers, I found both similarities and differences. Tupper and Boutilier (1995) in fact found over-compensatory mortality, that is, mortality at high densities was so severe that fewer individuals remained in populations with high initial densities than in populations with low initial densities. Like the present study, Forrester (1995) found compensatory mortality.

It is unclear why these three recent studies found strong density-dependent mortality in reef fishes while many earlier studies (e.g., Doherty 1982, 1983; Jones 1987a, b, 1988; Forrester 1990; Booth 1995; all done on damselfishes) did not. Forrester (1995; who studied a short-lived goby) suggested that studies on adults of short-lived species should be more likely to detect density-dependent effects on abundance because a greater proportion of the life span can be encompassed during the relatively short term of the experiments most commonly undertaken. While this may, in part, explain differences in the apparent strength of density-dependent modification of abundance between gobies and damselfishes, differing longevity is not a sufficient explanation. At the start of my experiments most or all of the fish I used were immature, yet, in both species, I found some density-dependent modification within a day. No such evidence for rapid density-dependent modification of juvenile abundance exists for damselfishes. Moreover, while a study of a short-lived fish (the wrasse, *Thalassoma bifasciatum*: Victor 1986) failed to detect density-dependent mortality, a study on juveniles of a longer-lived wrasse (*Tautogolabrus adspersus*) did detect strong density-dependent mortality (Tupper and Boutilier 1995).

In this study, density-dependent mortality reached its greatest strength (i.e., highest slope) or was least variable (i.e., highest r^2) around the time the fish attained maturity. This may have been unrelated to maturity: the density-dependent process(es) may have required a certain amount of time to exact its (their) toll. Alternatively, this could have been caused by increased territoriality at maturity, induced by the need to maintain a breeding territory. Indeed, Cole (1984) found that large *Coryphopterus nicholsii* maintain larger territories than do smaller individuals, and, moreover, recently settled *Coryphopterus* do not maintain territories at all. The finding of strongly regulated adult densities is similar to a number of studies that have found strong density dependence in the number of fish that reach maturity (e.g., Jones 1987a, 1990; Forrester 1990; Booth 1995), but the mechanisms are quite different. In the previously noted studies, survivorship did not differ (or differed only slightly) among density levels, but growth did. Since maturity is primarily determined by size in fishes, the reduced growth at high densities limited entry into the adult populations of the species in those studies. In my study, those individuals that did not reach maturity had died (or disappeared). The consequences of limiting adult density via growth versus death should be very different (Levitan 1989). Populations of organisms in which adult density is limited via growth should fluctuate much less in adult numbers than do species in which adult numbers are limited by mortality, because in the growth-limited species, when an adult dies it can be rapidly replaced by one of the existing stunted individuals already present. Moreover, the stunted individuals are still present and using resources and thus they can potentially influence growth and fecundity of other fish of all sizes (e.g., Jones 1987a; Forrester 1990; Steele 1995).

Mechanisms of density-dependent regulation of abundance

One possibility is that an artifact of handling actually induced density-dependent mortality in this study. For this to be the case, the handling artifact would have to have been density-dependent itself, i.e., the artifact would have to interact with the treatment (Peterson and Black 1994). This possibility seems highly unlikely. All of the fish used in the experiments were handled in exactly the same way, so while it may be reasonable to expect that handling could cause mortality rates to be elevated relative to natural rates of mortality, this elevated mortality should be density-*independent*. Moreover, in other experiments manipulating the densities of the two gobies and the presence of predators (Steele 1995; M. Steele and G. Forrester, unpublished work), in the absence of predators, mortality is density-independent, indicating that there is no density-dependent handling artifact. Experimental studies on density dependence in reef fishes have sometimes used an approach where fish are stocked on reefs repeatedly until the target density is maintained for some period of time (e.g., Doherty 1982; Jones 1987a, 1990). This approach may bias against detecting density-dependent mortality (and may partially explain why it has so rarely been found in reef fishes) because it will tend to result in high-density reefs that have populations of individuals that are exceptionally tolerant to high densities, because those fish not tolerant to high densities disappeared before the experiment was initiated.

It seems most likely that predators, and not some handling artifact, were the ultimate cause of the density-dependent mortality that I detected. In the absence of predators (i.e., in predator exclosure cages), mortality of *Lythrypnus* is density-independent (Steele 1995; M. Steele and G. Forrester, unpublished work), but in this and other experiments conducted in the presence of predators (Steele 1995; M. Steele and G. Forrester, unpublished work), mortality was density-dependent. The situation is very similar for *Coryphopterus*, in which mortality is density-independent or only weakly density-dependent in the absence of predators (Steele 1995; M. Steele and G. Forrester, unpublished work), but strongly density-dependent in the presence of predators (this study).

Predators can directly induce density-dependent mortality in their prey via four responses to prey density: an aggregative response, a functional response, a numerical response, or a developmental response (Murdoch and Oaten 1975). Numerical or developmental responses cannot be involved in the present study because the density-dependent mortality occurred too rapidly. Observations at the study site suggest that predators (mainly *Paralabrax clathratus*) are sufficiently abundant and active to induce density-dependent mortality via either an aggregative response or a functional response within 24 h (as found in this study) or less. In fact, other studies using cages to manipulate predator presence have found predator-induced mortality rates in the two gobies of *c.* 25% to >50% within 24 h of initiating experiments (M. Steele and G. Forrester, unpublished work), similar to the rates of mortality found early in this study. Future work aims to illuminate the roles of aggregative and functional responses in this system.

Effects of predators may also interact with intraspecific competition. Competition may cause individuals in high density populations to be more susceptible to predators. This may occur via reduced health which makes weakened individuals more susceptible to predators, reduced growth, if small individuals suffer higher risk of predation, competition for limited shelter from predators, or competition for some resource, such as mating sites, that also contains shelter.

Competition, presumably via exploitation of limited food, or interference among individuals, has widely been shown to cause reduced growth of reef fishes (Doherty 1982, 1983; Jones 1984, 1987a, b, 1988; Victor 1986; Forrester 1990; Booth 1995; Steele 1995), yet there is scant evidence that fish living at high densities and suffering reduced growth die at higher rates (Doherty 1982, 1983; Victor 1986; Jones 1987a, b; Forrester 1990; Booth 1995; and Steele 1995 all failed to find any large reductions in survivorship associated with density-dependent growth). So, it seems that competition alone probably cannot account for the compensatory mortality found in this study – predators appeared to play a key role in causing density-dependent mortality.

Population regulation: scale and spatial isolation

At the small spatial scales at which I worked, and for the reef configurations that I used, the consequences of the strong density dependence that I detected are clear: reduced mean density and convergence of densities (leading to reduced variability about the mean). On reefs like those I used, when larvae settle at densities greater than about 3–4/m^2 for *Coryphopterus* and *c.* 19/m^2 for *Lythrypnus*, then larval supply and settlement processes will play little role in determining mean adult density and variation about the mean. Density-dependent post-settlement processes will primarily set these population attributes. As noted above, these levels of input are often exceeded at Santa Catalina Island.

However, it is not clear how well these conclusions relate to population regulation on the large continuous reefs where most individuals of these two species live at Santa Catalina Island. There are three main areas of concern: the small size of the experimental reefs, their isolation, and their composition. The reefs I used were composed of rock rubble – a microhabitat that is common on large natural reefs and one that is used by both species. But other microhabitats are also commonly used (e.g., areas with large boulders or continuous sheets of rock), and since risk of predation is strongly affected by microhabitat type (M. Steele, unpublished work), it is difficult to predict how the results of this study apply to other microhabitats.

Another area of concern relates to the isolation of the reefs I used. The experimental reefs were sufficiently isolated that any emigration probably effectively became mortality because fish attempting to cross the sand that separated the reefs were likely to be eaten by predators. In the present study, I found no instances of successful migration to other reefs (although there may have been a few instances of migration among experimental reefs that I was unable to detect since all fish had the same batch mark). Prior studies at the same site, using similar or identical reefs with same degree of isolation, have also found very low rates of successful emigration – about 1% for both species (Steele 1995). This situation is somewhat unnatural: on large continuous reefs, migration to areas many meters distant sometimes occurs (M. Steele, unpublished work) and the risk of predation during such moves is probably lower than for movement over sand. Nonetheless, high-quality microhabitats (partly defined by abundant shelter) are patchily distributed on large reefs, and movement among good patches, through areas of low shelter, likely entails elevated risk of predation. The critical question is: how elevated is the risk of predation for emigrants? Studies that can distinguish between mortality and successful emigration, on large natural reefs, are required before we can evaluate how well the results of studies on small isolated patch reefs apply to populations living on larger reefs.

A third concern relates to spatial scale: a criticism leveled at studies conducted at small scales, like this one, is that they offer little insight into the importance of processes at larger scales (e.g., Doherty 1991). For reef fishes, no serious effort has been made to link the effects of processes that act at small scales to population dynamics at large scales, so such pronouncements are, to date, unfounded. Processes like competition and predation act at the scales over which the participating organisms interact. For reef fishes like those I studied, these interactions occur at scales of centimeters and meters. Hence, to best understand competition and predation, work should be conducted at the small scales over which the interactions occur. Indeed, testing for density dependence at larger scales can fail to detect strong density-dependent interactions that act at small scales (e.g., Heads and Lawton 1983; Hassell et al. 1987; Rothman and Darling 1990); and density dependence occurring at small scales can have important consequences for population dynamics at larger scales (Hassell et al. 1987; Murdoch 1994). Only by exploring the relative influence of input and subsequent modification at multiple scales within particular systems, will we come to understand how well small-scale studies relate to large-scale patterns.

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