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EARLY POST-SETTLEMENT MORTALITY IN A CORAL REEF FISH AND ITS EFFECT ON LOCAL POPULATION SIZE

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Abstract. The relative importance of recruitment and post-recruitment factors in controlling population fluctuations and determining population sizes in open marine systems is still poorly understood. To address this issue, I conducted an experiment investigating whether very early post-recruitment mortality of a coral reef fish, *Thalassoma bifasciatum,* is dependent on recruitment density. To quantify the extent to which local populations are likely to be controlled primarily by recruitment or by post-settlement density-dependent mortality, I also measured natural mortality rates and recruitment variation at sites around the island of St. Croix, U.S. Virgin Islands.

I manipulated densities of 1–3-d post-settlement *T. bifasciatum* on large natural patch reefs in Tague Bay, St. Croix, U.S. Virgin Islands. Manipulated recruits were followed for ~30 d. The loss rate over the initial 24-h period following placement of recruits on the reef was positively related to the density at the beginning of that period. After this period, initial recruit density had no effects on mortality.

Natural monthly mortality rates approximating the monthly mortality monitored during the experiment were measured for naturally recruited fish at sites around the island. Mortality was positively correlated with recruitment density. The effect was strong enough that across sites the relationship between recruit density and juvenile density the following month was not proportional; that is, juvenile density tended to reach an asymptote with increasing recruitment. The relationship between total recruitment per season at a site and adult abundance at the end of the season was similarly asymptotic, indicating the persistence of a density-dependent effect at the scale of the island.

Mortality rates around the island were extremely variable and density independent at densities below ~1 recruit/m^2. Above that level, mortality rates were higher and tended to increase with further increases in recruitment density. Around St. Croix, three out of eight sites consistently received recruitment above this "threshold," while five sites never experienced recruitment above that level during the study. Because spatial patterns of recruitment around St. Croix were consistent over time, some local populations may be controlled mainly by recruitment and density-independent mortality at all times, while others may be chronically affected by post-settlement density dependence. This study gives support to the idea that recruitment limitation and density dependence are not mutually exclusive. Rather, local populations must be characterized by the degree of recruitment, the resultant population density, and the subsequent degree of density-dependent regulation.

Key words: coral reef fish; density dependence; mortality; population regulation; recruitment; St. Croix; Thalassoma bifasciatum.

INTRODUCTION

Ecologists are concerned with understanding the factors that control fluctuations in abundance and determine the number of individuals in a population (limitation and regulation respectively, sensu Sinclair 1989). The debate surrounding the question of population regulation by density-dependent mechanisms has raged since the 1930s. As more long-term evidence accrues from both field and theoretical studies the debate appears largely resolved (Turchin 1995). It is generally agreed that population regulation requires the presence of density-dependent mechanisms (Murdoch 1994, Turchin 1995). Populations do not grow unchecked forever and in the absence of density-dependent factors they will eventually go extinct. This does not mean that all natural populations are regulated at all times. In addition, certain life stages (sizes or ages) of organisms may be more subject to the effects of density than other stages.

Historically, the theoretical and empirical studies that have fueled this long-standing debate in ecology have been based on "closed" terrestrial systems where local population density may effect demographic rates of local recruitment and/or death. More recently, interest has increased in the population dynamics of marine organisms with a dispersive larval stage (reviewed

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in Caley et al. 1996, see also Roughgarden et al. 1985, Bence and Nisbet 1989, Hughes 1990). Such "open" marine systems have very different dynamics due to a decoupling between local reproduction and input into the local population. That is, input results from recruitment of individuals that are likely to have been produced elsewhere. So for local marine populations, the demographic rates of interest are recruitment into the local population and mortality after settlement.

Much effort has been directed towards establishing patterns of recruitment of marine organisms, and it is well established that recruitment can be extremely variable in time and space (Underwood and Denley 1984, Caffey 1985, Connell 1985, Gaines et al. 1985, Gaines and Roughgarden 1985, Doherty and Williams 1988, Doherty 1991, Menge 1991). For reef fish, the patterns and potential causes of recruitment variability have been well studied (for reviews see Doherty and Williams 1988, Doherty 1991). Yet, despite major interest and controversy surrounding the role of recruitment in structuring populations, fewer workers have empirically demonstrated the consequences of variable recruitment to the dynamics of reef-based fish populations (for reviews see Jones 1991, Caley et al. 1996). Thus, the relative importance of recruitment vs. post-recruitment events in controlling population fluctuations and determining population size is still disputed (Jones 1991).

The earliest models for coral reef fishes described populations as saturated and stable entities, which are regulated by niche-differentiation and/or reef-based density-dependent processes such as competition for limiting resources (e.g., Smith and Tyler 1975, Gladfelter and Gladfelter 1978, Gladfelter et al. 1980, Anderson et al. 1981, Ogden and Ebersole 1981). Later, these ideas were eclipsed by a paradigm of recruitment limitation (Williams 1980, Doherty 1981). In its broadest interpretation, the recruitment-limitation model assumes that both recruitment and post-recruitment mortality are independent of the number of settled individuals (no density dependence) and that patterns of supply drive patterns of adult density. This idea arose because several studies (Williams 1980, Robertson et al. 1981, Doherty 1982, 1983, Victor 1983, 1986) indicated that some reef fish populations showed no evidence of density-dependent population regulation. Instead, population fluctuations appeared to be determined by low and variable recruitment rates (Williams 1980, Doherty 1982, 1983, Victor 1983, 1986, Wellington and Victor 1985).

In general, it has been difficult to assess directly the limiting nature of the supply of recruits. Thus, the recruitment-limitation hypothesis has been supported by evidence such as correlations between recruitment and population density (Victor 1983, 1986, Doherty and Fowler 1994), large year-to-year population fluctuations (Sale and Douglas 1984), the failure of recruitment to quickly restore reduced populations to their original sizes (Doherty 1983), and the persistence through time of strong age classes following large recruitment events (Doherty and Fowler 1994). Evidence of this nature should be accepted with caution, however, since these patterns can be characteristic of density-regulated populations as well (Hassell 1986, Warner and Hughes 1989, Holm 1990, Hughes 1990, Caley et al. 1996).

In contrast to the above observational studies, experimental evidence has accumulated that demonstrates that local population density of reef-associated stages can affect life history and demographic parameters. Although many early experimental studies on reef fish failed to detect density-dependent mortality (Doherty 1982, 1983, Jones 1987*a*, *b*, Forrester 1990), more recent work has demonstrated that mortality can be affected by density and in some cases, the effects can be quite strong (Jones 1990, Forrester 1994, Booth 1995, Hixon and Carr 1997). Given the difficulties in detecting density dependence from observational or correlative studies (Hassell 1986, Harrison and Cappuccino 1995), experimental manipulations such as the above studies are the most direct method of testing for density dependence.

However, even with experimental density manipulations, detecting density dependence and understanding the mechanisms of population regulation may still prove difficult. Whether or not the effects of density-dependent processes are detectable in individual studies depends on the spatial and temporal scale of the study, the strength of the density dependence, and the life stage of the organism. Ideally, an experimental study would be conducted at the scale of the entire lifespan of the target species. In reality, most studies of reef fish must focus on a particular stage of reef-based life. Lack of support for the importance of post-settlement processes in reef fish studies may in some cases be due to a failure to investigate the life stages most likely to be affected.

Although manipulative experiments may give insight on the manner and extent to which post-settlement processes may modify initial recruitment patterns, when taken alone they may be unable to explain local population density or dynamics. A complete study of reef fish population regulation should specify both (a) the degree to which biotic interactions may potentially modify the initial patterns established at settlement and (b) the extent in space and time over which these processes may affect naturally occurring populations. This goal is best achieved by conducting a thorough study of natural recruitment concurrently with an experimental investigation of the relative contributions of recruitment and post-recruitment processes in population regulation (Jones 1990). I used such an approach in an attempt to understand just how frequently and where recruitment is sufficiently high to activate reef-based limitations around a relatively isolated oceanic island.

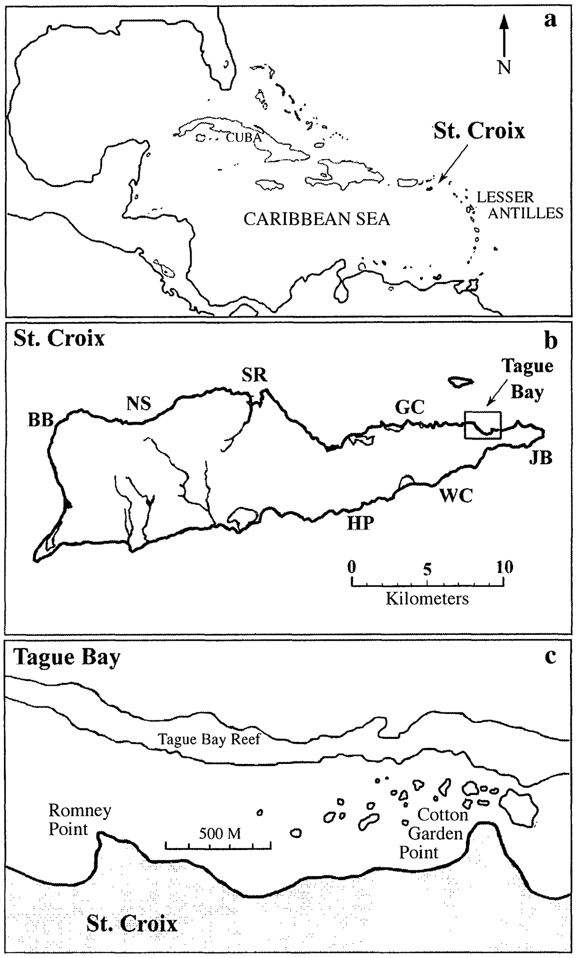

FIG. 1. (a) Location of St. Croix, U.S. Virgin Islands, in the eastern Caribbean. (b) Location of Tague Bay and the eight sites used for island monitoring: GC = Green Cay, SR = Salt River, NS = North Star, BB = Butler Bay, JB = Jacks Bay, WC = Wood Cottage, HP = Ha'penny. The eighth site was the Tague Bay forereef. (c) Location of patch reefs used for density manipulations within Tague Bay. Patch reefs were spread throughout the lagoon behind the Tague Bay reef.

METHODS

Study location and species

All work was conducted at St. Croix, U.S. Virgin Islands (17°45′ N, 64°35′ W). St. Croix is a sedimentary island located in the northeastern Caribbean, inside the arc formed by the lesser Antilles (Fig. 1a). All experiments were carried out on natural patch reefs in the lagoon of Tague Bay (Fig. 1b). I monitored recruits and juveniles monthly and censused resident adult populations intermittently at eight sites located around the island (Fig. 1b). For details of island monitoring see Caselle and Warner (1996).

The experiments were conducted using *Thalassoma bifasciatum,* the bluehead wrasse. Blueheads are short-lived sex-changing members of the family Labridae. Bluehead wrasse are abundant on shallow reefs in the lagoonal study area and throughout the Caribbean. There is an extensive literature on the behavior and mating system (e.g., Warner 1984*a*, *b*). The bluehead wrasse spawns daily throughout the year in Tague Bay. Individuals settle after spending an average of 45 d in the plankton at which time new recruits are ~10 mm standard length (SL) (Caselle 1997*a*). It has been reported that *T. bifasciatum* (and other labrids) may settle onto the reef and bury into sand or rubble for a period of up to several days (Victor 1986). This behavior is inferred from the presence of a "settlement check" or region of faint bands on the otoliths of settled fish and the absence of this check on larvae. In this study, "settlement" refers to emergence from the sand/rubble. Thus, the phrase "1–3 days post-settlement" is equivalent to "1–3 days post-emergence." Recruitment to St. Croix occurs throughout the year, with pronounced seasonal peaks in late summer and early fall (Caselle and Warner 1996). Recruitment also corresponds with the new moon of each month during the recruitment season (75% of new recruits appear in the two weeks surrounding the new moon; Caselle and Warner 1996). New recruits remain near the benthos, occupying low relief rubble or coral pavement habitats until they mature and move up into the water column. At this time, they assume a more planktivorous diet. Young mature at ~3 mo of age and most of the adult population consists of fish that settled the previous year (B. Victor, *unpublished data*).

The manipulations took place on eleven natural patch reefs, which ranged in size from 14.8 to 48.9 m^2 (mean = 26.9 m^2, Table 1). Reefs were measured by one of two methods: for oval-shaped reefs we ran a measuring tape over the reef from edge to edge (conforming the tape to the reef surface) in the longest direction and then orthogonal to the first measure. Reef area was calculated using the formula for the area of an oval. For larger or non-oval shaped reefs I approximated the center of the reef and measured radii at 30° intervals around the reef. The area between each radius was calculated based on the area of a triangle and the total area of reef was then summed from those measurements. All reefs had roughly similar adult densities (Table 1, overall mean density = 0.24 fish/m^2). Surveys taken over the last eight years on larger patch reefs in Tague Bay indicate that adult population densities at any point in time are similar over all reefs (R. R. Warner, *unpublished data*). Although reefs varied considerably in size, they were similar in terms of habitat type. All reefs had low relief and were characterized by dead coral pavement, the preferred habitat for newly settled *T. bifasciatum* (Caselle and Warner 1996). All reefs were separated from each other and from other reef areas by at least 3 m of sand, and most were well over 7 m away from any other reef.

1992 recruit density manipulation

To test the effects of recruit density, reef, and month on recruit survivorship and growth, I manipulated re-

TABLE 1. Characteristics of the patch reefs used in the 1991 and 1992 recruit density manipulations (1991, n = 8 reefs, marked with †; 1992, n = 11 reefs, marked with ‡).

Reef name	Reef area (m^2)	Max. height (m)	*T. bifasciatum* adult density (mean ± 1 SD)	Heterospecific density (mean ± 1 SD)	Predator density (mean ± 1 SD)
16½ C†,‡	27.5	0.72	0.23 ± 0.15	1.76 ± 0.18	0.07 ± 0.05
16 Huge†	31.7	2.37	0.27 ± 0.16	0.77 ± 0.33	0.08 ± 0.06
17½ C†,‡	15	1.48	0.39 ± 0.51	1.60 ± 0.09	0.06 ± 0
9 Mid A†,‡	14.8	1.4	0.15 ± 0.12	6.49 ± 1.05	0.34 ± 0.38
Ann Hi†,‡	27.1	7.7	0.10 ± 0.05	2.75 ± 1.28	0.33 ± 0.10
Ann Lo†,‡	29.2	1.4	0.08 ± 0.03	2.17 ± 0.65	0.15 ± 0.02
BBE‡	48.9	4.72	0.39 ± 0.16	1.43 ± 0.29	0.06 ± 0.02
BBW‡	31.4	2.45	0.46 ± 0.10	1.93 ± 0.20	0.11 ± 0.02
BR 1 and 2‡	18.9	0.94	0.13 ± 0.13	3.47 ± 0.11	0.16 ± 0.14
BR 10‡	18.9	1.1	0.11 ± 0.12	2.51 ± 0.04	0.03 ± 0.03
BR 7‡	32.6	4.12	0.33 ± 0.21	1.26 ± 0.35	0.03 ± 0.04
9 No. Big†	83.7	6.5	§	§	§
9 No. Sm.†	22.0	2.1	§	§	§
PR 14†	56.4	3.8	§	§	§

Notes: All censuses of unmanipulated fishes were done in 1992 only. Means and standard deviations are for censuses (adult *T. bifasciatum*, n = 12 censuses; heterospecifics and predators, n = 5 censuses). Heterospecific density included all other nonpredatory species on the reef except juvenile grunts (Family Haemulidae). Predators included harlequin bass (*Serranus tigrinus*), tobacco fish (*S. tabacarius*), red hind (*Epinephelus guttatus*), trumpet fish (*Aulostomus maculatus*), snappers (*Lutjanus mahogoni* and *L. analis*), squirrelfish (*Myripristis jacobus* and *Holocentrus sp.*), and lizardfish (*Synodus* spp.).

§ No censuses performed.

cruitment density on natural patch reefs in five separate months during the peak recruitment season (July–October) in 1992 (Table 2). Each month, just after the new moon pulse, all newly settled *T. bifasciatum* were removed from the experimental reefs. Additional recruits were collected from other patch reefs in Tague Bay and nearby areas. Tague Bay was an ideal location to conduct these experiments because recruitment is naturally low in this area of the island (Caselle and Warner 1996). Although that necessitated gathering additional recruits from other locations (primarily from Green Cay or Jacks Bay, Fig. 1b), it also meant that very few new recruits settled naturally during the course of the experiments. All fish were captured using aquarium dip nets without the use of quinaldine or any other anesthetic. Recruits were added haphazardly to reefs and all experimental fish received the same handling. Recruits were placed one at a time onto reefs by divers and were followed until they had settled on the substrate and remained in one spot for several minutes. Most reef fish appear to settle at night (Victor 1991), and thus all releases were initiated at dusk and continued for 1–3 h or well into darkness.

I treated starting density as a continuous variable in my experiments rather than a number of discrete "treatments." I attempted to establish a range of densities across reefs, spanning the range of naturally occurring recruitment around the island. This allowed me to use a regression approach to assess the exact form of the relationship between density and mortality (Forrester 1994, Hixon and Carr 1997), rather than simply looking for significant treatment densities. With a more precise idea of the relationship between density and mortality, I could make detailed comparisons between the experimental results and the results of the recruitment monitoring scheme around the island.

There were two phases to each monthly run of the 1992 experiment. In the manipulation phase, or phase 1, I measured loss over each 24-h period immediately following stocking (up to three periods per reef per

TABLE 2. Dates, mean initial density, and range of initial densities for the 1991 recruit density manipulation and phase 2 of the 1992 manipulation.

Year	Month number†	Date	N (d)	Mean initial density (1 SE)	Min. init. density	Max. init. density
1991	1	24 Jul–14 Aug	29	0.34 (0.03)	0.12	0.61
	2	16 Aug–10 Sep	26	0.37 (0.02)	0.23	0.60
	3	12 Sep–9 Oct	28	0.45 (0.05)	0.07	0.87
	4	13 Oct–11 Nov	30	0.34 (0.06)	0.04	0.73
1992	1	7 Jun–7 Jul	29	0.60 (0.06)	0.41	0.90
	2	13 Jul–1 Aug	21	0.50 (0.04)	0.34	0.68
	3	4 Aug–1 Sep	29	0.67 (0.08)	0.17	1.25
	4	5 Sep–5 Oct	30	0.74 (0.10)	0.27	1.43
	5	10 Oct–10 Nov	30	0.49 (0.07)	0.15	0.69

Notes: Means and ranges are across eight reefs in 1991 and 11 reefs in 1992. All densities are number of *T. bifasciatum* recruits/m^2.

† Number used throughout paper.

month). Phase 2 measured loss of fish for ~30 d following phase 1 (Table 2). Month 2 was terminated after 21 d when a pulse of natural recruitment occurred in Tague Bay. Although these new recruits were easily distinguished and could have been removed, I made the decision to use them for the following month's manipulation (month 3), requiring the early termination of the month 2 run of the experiment.

Phase 1.—Inoculations of reefs took place for as many as 3 d, with reefs intended for higher phase 2 densities receiving more transplants than others. New transplants were 1–3 d post-settlement. After no more than 3 d of stocking in the evening and censusing the following afternoon, phase 2 was started. Thus, at the end of phase 1, fish were 3–6 d post-settlement.

Phase 1 mimics natural recruitment in several ways. First, settlement in reef fishes is often pulsed, where fish settle in large numbers over several consecutive nights (Sponaugle and Cowen 1997). Each night (or day) some settlers will die, some will survive and new fish may settle. Phase 1 of this experiment mimics this type of settlement. Some transplanted fish might have survived the entire 3-d period, whereas others might not have survived a single night.

The procedures used during phase 1 are similar to those used in other experimental manipulations of density (e.g., Jones 1987*b*). Usually, fish are allowed to "acclimate" to the reef for a period of a day to several weeks before data are recorded. Phase 1 simply measures mortality during the "acclimation" phase. Little is known about the actual settlement event for reef fishes, but it is highly unlikely that new settlers are afforded an acclimation period of days before facing the risks associated with reef-based existence (e.g., predators). Thus, measuring mortality without an acclimation period, i.e., from the very beginning of the manipulation, may be a more realistic assessment of mortality following natural settlement, although the risks of artificial mortality induced by the transplanting process are greater (see *Methods: Potential biases*).

Phase 2.—The density remaining at the end of phase 1 was considered the starting density for phase 2 (Table 2). Thus, at the start of phase 2, all fish were 3–6 d post-settlement. During phase 2, fish were censused every day for the first week and every other day thereafter. Natural settlers (those settling after the start of phase 2) were removed. These fish could be distinguished from transplanted fish by their size, behavior, and location on the reef. Specifically, there is both a difference in size and color between 1-d post-settlement fish and 2–3 d post-settlement fish. One day post-settlement fish are ~2 mm smaller (Caselle 1997*a*) and more transparent in color (*personal observation*) than 2–3 d post-settlement fish. Observations of 1-d post-settlement fish show that these individuals are very closely associated with the benthos and remain in a particular spot (i.e., a small crack or depression) for at least one week and up to several weeks (*personal observation*). At the end of each experimental period, all survivors (including juveniles) were collected for otolith analysis (effects of density on growth are discussed elsewhere, Caselle 1997*b*) and the next manipulation was started. All natural settlers removed during the course of phase 2 were also aged. Otolith aging also allowed me to check the accuracy of my recognition and removal of natural recruits (see *Methods: Potential biases*).

Starting density ranges were assigned to reefs such that each reef was started at least once during the five monthly runs with a starting density in each range (high, medium, or low density). In addition, each month, a broad range of starting densities was achieved (Table 2). These densities encompassed and exceeded natural recruitment densities for *T. bifasciatum* (mean recruitment density around St. Croix = 0.53 fish/m^2, mean density in Tague Bay = 0.11 fish/m^2). Due to high mortality (with a density-dependent component) in the first phase (see *Results*), there were very few high starting densities for phase 2 (Table 2). Average starting densities and ranges of the second phase also varied slightly from month to month (Table 2).

For all months of the experiment, resident juvenile *T. bifasciatum* were manipulated to a constant 0.25 fish/m^2 so that the effects of recruits on other recruits would not be confounded by potential effects of juveniles on recruits. This involved removal of juveniles on some reefs and addition of juveniles on other reefs. Adult conspecifics and adult and juvenile heterospecifics (including potential resident predators) were unmanipulated and were censused periodically throughout the experimental period (Table 1).

Potential biases

There are several potential difficulties associated with a rapid assessment of mortality for such young fish. First, natural unaccounted recruitment at any point during the experiment would result in my having underestimated true mortality rates. Natural recruitment, if it occurred, could not be prevented during phase 1 (as opposed to phase 2) because there would be very little difference in size or behavior between transplanted and natural recruits. I suggest that natural recruitment was not a major source of bias for two reasons: (1) Tague Bay patch reefs tend to have very low levels of natural settlement (especially off-pulse) and the experiments were initiated after the monthly pulse of natural recruitment, and (2) although there were many instances where the mortality rate was zero during the 24-h periods, there was no case where the density of fish increased over this period, even among the lowest density treatments. If the experiments were contaminated by large amounts of natural settlement, some reefs should have increased in density by chance alone.

Natural recruits were removed during phase 2. Otolith aging allowed me to check the accuracy of my recognition and removal of these recruits. I back-calculated the date of settlement from the date of collection and the post-settlement age of each fish. If the settlement date was after the start of the experiment, that fish was a natural recruit. The following results indicate that additional natural settlement did not significantly influence the mortality estimates. (1) In no case was a transplant perceived as a natural recruit and subsequently removed. (2) Over the 5 mo of the experiment, 767 fish started phase 2. Of these, 495 fish survived and only 43 of these (9%) settled during the experiment and were not removed (i.e., 43 fish were not original transplants). All of these 43 natural settlers had settled only during the first 1–2 d of phase 2. No fish that naturally settled after the first 2 d were mistakenly allowed to remain. (3) Natural recruitment was not density dependent. Thus, low levels of natural settlement that did occur should not have biased mortality rates in any systematic way.

Second, although natural settlers were removed during phase 2, migration between reefs could have occurred (Frederick 1997, Lewis 1997). Fish were not individually marked due to their small size. However, during phase 2, no reefs increased in number from one census to the next by the appearance of a larger individual. Some reefs did increase in density between censuses, but the increase was always caused by the arrival of small, newly settled fish. Given that there were many days with zero mortality between censuses, if migration played a large role I would expect some reefs to increase occasionally in density. This never happened. Thus, I equate all losses from reefs with mortality and for the rest of this paper use the term mortality. In addition, I rarely observed any emigration by newly released fish during phase 1 and never during phase 2. In the few cases in which I did observe a recruit leaving a reef, it was almost immediately eaten by a small piscivorous fish (primarily lizardfish, *Synodus* spp., or small serranids *Serranus tigrinus* and *S. tabacarius*). In general, new recruits stayed very close to the substrate, often remaining in the same location on the reef for several weeks.

A third potential bias is that the effects of handling and transplantation may have artificially inflated mortality rates by causing fish to be more susceptible to predation or emigration. Therefore, two preliminary control experiments were done prior to the large-scale 1992 manipulation. In a 1990 pilot study, I examined the effect of transplantation to a new reef. On nontransplanted or "native" reefs ($n = 3$), recruits were caught and handled and each recruit was subsequently released onto the same reef from which it was caught. On transplanted or "nonnative" reefs ($n = 3$), recruits were caught elsewhere, handled, and added to different reefs. The density of manipulated recruits on all reefs in both treatments was ~0.25 fish/m^2, which was similar to the densities on the native treatment reefs at the time. Fish were censused daily for 2 wk.

In 1991, a recruit density manipulation similar in design to phase 2 of the 1992 experiment was run with an additional nonhandled treatment. Fish were manipulated using the methods of the 1992 experiment and the experiment ran for 4 mo on eight natural patch reefs. Three differences in the design of the 1991 experiment were the following: (1) new recruits were allowed to acclimate for 3 d after placement on the reef during which mortality was not assessed (thus this experiment is equivalent to phase 2 of the 1992 experiment), (2) at the end of each month, the transplanted recruits (now juveniles) were allowed to remain on the reef and new recruits were added (all fish were removed at the end of the 4 mo), and (3) two reefs each month were nonhandled controls. On the control reefs, fish were allowed to settle naturally and were censused following my standard protocol. Control treatments in this experiment were necessarily low density because the experiments were done in areas of naturally low recruitment (to avoid problems with naturally occurring settlement).

Finally, unaccounted natural recruitment can cause a "false" density-dependent effect. If both natural (unaccounted) recruitment numbers and true per capita mortality are the same among reefs, higher density reefs will have higher estimated per capita mortality because per capita recruitment on such reefs will be lower. This numerical effect could falsely indicate a density-dependent effect on per capita mortality estimates, but my results suggest that the role played by such an effect was negligible (see Appendix).

Island-wide monitoring

To examine island-wide patterns of density dependence, I monitored recruits and juveniles monthly at eight sites around the island from June–October of 1991 and May–November of 1992 (Fig. 1b). Fish were visually censused by two observers on five or six permanent linear transects (20 × 2 m) at the eight sites. (For details of the methods and results see Caselle and Warner 1996.) Adults were visually censused using the same permanent transects at the end of each recruitment season (November 1991 and 1992). New recruits, for the island monitoring, were fish that had settled during the monthly pulse, and were distinguished from juveniles on the basis of size, behavior, and location. Juveniles were fish that had settled during the prior month, as determined by size. Mortality estimates were made by counting a cohort of recruits settling to a site in a particular month and counting the number remaining in that cohort at that site 1 mo later. All estimates of age that were based on fish size were verified by otolith analysis prior to the onset of the monitoring program. In addition, observers were repeatedly tested on the accuracy of their visual size estimation by capturing and measuring fish after visually estimating size.

Statistical analyses

For both the experiments and the island-wide data, standard analyses of variance (ANOVA) and analyses of covariance (ANCOVA) were used to test the effects of various parameters on per capita mortality rates. Per capita mortality rates were arcsine square-root transformed whenever necessary to stabilize variances (Zar 1996). In all ANCOVA models, I first tested the assumption of homogeneity of slopes (interaction terms). Whenever this assumption was satisfied, the interaction term was dropped from the model. In some analyses, I used variance components analysis to compare the percentage of the total variance (ω^2) that is explained by the individual terms in the model (Winer et al. 1991).

Controls.—For the 1990 transplantation control, I compared per capita mortality over the two-week experimental period with one-way analysis of variance. For the 1991 density manipulation with a handling control, I tested the effects of handling and initial density on mortality using ANCOVA with initial density as a covariate. Post hoc power analyses were done in both cases.

1992 density manipulation (phase 1).—To address very early post-settlement mortality, I analyzed the pattern of losses during the 24-h period immediately after stocking. I tested the effect of initial density, reef, and experimental month on 24-h per capita mortality during phase 1 using ANCOVA. In this case, both reef and month could be included as factors in a model with density as the covariate because there may be up to three mortality measures per reef per month.

1992 density manipulation (phase 2).—For the second phase, I tested for the effect of the phase-2 starting density on per capita mortality over the entire 30-d period. A mortality rate was calculated for each reef for each month. Reefs were considered as replicates. However, because natural reefs were used in the experiment, the potential for a reef effect existed. Reef and month cannot both be included in a model with initial density as a covariate, because these three factors together uniquely characterize every data point. I first tested for a reef effect by running an ANCOVA model with reef as a factor instead of month. The reef term was nonsignificant (ANCOVA, $F_{10,50} = 0.97$, $P = 0.48$) and was dropped from the final model which tested the effect of initial density (covariate) and month (fixed factor).

Effect of "mortality interval."—In these experiments, where densities are not maintained by addition of animals throughout the experiment, densities obviously do not remain constant throughout the experiment. Thus, it may be more relevant to ask if there is an effect of initial density over shorter periods of time and if that effect is lost by integrating over longer time periods. To answer that question, I used separate ANCOVA models to test the effect of initial density on per capita mortality over increasingly shorter time periods, effectively truncating the experimental data set after different intervals (25, 21, 15, 11, 7, and 5 d). This method asks, over what time period(s), if any, following a pulse of recruitment, does the density of that pulse affect the ensuing mortality? Again, the reef term was tested first, found to be nonsignificant in all cases, and subsequently dropped from the final models.

Island-wide monitoring.—I used ANCOVA models analogous to the whole experiment models described above to test the effect of month, site, and recruit density on per capita mortality around the island. As before, site and month cannot both be included in a model with recruit density as a covariate because these three factors together uniquely characterize every data point. Again, I first tested for a month effect and a site effect in separate ANCOVA models. Both month and site were nonsignificant in respective models. I dropped the "site" term from the final models for the following reasons: (1) the month term was only marginally nonsignificant compared to the site term ($P = 0.07$ vs. $P = 0.59$, respectively), (2) the model including the site term explained less variance in mortality than that including "month" ($R^2 = 0.39$ vs. $R^2 = 0.45$, respectively), and (3) site is functionally equivalent to "reef" in the experimental data set. Dropping the site term and including the month term allowed a direct comparison between the ANCOVA model from the experiment and that from the island monitoring. Thus, the final model tested the effect of initial density (covariate) and month (fixed factor).

Relationship between initial and final density.—For both density manipulations (1991 and 1992) and the island-wide mortality estimates, I investigated the relationship between initial recruit density and final density (at the end of ~30 d) using least-squares regression. The shape of this relationship will give insight into the occurrence, if any, of density dependence. An asymptotic relationship between initial density and final density indicates a density-dependent effect; a linear relationship indicates density independence. However, the data were first log-transformed to stabilize variances. For log-transformed data, if final density is proportional to recruit density (i.e., density independence), a regression coefficient (β) equal to 1 is expected. That is, a linear relationship between two variables will have a slope $=1$ when log-transformed. A relationship between these two log-transformed variables with a regression coefficient significantly <1 indicates that the true relationship is asymptotic (i.e., density dependence). Regression coefficients were tested using the Student's t statistic (Fisher 1922, as cited in Zar 1996).

RESULTS

Transplantation control

The transplantation control experiment investigated whether moving new recruits to unfamiliar reefs artificially affected their mortality on those reefs. Despite a low sample size and hence low power (Table 3), there was virtually no difference in per capita mortality rate

TABLE 3. One-way, single-factor ANOVA comparing per capita mortality (arcsine square-root transformed) over a 2-wk period between transplanted "nonnative" and nontransplanted "native" treatments.

Source	df	SS	F	P
Transplant treatment	1	0.002	0.079	0.79
Error	4	0.112		

over the 2-wk period between native and nonnative treatments. Mean per capita mortality rate (±1 SE) was even slightly greater for the native treatment (0.53 ± 0.09) than for the nonnative treatment (0.50 ± 0.10). Power analysis indicated that given this similarity in mean mortality rate, detecting a significant difference (alpha = 0.05) between the two treatments would require an extremely large sample (n = 292 reefs). Given that the means of the experimental treatments were virtually identical, it is unlikely that the conclusion of no transplant effect is a Type II error.

1991 density manipulation

I explicitly tested for the effects of handling on mortality in new recruits in the 1991 density manipulation. There was no difference in per capita mortality rates between handled and nonhandled fish in this experiment (Table 4). Mean per capita mortality rate over 30 d (±1 SE) was 0.46 (±0.04) for handled fish and 0.35 (±0.15) for nonhandled fish. Post hoc power analysis indicated that, given the mean mortality values, detecting a significant difference (alpha = 0.05) between the two treatments would have required a sample size of 104 reefs. In addition, the initial densities were on average higher on the handled reefs (mean [±1 SE] = 0.40 fish/m^2 [±0.03]) than on the control reefs (mean = 0.29 fish/m^2 [±0.12]). There was one case in which density was particularly high on a control reef (0.87 fish/m^2), when a large pulse of natural recruits settled. Although the rate of mortality on this reef was low compared to the other high-density noncontrol reefs, it was not the lowest (Fig. 2a).

In addition to a handling control, the 1991 density manipulation tested the effects of recruit density on mortality and was similar in design to phase 2 of the 1992 manipulation. There was no significant effect of initial density on per capita mortality measured over ~30 d during the 1991 density manipulation (Table 4, Fig. 2a). Initial density accounted for 64% of the variation in final density (Fig. 2b). The regression equation is $\log_{10}$(final density) = 0.88 × $\log_{10}$(initial density) − 0.33 (Fig. 2b). The slope of this relationship was not significantly different from 1 (Student's t: $t = 0.94$, $n = 31$, $P > 0.05$) indicating that final density increased proportionally with initial density, that is, there was no density dependence.

In general mortality rates during the 1991 density manipulation were quite variable. However, the variance was significantly greater at lower initial densities ($\leq$0.5 fish/m^2) than at higher initial densities ($>$0.5 fish/m^2) (Fig. 2a, F test on variance in mortality at initial densities above and below 0.5 fish/m^2: $F_{22,8} = 3.75$, $P < 0.05$). This pronounced variation was primarily due to low numbers of fish on low-density reefs and thus a presumably greater influence of stochastic events. Overall, the mean per capita mortality rate over 30 d (±1 SE) for all reefs during this manipulation was 44% (±4%).

1992 density manipulation

Phase 1.—Daily per capita mortality rates during phase 1 of the 1992 density manipulation were significantly and positively related to the density of recruits placed on the reef during the prior evening (Table 5a, Fig. 3). However, these 24-h mortality rates were extremely variable (density explained only 14% of the variance in mortality, Table 5a), indicating that a large component of mortality was due to density-independent causes. Although mortality rates ranged from 0 to 100% at lower initial recruit densities, there were fewer cases of zero mortality when initial densities were $\geq$1 fish/m^2. Mortality was zero for 11% of the samples in which density was $\geq$1 fish/m^2 and 23% of the samples at densities $<$1 fish/m^2 (Fig. 3).

Phase 2.—During phase 2, recruitment density explained virtually none of the variance in per capita mortality rate over the ~30-d experimental period (Table 5b, Fig. 4a). This result was similar to the results for the 1991 density manipulation. Initial phase 2 recruit density accounted for 62% of the variation in the final density (Fig. 4b) and the slope of this relationship (log-transformed data) was not significantly different from 1 (Student's t: $t = 0.32$, $n = 49$, $P > 0.05$). Thus, final density increased proportionally with initial density indicating that there was no density dependence. The regression equation is $\log_{10}$(final density) = 1.004 × $\log_{10}$(initial density) − 0.25 (Fig. 4b).

Mortality rates during phase 2 were also extremely variable both within and among the experimental months (Table 5b). Variability was slightly but not significantly greater at lower initial densities ($\leq$0.5 fish/m^2) where mortality rates ranged from 0 to 75% (Fig. 4a, F test on variance in mortality at initial densities above and below 0.5 fish/m^2: $F_{18,30} = 1.45$, $P > 0.05$). Overall, the mean per capita mortality rate over 30 d (±1 SE) for all reefs during this manipulation was 42% (±3%). The overall mean per capita mortality rates, the pattern of variability in mortality across den-

TABLE 4. ANCOVA on the effects of handling and initial density on per capita mortality (arcsine square-root transformed) over a 30-d period.

Source	df	SS	F	P
Initial density	1	0.001	0.007	0.93
Handle/control	1	0.116	1.208	0.28
Error	29	2.79		

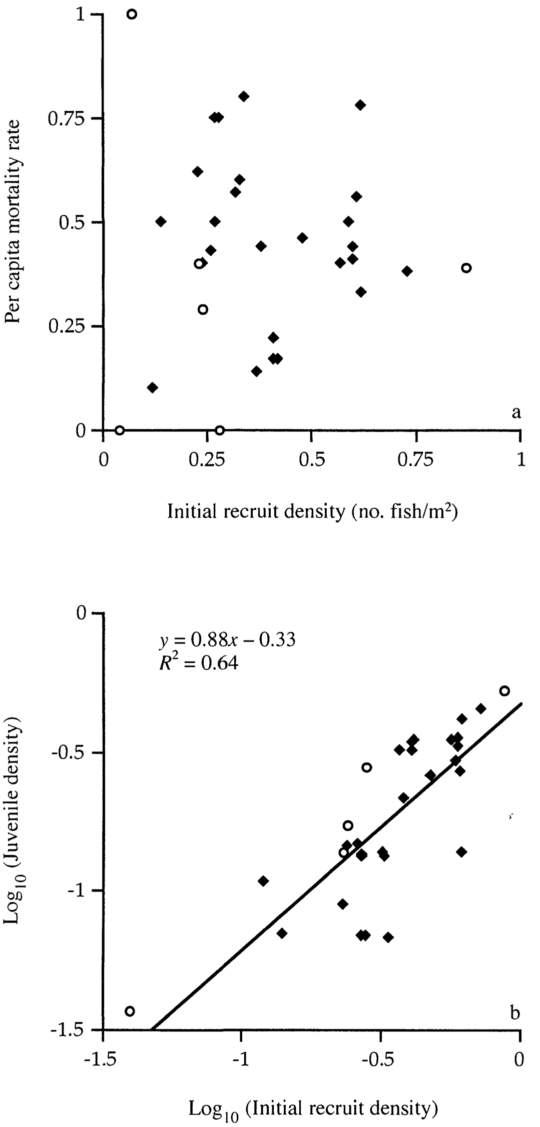

FIG. 2. (a) Relationship between initial recruit density and per capita mortality rate for the 1991 recruit density manipulation with a handling control. Per capita mortality rates were calculated based on the entire duration of the manipulation (~30 d). Each point represents the mortality rate on one patch reef during one monthly manipulation. (b) Relationship between log-transformed initial recruit density (measured in no. fish/m^2) and log-transformed juvenile (final) density (measured in no. fish/m^2) for the 1991 recruit density manipulation. Juvenile density was the density of fish remaining at the end of the manipulation, 30 d after the start of the experiment. In both (a) and (b), handled reefs are shown with filled diamonds, nonhandled controls are shown with empty circles.

sities, and the lack of effect of initial density on 30 d per capita mortality were all very similar between the 1991 density manipulation and phase 2 of the 1992 manipulation.

TABLE 5. ANCOVAs of per capita mortality (arcsine square-root transformed) during the 1992 density manipulation for (a) phase 1 (24-h period) and (b) phase 2 (~30-d period).

Source	df	MS	*F*	*P*	ω^2 (%)
a) Phase 1					
Initial density	1	2.997	40.484	<0.001	14.08
Month	4	0.794	10.723	<0.001	13.86
Reef	10	0.325	4.388	<0.001	12.08
Error	138	0.074			
b) Phase 2					
Initial density	1	0.011	0.248	0.621	0
Month	4	0.120	2.586	0.05	11.65
Error	43	0.046			

Note: Nonsignificant interactions were dropped from the final models. Percentage variance explained (ω^2) was calculated according to Winer et al. (1991).

For graphical comparison, I grouped initial density into four classes and compared the mean mortality rates for all experiments and for the island-wide mortality estimates (see *Results: Island-wide recruit mortality*) (Fig. 5). During phase 1 of the 1992 manipulation, average daily mortality rate for density classes steadily increased from ~20% for the lowest density class (<0.5 fish/m^2) to ~50% for the third density class (1.0–1.49 fish/m^2) (Fig. 5). Mortality was 70% when density was ≥1.5 fish/m^2, but this mean was based on a sample size of three (Fig. 5). For the 1991 manipulation and for phase 2 of the 1992 manipulation, mortality rates were similar and low among the first two and three classes of initial recruit density, respectively (Fig. 5). Notably, in phase 2 of the 1992 manipulation recruit densities >1 fish/m^2 were rarely present (n = 4) and densities >1.5 fish/m^2 were never present, despite stocking reefs with densities >2 fish/m^2.

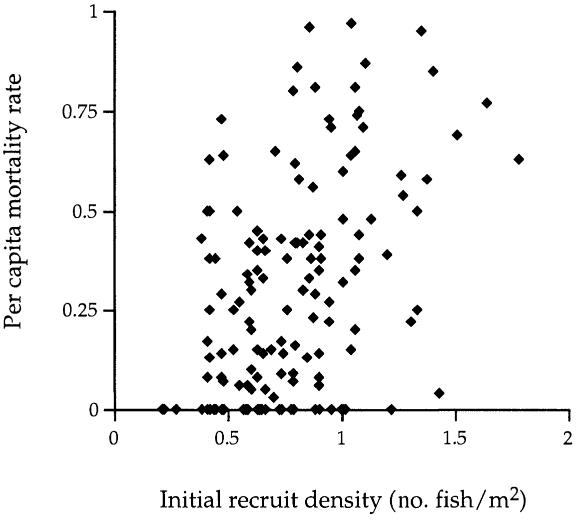

FIG. 3. Relationship between initial recruit density and per capita mortality rate for phase 1 of the 1992 recruit density manipulation. Mortality was measured over ~24 h following placement of new recruits on the reef. Each data point represents one reef for one 24-h period. Each of the 11 reefs is represented up to three times per monthly manipulation.

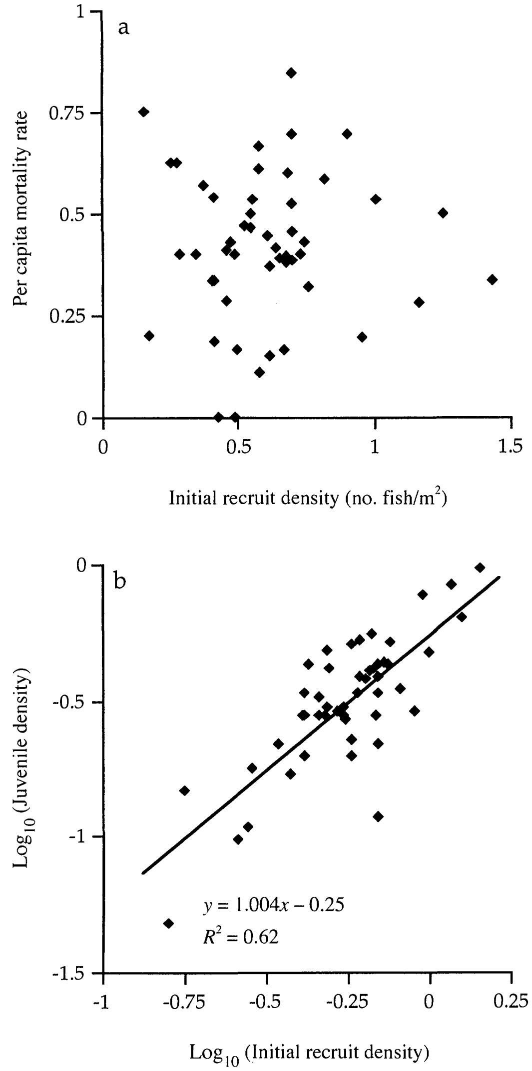

FIG. 4. (a) Relationship between initial recruit density and per capita mortality density for phase 2 of the 1992 recruit density manipulation. Per capita mortality rates were calculated based on the entire duration of phase 2 of the experiment (~30 d). Each point represents the mortality rate on one patch reef during one monthly manipulation. (b) Relationship between log-transformed initial recruit density (measured in no. fish/m^2) and log-transformed juvenile (final) density (measured in no. fish/m^2) for phase 2 of the 1992 recruit density manipulation. Juvenile density was the density of fish remaining at the end of phase 2 of the experiment.

Effect of varying "mortality interval"

The effect of initial density on per capita mortality during phase 2 of the 1992 manipulation was stronger as the time period over which mortality was measured ("mortality interval") was decreased (Table 6). Although the effect of initial density was not statistically significant for any mortality interval during the experiment (5-d interval to 29-d interval), P values decreased from 0.67 to 0.06 as the mortality interval decreased from 29 d to 5 d (Table 6).

Similarly, the variance in mortality that was accounted for by initial density (ω^2, Winer et al. 1991) decreased with increasing mortality interval (Table 6). This result was most clear when the 1-d mortality interval from the first phase was included in the comparison (Table 5a). There was a major decrease in variance explained between the 1-d and 5-d mortality intervals (1-d variance: $\omega^2 = 14.08$, 5-d variance: $\omega^2 = 4.94$).

Temporal variation in mortality

Mortality rates during both the first and second phases of the 1992 experiment varied significantly among months (Table 5a, b). Interestingly, although daily mortality rates were dramatically lower in the second phase, the rankings of mortality among months were the same in both phases (Spearman rank-order correlation, $R_S = 1$, Fig. 6). These data (from the two phases) are independent of one another so a similar pattern of monthly variation implies that the factor(s) affecting mortality during the early phase continued to affect mortality throughout the ~30-d experiment across all reefs. This result also implies that mortality rates during the first phase did not bias the second phase starting densities in a consistent manner. For example, mortality was greatest in month 5 for both phases of the experiment. Thus, for the second phase, the high mortality rate in month 5 was not a result of low phase 1 mortality causing high initial densities during that month. In fact, the high mortality during the first phase in this month resulted in relatively low average starting densities for the second phase (Table 2). Despite the resulting low starting densities, mortality was still greatest in this month.

Island-wide recruit mortality

Overall mean per capita mortality of new recruits (measured for the 1st mo on the reef) was slightly lower at various sites around the island than for phase 2 of the 1992 manipulation at Tague Bay (mean ± 1 SE, island sites: 0.35 ± 0.04, Phase 2: 0.44 ± 0.03). However, mortality at the island-wide sites showed a clear increase with increasing recruitment density and was generally much less variable (Figs. 5, 7a).

I tested the effect of recruit density and month on per capita mortality over 30 d at sites around the island of St. Croix. Recruitment density explained a significant amount of variance in per capita mortality rate and there was a slight but nonsignificant month effect (Table 7). Variance components analysis revealed that initial recruitment density accounted for 24.2% of the variance in mortality at sites around the island (Table 7).

Density-dependent mortality around the island was strong enough to cause the relationship between initial density and final or "juvenile" density (30 d later) to deviate from linear (Fig. 7b). Linear regression on the log-transformed data indicated that initial recruit den-

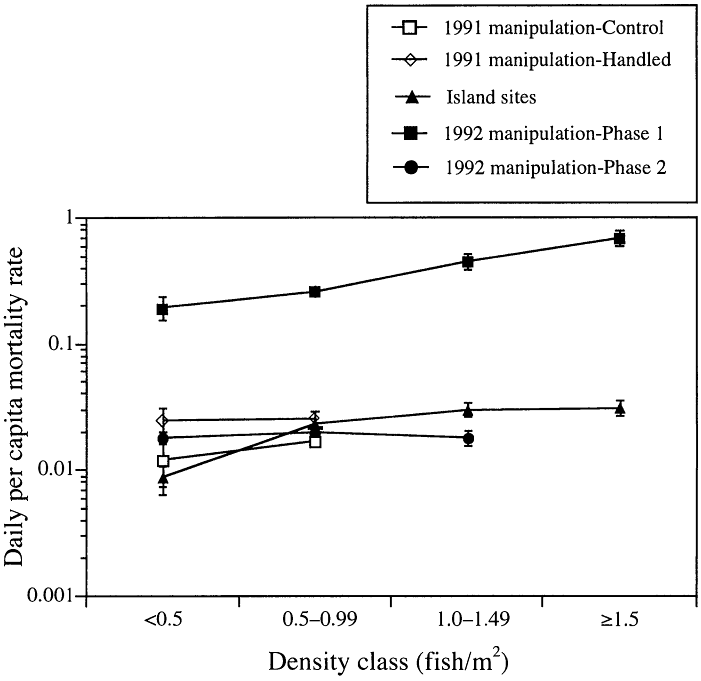

FIG. 5. Mean daily per capita mortality rates (±1 SE) for the 1991 experiment, with handled reefs shown separately from nonhandled controls; for phase 1 of the 1992 manipulation; for phase 2 of the 1992 manipulation; and for the island-wide monitoring as a function of initial density class. The 1991 manipulation, phase 2 of the 1992 manipulation, and the island-wide mortality estimates were measured over 30 d and transformed to daily rates, whereas phase 1 mortality was measured as daily. Experimental estimates of mortality rates are averaged over reefs and months (1992, $n = 11$ reefs, $n = 5$ mo; 1991, $n = 8$ reefs, $n = 4$ mo); island-wide rates are averaged over sites ($n = 8$) and months ($n = 12$). Note that the y-axis is on a log scale.

sity accounted for 67% of the variance in juvenile density: $\log_{10}(\text{final density}) = 0.64 \times \log_{10}(\text{initial density}) - 0.40$. The slope of this relationship was significantly less than one (Student's t test: $t = 5.14$, $n = 46$, $P < 0.001$), indicating that juvenile density did not increase proportionately with increasing recruitment density. This relationship signifies the presence of a density-dependent effect.

Natural recruitment variation

Natural recruitment varied considerably at all spatial and temporal scales examined (spatial and temporal patterns of recruitment are described in Caselle and Warner 1996). I examined this natural recruitment variation in light of the relationship between recruit density and mortality found in the experiments and the island

TABLE 6. Summary of separate ANCOVA models of per capita mortality rate (arcsine square-root transformed) over varying time periods ("mortality intervals") from the beginning of each experimental month during phase 2.

Mortality interval	Source	df	SS	F	P	ω^2 (%)
5 day	Month	4	0.489	2.660	0.045	11.99
	Initial density	1	0.172	3.738	0.060	4.94
	Error	43	1.976			
7 day	Month	4	0.354	1.823	0.142	6.30
	Initial density	1	0.138	2.844	0.099	3.50
	Error	43	2.090			
11 day	Month	4	0.557	2.881	0.034	13.26
	Initial density	1	0.154	3.181	0.082	3.84
	Error	43	2.078			
15 day	Month	4	0.637	3.189	0.022	15.08
	Initial density	1	0.154	3.084	0.086	3.59
	Error	43	2.148			
21 day	Month	4	0.723	4.500	0.004	22.34
	Initial density	1	0.089	2.210	0.144	1.93
	Error	43	1.728			
25 day	Month	3	0.555	4.779	0.007	23.34
	Initial density	1	0.036	0.939	0.339	0
	Error	33	1.278			
29 day	Month	3	0.434	3.699	0.021	17.95
	Initial density	1	0.007	0.183	0.672	0
	Error	33	1.290			

Notes: Nonsignificant interactions were dropped from the models. Percentage variance explained (ω^2) was calculated according to Winer et al. (1991).

sites. All density–mortality relationships indicated that at densities greater than ~1 fish/m^2, the mortality rate was high and increased with increasing density. As an example, I used 1 fish/m^2 as a rough threshold density and counted the number of recruitment events of greater and less than that density around St. Croix. The number of monthly censuses in which I recorded densities >1 fish/m^2 was 6 (out of 32 total censuses) in 1991 and 11 (out of 54 total censuses) in 1992 (Table 8). Although relatively few high-density recruitment events occurred, the total number of fish that faced densities >1 fish/m^2 was 2004 (out of 3649 total fish) in 1991 and 3635 (out of 6061 total fish) in 1992 (Table 8).

There was a strong spatial pattern of recruitment. Over 2 yr of monitoring, five sites never received recruitment levels >1 fish/m^2 while three others received recruitment above that level 20–67% of the time (Table 9). Consequently, ~50–90% of the fish recruiting to the three highest density sites faced densities >1 fish/m^2. These sites of high and low recruitment were spatially clumped around the island. Highest density sites are located on the western end of the north shore (NS, BB) or the eastern end of the south shore (JB). These spatial patterns are largely determined by physical oceanographic processes influencing larval delivery to the island and are further discussed in Caselle and Warner (1996).

Recruit–adult relationship

Adults were censused at the end of each recruitment season (November 1991 and 1992). Adult density at the end of each season at each site was regressed against total recruit density for that site (summed over monthly censuses). There was a clear increasing relationship between the number of fish recruiting to a site and the number of adults at that site (Fig. 8). Since *T. bifasciatum* is relatively short-lived, the adult population at the end of a recruitment season is mainly comprised of recruits from that season. In addition, recruitment levels to sites were consistent between the two years (Caselle and Warner 1996), and so a high recruitment site in 1991 was also a high recruitment site in 1992.

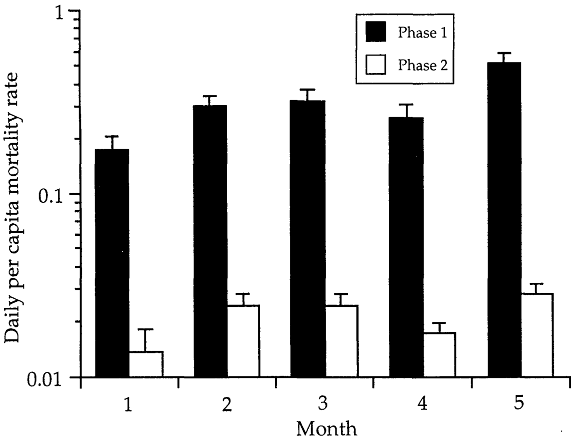

FIG. 6. Mean daily mortality rate (±1 SE, for $n = 11$ reefs) during each monthly run of the experiment during phase 1 (black bars) and phase 2 (white bars) of the 1992 density manipulation. Note that the y-axis is on a log scale.

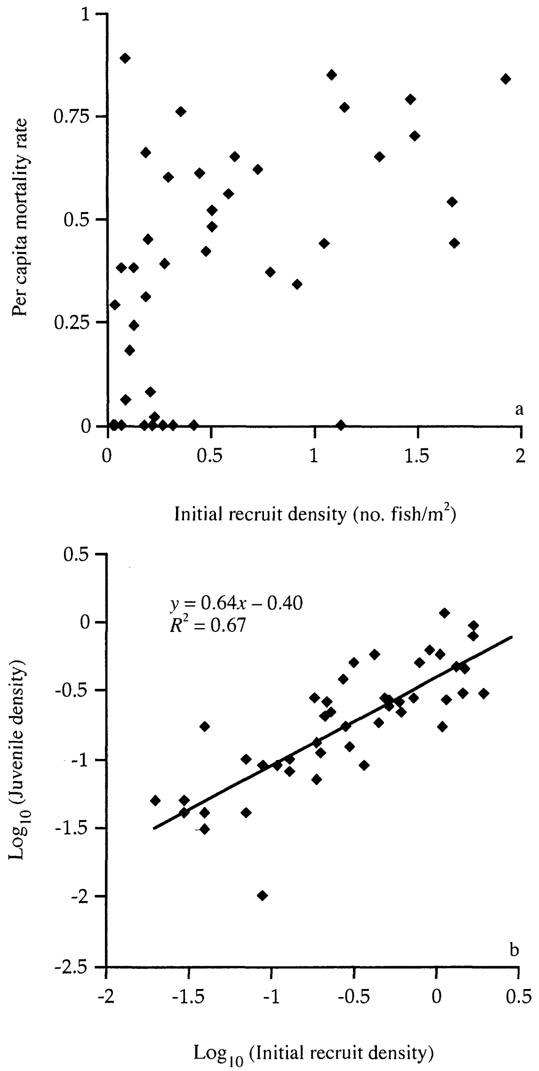

FIG. 7. (a) Relationship between initial recruit density and per capita mortality over 30 d at sites around St. Croix during 1992. Per capita mortality rates were estimated based on the number of new recruits censused at a site in one month and the number of juveniles censused at that site the following month (~30 d between censuses). Each point represents one monthly mortality estimate at a site (8 sites total, 6 mo). (b) Relationship between log-transformed recruit density (measured in no. fish/m^2, censused at time t) and log-transformed juvenile density (measured in no. fish/m^2, censused at time t + 30 d) at sites around St. Croix during 1992. The regression equation is discussed in the *Results: Island-wide recruit mortality.*

The fact that there is a relationship between recruitment and population density indicates that recruitment is an important determinant of local population size.

TABLE 7. ANCOVA comparing the effects of initial density and month on per capita mortality (arcsine square-root transformed) over ~30 d at the island sites.

Source	df	MS	F	P	ω^2 (%)
Initial density	1	2.003	18.563	<0.001	24.21
Month	5	0.244	2.206	0.067	8.69
Error	39	0.108			

Notes: Nonsignificant interactions were dropped from the final models. Percentage variance explained (ω^2) was calculated according to Winer et al. (1991).

TABLE 9. Spatial pattern of recruitment around St. Croix in 1991 and 1992.

Site†	No. fish facing densities ≥1 fish/m^2	No. fish facing densities <1 fish/m^2	No. censuses with densities ≥1 fish/m^2	No. censuses with densities <1 fish/m^2
FR	0 (0%)	283 (100%)	0 (0%)	12 (100%)
GC	0 (0%)	461 (100%)	0 (0%)	12 (100%)
SR	0 (0%)	609 (100%)	0 (0%)	12 (100%)
NS	2405 (86.7%)	370 (13.3%)	8 (66.6%)	4 (33.3%)
BB	2369 (83.2%)	480 (16.8%)	7 (58.3%)	5 (41.7%)
JB	865 (50.5%)	849 (49.5%)	2 (20.0%)	8 (80.0%)
WC	0 (0%)	594 (100%)	0 (0%)	9 (100%)
HP	0 (0%)	126 (100%)	0 (0%)	7 (100%)

Notes: Data are from monthly recruitment surveys at eight sites around the island (1991, $n = 32$ surveys; 1992, $n = 54$ surveys). Numbers in parentheses are the percentage of the total number of fish and the percentage of the total number of censuses, respectively, facing different densities.

† FR = Forereef, GC = Green Cay, SR = Salt River, NS = North Star, BB = Butler Bay, JB = Jacks Bay, WC = Wood Cottage, HP = Ha'penny.

However, the shape of the relationship gives insight into the occurrence, if any, of density dependence. In this case, the linear fit to the log-transformed data was best described by a function of the form: $\log_{10}(\text{adult density}) = 0.33 \times \log_{10}(\text{recruit density}) - 0.27$. Recruitment density explained 50% of the variance in adult density and the slope of this relationship was significantly <1 (Student's t test: $t = 6.98$, $n = 14$, $P < 0.001$). Hence, adult densities were not simply a reflection of recruit densities but were modified by density-dependent processes.

DISCUSSION

For open marine systems, discussion regarding population regulation has centered on the relative importance of post-settlement density-dependent processes and variable recruitment. For highly fecund marine animals, whose young disperse from natal areas, local population regulation by density-dependent effects on birth rates per se is highly unlikely (Hughes 1984, Roughgarden et al. 1985, Warner and Chesson 1985, Bence and Nisbet 1989). Rather, in these open systems, rates of recruitment and/or post-settlement mortality may respond to the density of individuals already present in a local population. In another study, settlement rate of *T. bifasciatum* was shown to be, first, poorly correlated with the disappearance of juveniles in the days prior to settlement (e.g., space did not appear to limit settlement), and second, strongly correlated with larval abundance the night before settlement (Victor 1986). Since settlement rate for this species in Panama appeared to be density independent and determined primarily by availability of competent larvae, I focused my study on early post-settlement mortality. In this study I asked whether very early post-settlement mortality was density dependent and if so, was there a "threshold level" of density at which this occurs (i.e., can populations potentially be regulated by density-dependent effects on very early stages on the reef?). Equally important, I asked whether that threshold level was ever reached naturally and if so, when and where? That is, to what extent does variable recruitment influence local population fluctuations around St. Croix?

I distinguish between these questions because variable recruitment will clearly drive fluctuations in local population density in open systems much, if not the majority, of the time (Caley at al. 1996). Strong correlations will occur when recruitment levels are low (Warner and Hughes 1989) or density dependence is weak. However, demographic rates will inevitably respond in a density-dependent manner at some upward limit of recruitment or established population density (e.g., reef-based adults). The essence of the problem is to discover those limits, as well as where and when, if ever, those limits are reached in natural populations.

Early post-settlement mortality

My results suggest that recruitment density had a negative effect on recruit survivorship in the short-lived *T. bifasciatum.* More importantly, the density-dependent reduction occurred only in the first 24-h post-settlement and occurred only at high densities. However, the effect was not strong enough to be com-

TABLE 8. Summary of (a) the number of recruitment censuses at sites around the island of St. Croix in which densities of new recruits were >1 fish/m^2 and (b) the number of individual fish around the entire island facing densities >1 fish/m^2.

Parameter	1991	1992
a) Recruitment censuses		
No. of censuses where density >1 fish/m^2 (% of total censuses)	6 (18.7%)	11 (20.3%)
Total no. of censuses	32	54
b) Individual fish		
No of fish facing densities >1 fish/m^2 (% of total fish)	2004 (54.9%)	3635 (60.0%)
Total no. of fish	3649	6061

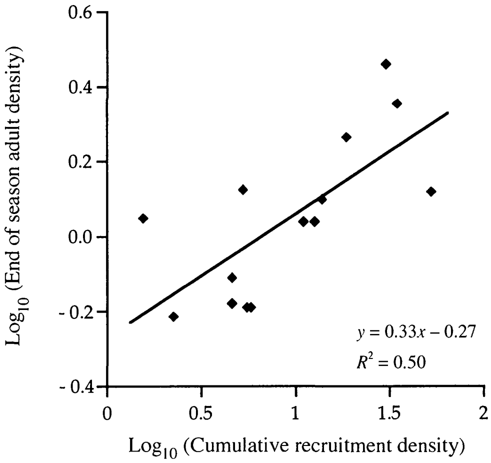

FIG. 8. Log-transformed cumulative recruitment per site per season plotted against log-transformed adult density (measured in no. fish/m^2) at the end of each season for 1991 and 1992. Cumulative recruitment is the sum of all recruits over the season expressed as density (no. fish/m^2). Regression equation is discussed in the *Results: Recruit–adult relationship*.

pletely compensatory, and density only explained a small proportion of the large variance in mortality. Many past studies have failed to detect short-term density-dependent effects on mortality in reef fishes (reviewed in Jones 1991). The majority of these density manipulations examined the effects of juvenile and/or adult density on demographic parameters of juveniles. They also tended to focus on relatively long-lived and highly socially organized damselfish (primarily in the genera *Dascyllus* and *Pomacentrus*: e.g., Jones 1987*a*, *b*, Doherty 1982, 1983). Several studies have recently demonstrated density-dependent mortality in coral reef fishes. They differ from earlier studies by focusing on very early post-settlement stages and/or less socially organized species (Forrester 1990, 1994, Booth 1995, Hixon and Carr 1997, Schmitt and Holbrook 1999). This study contributes to the growing list of studies showing density effects on mortality very early after settlement.

During the first phase of the 1992 manipulation, daily mortality was strongly affected by density, increasing sharply from ~20% at low initial densities to >70% mortality at high densities. The increase was most noticeable at initial densities >1 fish/m^2. After phase 1, mortality was reduced to ~40% over the remaining month, equivalent to ~2% daily mortality. The 1991 experiment, which was equivalent in design to phase 2 of the 1992 manipulation, showed similar results. Mortality rates for these slightly older fish were similar to those found for comparably aged bluehead wrasse in other areas of the Caribbean. Monthly mortality rates for *T. bifasciatum* ranged from 18 to 57% in Barbados (Hunte von Herbing and Hunte 1991) and averaged 62.2% in the Bahamas (Carr and Hixon 1995). Only one other study has investigated mortality immediately following settlement (i.e., comparable to my phase 1 mortality rates). Victor (1986) found that 11.6% of unmanipulated newly recruiting *T. bifasciatum* in Panama disappeared from small patch reefs during the first day after settlement, and an additional 10.6% disappeared over the second and third days. These levels are substantially lower than the phase 1 mortality that I found in this study. A possible explanation is that natural recruitment levels in that study (and in Panama in general) were much lower than both my manipulated levels and naturally occurring levels in St. Croix. Thus at least some component of the difference in mortality rates may be the density-dependent mortality observed in my study but not observed in Victor's study. In addition, recruits in my experiment were handled while those in Victor's study were natural. Another part of the difference may be due to a handling effect, although the pilot studies reported here showed no effect of handling.

The control manipulations presented in this paper directly assessed the effects of transplantation and handling on mortality estimates. Because the manipulations were performed in areas with naturally low levels of recruitment, all controls were, necessarily, low-density treatments. Conceivably, a handling and transplantation procedure itself could cause density-dependent mortality. The ideal control for a manipulation designed to detect density-dependent mortality, would investigate the effects of handling at different densities by comparing a range of manipulated recruitment densities with a similar range of naturally occurring densities in the same place at the same time. To do this control, one would need to conduct experiments in areas with a wide range of natural recruitment density over a small spatial area. Perhaps because of extremely difficult logistics, to date, these controls have not been done. However, as more of these types of recruit density manipulations are done, this will be an important future step.

Although the experiment was not designed for this purpose, the temporal pattern of mortality from the 1992 manipulation may give some insight into the possible mechanisms involved. Daily per capita mortality rates during phase 1 were almost an order of magnitude greater than during phase 2 (Fig. 6), but the temporal pattern of mortality was similar during both phases (e.g., for both phases: month 5 > month 3 > month 2 > month 4 > month 1). Since mortality during phase 2 was independent of density and mortality during phase 1 was composed of both a density-independent and density-dependent component, similar temporal patterns suggest that at least the density-independent component to mortality was due to a process or processes acting at the scale of Tague Bay or possibly the entire island. In terms of the density-dependent component to mortality observed only during phase 1 of the experiment, several potential explanations exist. It is unlikely that competition for food or shelter space was the primary cause of mortality because of the short duration (24 h) and the absence of a reef effect in the analyses. Predation has been found to cause density-dependent mortality in at least one study of reef fish (Hixon and Carr 1997) and in addition, may differentially affect young or newly settled individuals (Johannes 1978). There are a variety of both resident and mobile predators on and around the patch reefs in Tague Bay. Although the scale of movements of these predators is unknown, certainly some are capable of moving from patch reef to patch reef throughout Tague Bay, possibly aggregating at patch reefs with a high abundance of new recruits (for a complete discussion of the effects of predation and competition in reef fishes see: Hixon 1991, Hixon and Beets 1993, Carr and Hixon 1995).

Since the results of the present study showed that per capita daily mortality of 1–3 d old fish had a density-dependent component, future studies of the effects of recruit variation on populations may benefit from concentrating on this early phase. In other words, recruitment monitoring schemes need to account for early mortality. Measuring recruitment weeks following the actual settlement event may lead to inaccurate assessment of the importance of recruitment and post-settlement processes in determining population size, simply because such processes have already operated.

This experimental design clarified when during the first month on the reef the density of a large pulse was likely to affect ensuing mortality. Natural recruitment in blueheads occurs in pulses, a pattern common for many reef fishes (Williams 1983, MacFarland et al. 1985, Robertson et al. 1988, Robertson 1992, Sponaugle and Cowen 1997). This study showed that mortality was severely affected by density in the first day following such a pulse. As the interval over which mortality was measured increased, the effect of density decreased. Mortality measured over the entire 30-d period of the 1992 manipulation showed no clear relationship with density on the first day of that period. That is, after 2–3 d, densities were already below the level at which mortality was density dependent. Density-dependent mortality during the initial 24-h phase reduced densities below the critical level. Two points emerge from this result. First, the extremely rapid reduction in density highlights the need for monitoring recruitment at appropriately short intervals. Second, equating recruitment with settlement, which may be misleading for most reef fish species, may be particularly so for species such as *T. bifasciatum,* which settle in large pulses. For species with highly synchronized patterns of recruitment, densities will be highest on the reef just following settlement, and this may be the critical stage for setting local population size.

Mortality and natural recruitment levels

The second question posed in this study was whether natural recruitment around the island of St. Croix ever reached levels at which processes begin to be affected by density. Even over small geographic areas, the dynamics of local populations may be radically different. By combining experiments and observations of mortality with observations of naturally occurring recruitment variation, it was clear that fluctuations in the size of certain local populations (sites, in this study) are likely to be driven mainly by recruitment while others commonly experience the effects of density-dependent mortality. Above a density of ~1 fish/m^2, mortality at the island sites was high and increased with increasing recruit density. Approximately 20% of all monthly censuses of recruitment recorded densities >1 fish/m^2 and because of the consistent spatial pattern of recruitment to St. Croix, all of these occurred at only three sites. Five other sites never experienced recruitment above that level. Although fish at all sites certainly experience variable, and sometimes high density-independent mortality, these five sites may never experience any added effects of density-dependent mortality while the three high recruitment sites may consistently experience it.

It should be noted that the mortality estimates at island sites encompass both phase 1 and phase 2 of the 1992 manipulation, in that fish recorded as new recruits at the island sites may be anywhere from 1–7 d post-settlement. Despite the potential for underestimating recruitment at the island sites (due to early mortality), recruitment densities to the sites were still higher than commonly achieved in the experiments. I attribute this difference to two possible effects: (1) handling of very young fish in the experiments may have led to overall higher rates of mortality (at all densities) and hence lower recruitment densities and (2) differences in habitat between the patch reefs and the island sites may be responsible for the lower manipulated recruitment levels in the experiment. Regarding the second point, previous work in St. Croix has shown that consistent differences in naturally occurring recruitment levels among the island sites are not due to differences in habitat among those sites (Caselle and Warner 1996). Instead, the differences appear due to local oceanographic conditions that favor delivery of larvae to certain sites and not others. Thus it seems likely that density-dependent mortality at the island sites was underestimated. If the period from actual settlement to recruitment (e.g., census time) was included for all fish, an even stronger density effect would emerge.

How does variation in recruit mortality among sites affect juvenile abundance? As an example, I applied the average monthly mortality rate at a consistently low recruitment site, Green Cay (average recruitment density = 0.16 fish/m^2, average monthly per capita mortality rate = 13%) to a consistently high recruitment site, Butler Bay (average recruitment = 1.50 fish/m^2, average monthly per capita mortality rate = 60%) and examined the difference in the abundance of 1-mo-old juveniles under the two mortality regimes. Less than 20 km away from Green Cay, the Butler Bay site received 2109 recruits in 1992, and 790 survived for 1 mo. If the mortality at Butler Bay occurred at the same rate as at Green Cay (i.e., 13%), 1841 of 2109 recruits would have survived to be juveniles. Applying the lower mortality rate experienced by fish at a low recruitment site more than doubled the abundance of juveniles at the high site.

A strong relationship between recruitment and some stage following recruitment implies that population fluctuations are mainly driven by recruitment fluctuations. This result is not incompatible with the presence of density-dependent mortality. Holm (1990) demonstrated with a simple model that population age structure may directly reflect larval settlement despite density-dependent mortality of settlers. This may often occur when settlement densities are low. In the 1992 manipulation, recruitment variation accounted for 62% of the variance in juvenile density (phase 2). The relationship was linear which fits the model for density-independent mortality. Around the island, a similar amount of variance in juvenile density was accounted for by the variation in recruit density (67%), but the relationship reaches an asymptote and thus there was a density-dependent component. Small amounts of density dependence, perhaps at only one life stage, can act to regulate populations on longer time scales than commonly investigated. For example, Yoshioka's (1982) simulations over long time periods showed that although seasonal fluctuations in the population size of a bryozoan were primarily controlled by fluctuating recruitment, a small density-dependent effect accounting for only 7% of the total variance in the numbers of one life stage was capable of regulating the population. Since the experiment reported here was conducted over a very short time period, I cannot draw strong conclusions regarding long-term population regulation of *T. bifasciatum.* Simply documenting a density-dependent mechanism does not necessarily mean that one has found the primary regulating factor, since the possibility exists that direct density dependence in one stage may be balanced by inverse density dependence in another life stage (Turchin 1995). In addition, the density-dependent effects found in this study only partially explain the extremely variable mortality rates. In any event, the identification of a life stage in which mortality is density dependent will certainly be a useful guide for further studies of reef fish population dynamics.

Currently, a consensus view is emerging that the ultimate abundance and distribution of reef fishes may be influenced by both pre- and post-recruitment processes, and thus there is a need for a better understanding of the circumstances under which each is important (Warner and Hughes 1989, Jones 1991). Factors affecting the ultimate abundance of individuals in a population can occur before, during, and after settlement, and the relationship between recruitment limitation and density dependence should no longer be thought of in terms of a dichotomy (Warner and Hughes 1989, Caley et al. 1996). Given the extreme variability in recruitment, it is not difficult to imagine that at certain times or places, recruitment may be limiting whereas at other times or places, post-settlement processes may be important (Jones 1991). This study demonstrates that at the scale of a single island, some local populations are more influenced by post-settlement processes whereas others are primarily determined by recruitment. In addition, this study highlights the importance of investigating very early post-settlement stages in marine organisms.

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APPENDIX

EFFECTS OF UNACCOUNTED RECRUITMENT ON PER CAPITA DEMOGRAPHIC ESTIMATES

There is a theoretical problem related to the use of per capita rates of mortality (or survival) calculated from changes in population size when migration (or settlement) into the populations is not accounted for. When absolute rates of settlement into populations with differing initial densities are the same, per capita rates of mortality will be higher in higher density populations. This numerical effect could have the result of indicating a density-dependent mortality process when, in fact, there is none.

Here I explore whether this could explain the patterns presented in this paper. I was not able to control for additional settlement in phase 1 of the 1992 experiment. Below, I show that the large differences in per capita mortality rates between the high-density and low-density reefs in this experiment could not be a simple numerical artifact.

A simple model of an open population is given by

$$N_{t+1} = N_t(1 - m) + S \tag{1}$$

where N_t and N_{t+1} are equal to the initial and final numbers (or density), S is equal to settlement between time t and $t + 1$, and m is the mortality rate. Notice that there is no density-dependent mortality in this model. Mortality is strictly density independent.

The estimated mortality obtained by comparing the number of individuals after one time interval (as in my experiments) is

$$M_{\text{calc}} = 1 - (N_{t+1}/N_t) \tag{2}$$

where M_{calc} is the estimated per capita mortality. Substituting Eq. 1 into Eq. 2 gives

$$M_{\text{calc}} = m - S/N_t. \tag{3}$$

The estimated mortality rate is clearly density dependent since it increases as N increases. This is the density-dependent artifact.

One can use this model to see how this artifact may have affected my data. There are several pairs of values of M_{calc} and N_t for phase 1 (Fig. 5). The most extreme values are from the lowest density class and the highest. So, with two equations and two unknowns, one can solve for S and m and check if these values are realistic. This asks, what would the density-independent mortality rate and settlement rate have to be to give me the density-dependent rate of mortality that I measured in my experiment.

For simplicity, I use N_t and M_{calc} for the lowest and the highest density classes for phase 1 of my experiment (from Fig. 5):

low density: $N_t = 0.25$ fish/m^2, $M_{\text{calc}} = 0.2$

high density: $N_t = 1.5$ fish/m^2, $M_{\text{calc}} = 0.7$.

Substituting these values into Eq. 3 and solving for S and m gives $S = 0.75$ fish/m^2 and $m = 3.2$. If the numerical artifact were the primary cause of the relationship between density and estimated per capita mortality that I observed in phase 1 of my experiment, the true density-independent mortality rate would have to be impossibly high. That is, 320% of the fish would have had to die, or more than three times the number present. Clearly this numerical density dependence could not have caused the extreme variation in mortality between high-density and low-density reefs. It is apparent from Eq. 3 that settlement will always *reduce* the effective mortality rates measured ($M_{\text{calc}} < m$). In no case can additional settlement raise the estimated mortality. Although settlement could have the effect of slightly lowering the per capita mortality estimates at lower densities, it could not have caused the steepness of the phase 1 curve in Fig. 5.

Additional settlement was also not accounted for in the island-wide monitoring. In addition to the reasons stated above, there are several other reasons why my estimates of per capita mortality around the island are unlikely to be biased. First, simply because of the methods and timing of the censuses, it is unlikely that many additional settlers were included in the counts of one cohort to the next. Unlike phase 1 of the experiment, during an island census, most fish were already several days to 1 wk old (10–13 mm). At the next census (following month), fish in the same cohort would be 4–5 wk old (17–20 mm). For *T. bifasciatum,* with its discrete recruitment pulses, monthly cohorts are easily distinguishable from one another for ~3 mo, at which time growth slows and cohort size boundaries tend to merge. More importantly, even if some additional settlement occurred, it is extremely unlikely that it was constant among sites. In St. Croix, there are large and consistent spatial differences in the amount of natural recruitment to the sites (Caselle and Warner 1996). We have shown previously that these differences are likely due to oceanographic processes influencing larval delivery (Caselle and Warner 1996). In fact, these sites have different established adult and juvenile population densities because of the differences in recruitment. For estimated per capita mortality rates to be biased by the numerical effect discussed above, the absolute numbers of additional settlers among sites must be relatively constant. Thus the settlement *rate* will be inversely density dependent. But in St. Croix, the settlement rate is similar among sites and thus should not bias estimates of per capita mortality.