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THE INTERACTION OF RETENTION, RECRUITMENT, AND DENSITY-DEPENDENT MORTALITY IN THE SPATIAL PLACEMENT OF MARINE RESERVES

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ABSTRACT Population density can affect rates of mortality and individual growth. We measured these for the non-exploited bluehead wrasse, *Thalassoma bifasciatum*, at three sites around St. Croix, US Virgin Islands. Previous work demonstrated that differences in the degree of larval retention in these sites results in very large differences in recruitment intensity. Post-settlement mortality differed among sites and was positively related to recruitment density. Post-settlement growth differences were small. Because of strong mortality effects early in life, adult densities and size/age distributions differed among sites and did not reflect differences in recruitment rate. The site with the highest retention and recruitment (Butler Bay) had many small fish, while the two other sites with lower recruitment rates (Jacks Bay and Green Cay) had proportionally more large fish. These differences resulted in large differences in egg production. Per capita production was highest at the lowest density site (Green Cay). Total egg production at Green Cay was 75% that at Butler Bay, despite only having half the population size, and the highest overall production was at Jacks Bay, with low retention and moderate recruitment. In terms of marine reserve location, sites predicted to have high retention and recruitment may not always be the sites of highest egg production due to density-dependent processes, and it is important to consider the relative values of self-recruitment and larval export in reserve design.

INTRODUCTION

Marine fisheries throughout the world are generally in decline due to increasing human influence on our oceans (Norse 1993, Dayton et al. 1995). Demersal, nearshore reef fisheries appear to be in particular trouble because of the variety and intensity of human impacts on nearshore areas as well as the fact that many of the species comprising these fisheries have life histories that make them susceptible to overexploitation (e.g., long-lived, reproduction in mass spawning aggregations, etc.). In addition, nearshore reef fisheries pose complex management problems because they are multi-specific and employ a variety of gear types (Roberts and Polunin 1991). Traditional management models of setting catch levels (e.g., with quotas or gear restrictions) or controlling effort (e.g., with limited entry or seasonal/daily closures) have been employed with mixed success even for the single-species and usually temperate fisheries they were designed to manage (NRC 2001). These models of management may not be at all effective in managing tropical, mixed species reef fisheries where basic knowledge of the stocks and management budgets may be limiting (Roberts and Polunin 1991)

Marine reserves have been proposed as a potentially effective tool for managing fisheries in areas where traditional management is either impractical or ineffective (Bohnsack 1990, NRC 2001). Marine reserves offer types of protection not afforded by other management strategies, including intrinsic protection from overfishing (Dugan and Davis 1993, Allison et al. 1998) and potential enhancement of fisheries (Rakitin and Kramer 1996, Russ and Acala 1996, Allison et al. 1998, Chapman and Kramer 1999).

As the number of marine reserves increase, so do the empirical studies comparing these sites to nearby outside areas. It has been well established at this point that both population size and individual sizes tend to be larger inside of reserves relative to nearby fished areas (reviewed in Roberts and Polunin 1991, Dugan and Davis 1993, Halpern in press). This effect of protection occurs despite the fact that virtually all marine reserves to date have been designed and located rather opportunistically (e.g., for social and political reasons) without much consideration of optimal reserve size or the biological, oceanographic, and physical characteristics of the site. However, in recent years, there has been a tremendous upsurge in public interest in reserves and many countries, including the U.S. are moving towards regional and national programs of reserve establishment. Not only is it important that we gain a better understanding of how reserves affect both the areas they are intended to protect and the various stakeholders who use marine resources, but we need to move towards a better "science" of reserve design and siting.

There are a myriad of issues involved in reserve placement including simple opportunity, local and regional-wide politics and community support, enforceability, and economics as well as biology and oceanography. Unfortunately, biological and oceanographic considerations often sit low on the list of decision-making priorities for determining reserve design and siting, while social and political interests ultimately influence the size, location, and implementation of marine reserves. Recent application of source-sink theory to marine reserve design (Roberts 1998, Crowder et al. 2000), by integrating biological (i.e., population demographic) and oceanographic (i.e., ocean current) information, may increase our power to predict long-lasting reserve effects. To be an effective fisheries management tool reserves should be placed in source areas (i.e., sites of positive population growth and export of young) while managers should avoid sink locations (i.e., sites of negative population growth and import of recruits). Reserves situated in source locations have the potential to enhance nearby fisheries through the export of recruits and adults. However, fishermen recognize the most productive areas and avoid habitats not worth fishing. They often resist establishment of no-take reserves in these good habitats, which are also likely to be population sources (Crowder et al. 2000, Dayton et al. 2000). Reserve benefits may be minimized or even detrimental to fisheries if put in sink habitat (Crowder et al. 2000).

It is clear that for optimal design of marine reserves, some knowledge of dispersal patterns is needed. Since the vast majority of nearshore reef fishes have pelagic larvae, the common view has been that recruitment into local populations is effectively decoupled from production in the same population (Caley et al. 1996). As recent work brings us closer to understanding the patterns of connectivity between local populations, it appears that localized dispersal may be more prevalent than previously thought (Schultz and Cowen 1994, Cowen and Castro 1994, Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000, Swearer et al. 2002). Thus, local reproductive output may play a more important role in determining local dynamics and certainly will play a role in regional dynamics. Our past work has shown that certain areas of St. Croix, US Virgin Islands receive many more recruits than others, and that large recruitment pulses tend to be retention events (that is, the recruits tend to be the result of local production; Swearer et al. 1999). There have been some suggestions that marine reserves might best be placed in areas of larval retention, since this should increase recruitment rates and enhance the ability of a local reserve to be self-sustaining (e.g.,

Roberts et al. in press). However, as we show here, increased recruitment does not necessarily result in increased local production.

Hotspots of recruitment may lead to large population sizes and the action of density-dependent processes. For example, variable growth and mortality rates caused by differences in initial density among local populations may affect the total numbers maturing, which in turn will affect the reproductive output of a population (Jones 1987, Weeks 1993, Booth 1995, Owens and Noguchi 1998). The consequences of variable and density-dependent rates of recruitment, growth and mortality to production from marine reserves are rarely examined (but see Tupper and Juanes 1999, Sanchez Lizazo et al. 2000).

Given that marine reserves will usually accumulate larger individuals and populations relative to unprotected areas, are there locations where those effects will be greater? That is, can we place reserves in locations where we expect a larger effect of protection? We focus on the effects of variable demographic rates on the *a priori* choice of locations for marine reserves. We investigate rates of recruitment, mortality and growth for an unexploited coral reef fish at several sites around the Island of St. Croix, U.S.V.I. and the influence these demographic rates have on potential production from these areas.

MATERIALS AND METHODS

Study location and species

All work was conducted at St. Croix, US 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 (Figure 1A). We monitored recruitment and juvenile densities monthly at sites around St. Croix. Fish were visually censused by two observers on 5 or 6 permanent linear transects (20 m x 2 m) at all sites. (For details of the methods and results see Caselle and Warner 1996). Adults were visually censused using the same permanent transects twice during the recruitment season. We collected adults for length frequency estimates intermittently at these sites. Three sites were used for this study: Butler Bay, Green Cay and Jacks Bay (Figure 1B). Green Cay (GC) is located on the eastern part of the leeward shore, Jacks Bay (JB) on the eastern end of the windward shore, and Butler Bay (BB) on the western end of the island. Previous work (Caselle and Warner 1996) has shown that these sites receive consistently different levels of recruitment. Butler Bay is consistently a high recruitment site in summer months, while Jacks Bay occasionally receives large pulses of recruit-
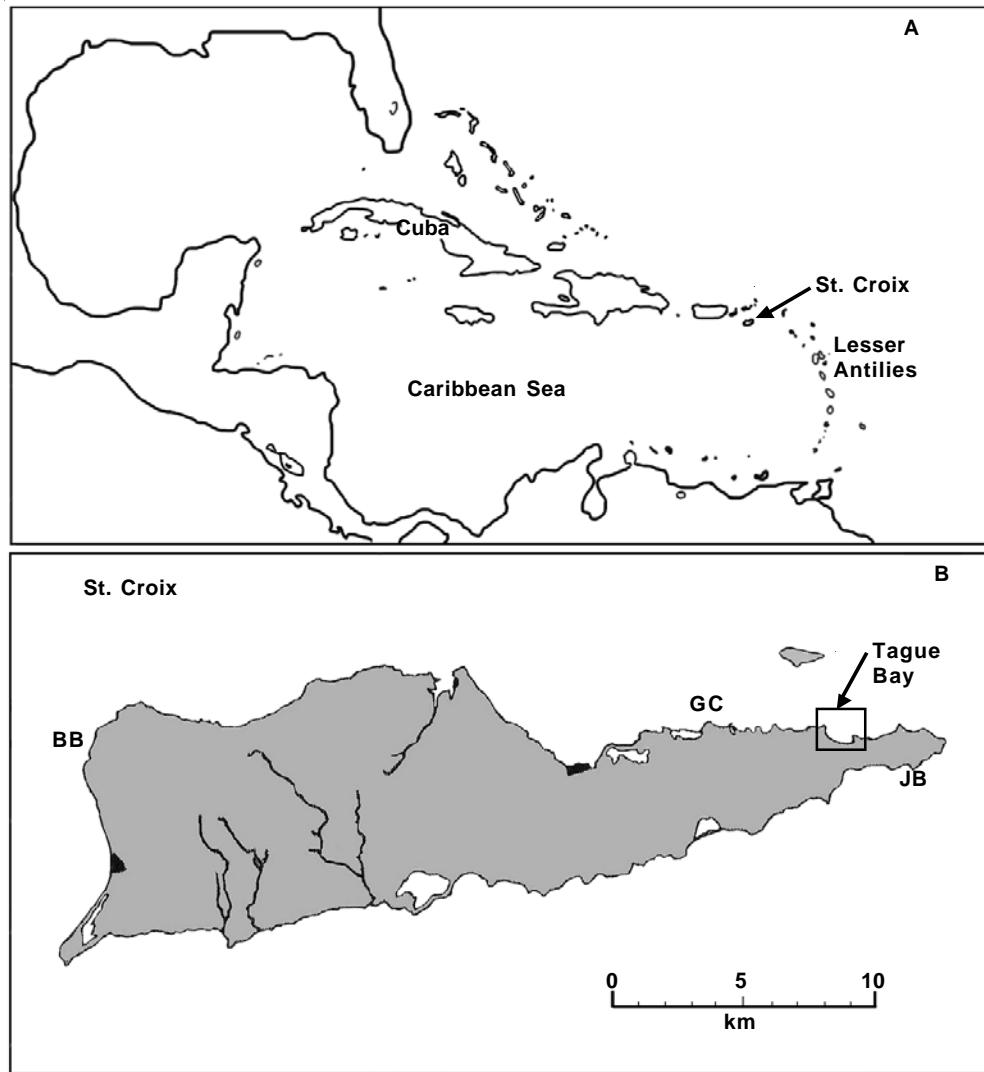
Figure 1. A. Location of St. Croix, US Virgin Islands in the Caribbean. B. St. Croix, showing the location the three sites used in this study; Jacks Bay (JB), Green Cay (GC) and Butler Bay (BB).

ment (particularly in Fall), but on average has lower recruitment levels. Green Cay always has lower recruitment. Swearer et al. (1999) related these recruitment differences to larval retention: Butler Bay is located nearest the downcurrent end of the island, and the presence of persistent oceanographic features in the island wake in summer is associated with large recruitment pulses consisting of fish that are the result of local island production.

All results presented here are for *Thalassoma bifasciatum*, the bluehead wrasse. Bluehead wrasse are short-lived sex-changing members of the Family Labridae. Bluehead wrasse are abundant on shallow reefs in the study areas 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 days in the plankton (Caselle 1996) at which time new recruits are about 10 mm SL. Recruitment to St. Croix occurs throughout the year, with pronounced seasonal peaks in late summer and early fall (Caselle 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).

Otolith preparation

Growth rate estimates in this study were made using otoliths. The two larger pairs of otoliths (sagittae and lapilli) were removed from the cranium, cleaned, and air dried. Otoliths of newly recruited bluehead wrasse were

placed on slides in immersion oil. Otoliths were left in oil for at least one month before reading, since the rings become more distinct after this time. For adult fish, sagittal otoliths were embedded in Crystalbond™ and ground on a frontal plane using 9 mm and 3 mm lapping film until the core was exposed. We examined the otoliths and counted daily rings under a compound microscope with transmitted light at 400 to 1000x with a polarizing filter between the light source and the slide. Daily rings were counted twice for each otolith by one observer and averaged to estimate the age of each fish. Otoliths were counted a third time if the first two counts differed by more than 5 days. The nearest counts were then averaged and the outlier discarded. There has been much work on the otoliths of bluehead wrasse and daily formation of increments has been validated (Victor 1982).

Age, growth and mortality.

Bluehead wrasse recruits and juveniles were visually surveyed and collected monthly using SCUBA and aquarium dipnets from sites around St. Croix. We calculated juvenile mortality rates by counting a cohort of new recruits settling to a site in a particular month and counting the number remaining in that cohort at that site one month later. New recruits 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. 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. We measured mortality for 6 consecutive months (May-November of 1992).

Post-settlement growth rates were estimated from length at age relationships determined from the standard length (SL) of individuals at capture and the total number of otolith increments after the settlement mark (post-settlement age). The slopes of linear least squares regression of SL on post-settlement age provided an estimate of juvenile growth rate and the intercept approximated the standard length at settlement. We compared the slopes and intercepts using analysis of covariance (ANCOVA) with age as the covariate according to Zar (1974). Pair-wise t-tests of means were corrected with Bonferroni adjustments were necessary. The interaction term (site x age) tests for differences in slopes (growth rates among sites). If slopes are not different, the site term tests for differences in elevation.

Adult bluehead wrasse were collected from each of the island sites during spring and fall of 1992. Both collections were combined to construct length-frequency histograms. Fish were captured using liftnets baited with the sea urchin, *Diadema antillarium* (liftnet technique is described in Roede 1972). For each season, fish were collected from all sites within a one week period. A sample of adults from BB and JB were aged using methods described above. The adult age distribution at each site was reconstructed using the equation of the linear least squares regression of age on SL for all fish that were aged at that site (BB: age = 4.2 x SL−48.2, $r^2 = 0.98$, $P < 0.001$, JB: age = 3.9 x SL−42.6, $r^2 = 0.86$, $P < 0.001$). No adult fish were aged from GC; the growth rates of the juveniles at BB and JB were not markedly different from the life-time growth rates at those sites and we used the slope of the regression for juveniles to estimate ages for all fish at GC (age = 3.2 x SL−30.6, $r^2 = 0.86$, $P < 0.001$). Adult population density was assessed with visual surveys at each site during the fall (after the recruitment season). These surveys were done on the same permanent transects used for the recruit censuses. A total of 240 m^2 was censused at each site. Differences among sites in per capita mortality, standard length and age were tested with separate one-way analyses of variance (ANOVA). Data were tested for normality using a Shapiro-wilk test.

Population production estimates

In order to compare the reproductive output of the three target populations on St. Croix, we estimated their total fecundity. We used the relationship between SL (mm) and number of eggs for female bluehead wrasse from Schultz and Warner (1991), and the measured length frequency distribution and population densities from each of the island sites. We started with the population size at each site from the empirical census data and distributed the fish according to the length frequency data from the collections at the three sites. Although we did not measure the sex ratios in this study, previous work has shown that sex ratios in large populations of bluehead wrasse in St. Croix are slightly biased towards females (proportion of males ranges from 0.38 ± 0.03 to 0.48 ± 0.03) and vary little among sites (Warner 1995).

RESULTS

The rate of growth of juvenile bluehead wrasse was not significantly different among the three island sites (Table 1A, Figure 2), despite large differences in mean recruitment density and established population size at those sites (Figure 3). While juvenile fish from BB and JB

TABLE 1

A) Summary of ANCOVA results testing the effects of site on growth rates of juvenile bluehead wrasse collected from island sites in 1992. B) Pairwise t-tests on elevations (y-intercepts) (Bonferroni corrected p-values).

A)	Source	df	SS	F Ratio
	Site	2	13.46	3.54*
	Age	1	3046.03	1600.76***
	Site * Age	2	2.41	0.63ns
	Error	409	778.27	

df = degrees of freedom, SS = sums of squares,
ns = $P > 0.05$, * = $P < 0.05$, *** = $P < 0.001$

B)		T	df	
	BB-JB	2.96	293	$P < 0.01$
	BB-GC	2.85	252	$P < 0.05$
	JB-GC	0.31	279	$P > 0.05$

grew at almost exactly the same rate of 0.25 mm/day, fish at GC, the lowest recruitment site, grew 0.27 mm/day. However, the intercepts of the age at length relationships were significantly different, indicating that fish settle to the sites at different sizes. New settlers are significantly larger at BB (11.3 mm) than at JB and GC (10.6 mm and 10.5 mm respectively; Table 1B).

Juvenile per capita mortality rates (for the first 30 d after settlement) were significantly different at the three sites (ANOVA $F_{2,17} = 4.99$, $P = 0.02$, Figure 3). We previously demonstrated that juvenile mortality was density-dependent at 8 sites on St. Croix (Caselle 1999). Mortality (and recruitment) was highest at BB (60% over the first month after settlement), intermediate at JB (33%) and lowest at GC (13%).

Size and age structures of adult fish varied among the three sites. Mean lengths and ages of adults differed significantly (Figures 3, 4, SL: ANOVA $F_{2,425} = 18.6$, $P < 0.001$, Age: $F_{2,428} = 55.9$, $P < 0.001$). Adults at JB were larger and older than at the other two sites (Figure 4). Adults at GC were relatively large but young, and adults at BB were the smallest and intermediate in age to the other sites. In addition, the range of fish lengths was smaller at BB than at either of the other two sites (Figure 4). Although the minimum length is set primarily by the liftnet method (which is effective only for fish greater than about 25 mm), there is no upper size limit using this collection technique for bluehead wrasse. The maximum SL of fish collected at BB was 70.7 mm, the maximum at JB was 88.9 mm and the maximum at GC was 90.5 mm (Figure 4).

Adult population sizes in the fall after the majority of the yearly recruitment had occurred were similar at BB and JB (313 fish/240 m² and 299fish/240 m², respectively) and much lower at GC (154 fish, Figure 3).

Our estimate of the total number of eggs produced in one day in each of the local populations is shown in Figure 3. Although Green Cay has only half the population size of Butler Bay, production per 240 m² is 62% of that at Butler Bay. The population size at Butler Bay is almost the same as that at Jacks Bay, but production at Butler Bay is about 75% of that at Jacks Bay (Figure 3).

DISCUSSION

The focus to date of studies of marine reserves has largely considered total numbers of adults (Warner et al. 2000) and population size structure inside of reserves compared to outside areas (see Halpern in press for a summary). Other important aspects of populations such as recruitment, age structure, numbers of mature individuals, and reproductive output have been less frequently examined. Importantly, reproductive output is the main metric of functionality for marine reserves designed for fisheries enhancement. If a particular population is recruitment-limited (as has been suggested for the Panamanian populations of bluehead wrasse, Victor 1983), then it is reasonable to expect that enhanced recruitment will result in larger adult population sizes and higher local production.

This expectation was not realized in the three local populations of bluehead wrasse that we studied around St. Croix, a pattern summarized in Figure 3. In fact, the site of highest retention and recruitment, Butler Bay, is characterized by high juvenile mortality and the adult population is composed of large numbers of smaller adults that are relatively young. The Jacks Bay site has lower recruitment and lower mortality and thus has a large adult population size composed of large, old individuals. Green Cay has very low recruitment and very low mortality, and consequently has a low adult population size consisting of larger, young adults. These differences in adult size structure can result in large differences in egg production. Estimated per capita production was highest at the lowest density site (Green Cay). Total egg production at Green Cay was about 62% of total production at Butler Bay, despite only having half the population size, and the highest overall production was at the site with low retention and moderate rates of recruitment (Jacks Bay).
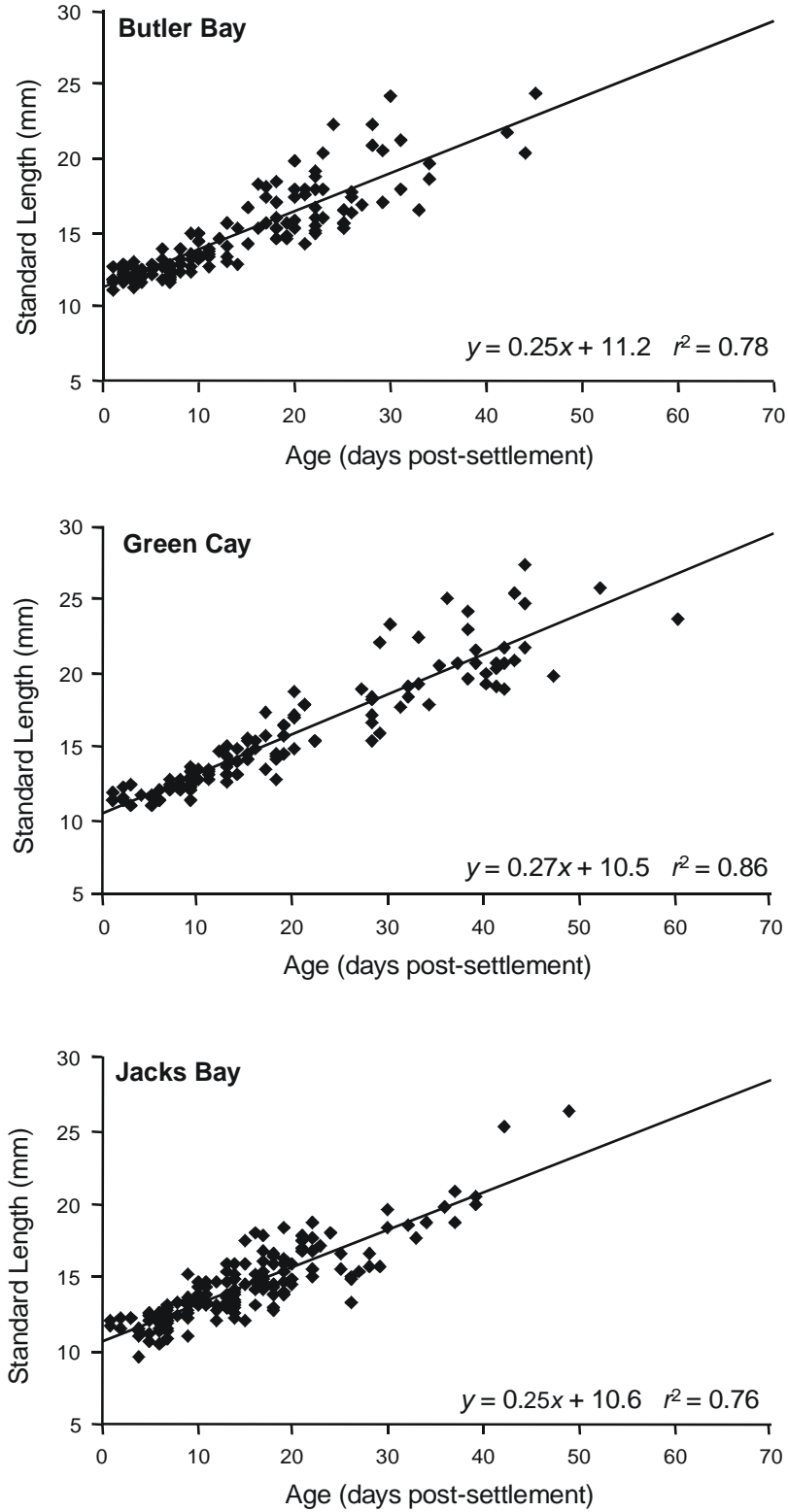
Figure 2. Length at age relationships for *T. bifasciatum* at three sites around St. Croix. Equations for least-squares regression (line shown) are given. The intercepts are a measure of the size at settlement. The test on these elevations is shown in Table 1B.
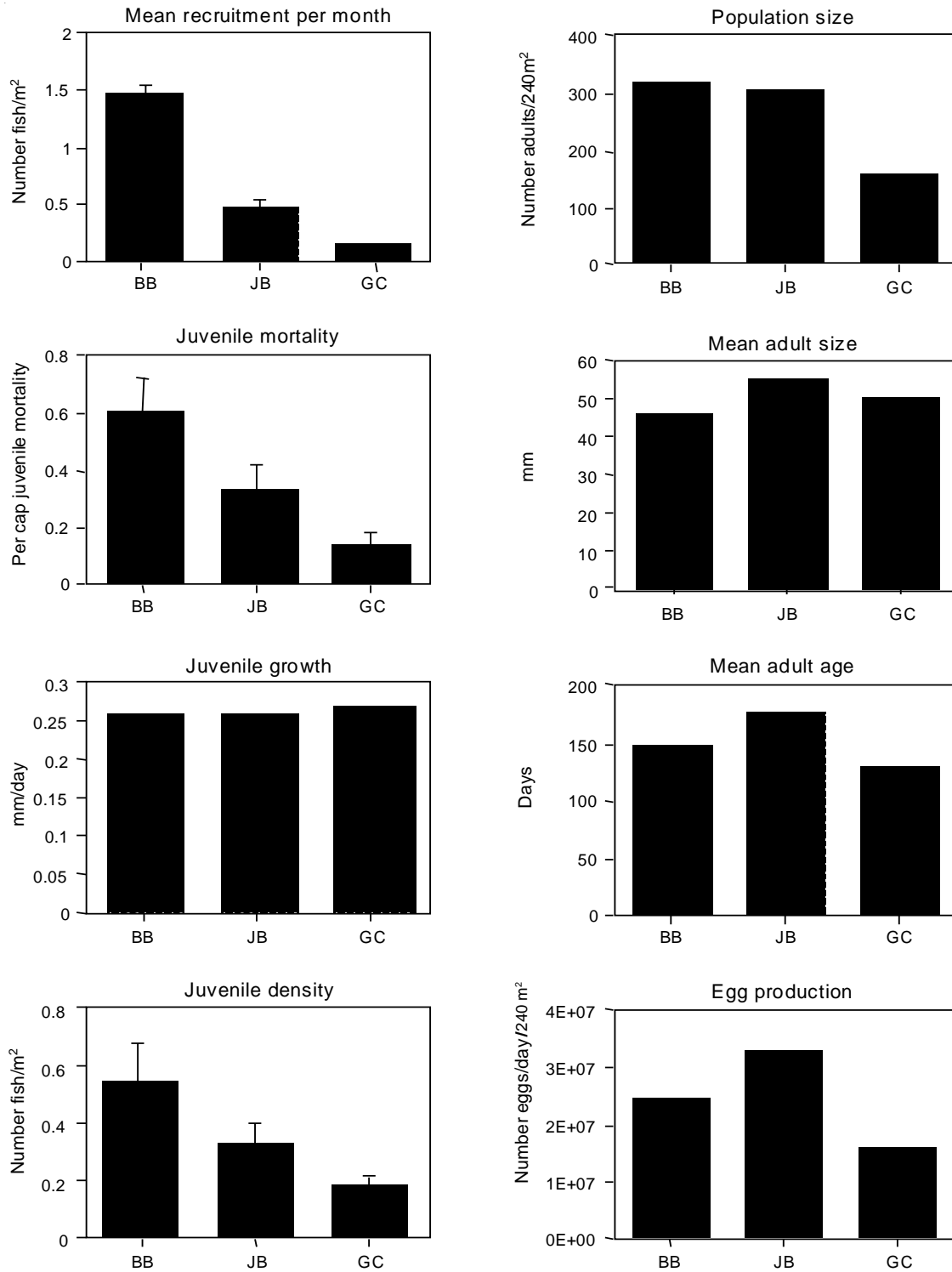
Fig. 3. Plots showing variation in demographic variables for *T. bifasciatum* among sites in St. Croix, US Virgin Islands. Recruitment density and juvenile density were measured monthly. Population size was assessed twice annually. Juvenile mortality was for the first 30 days on the reef. See methods sections for details of juvenile growth, adult age and size and egg production estimates.
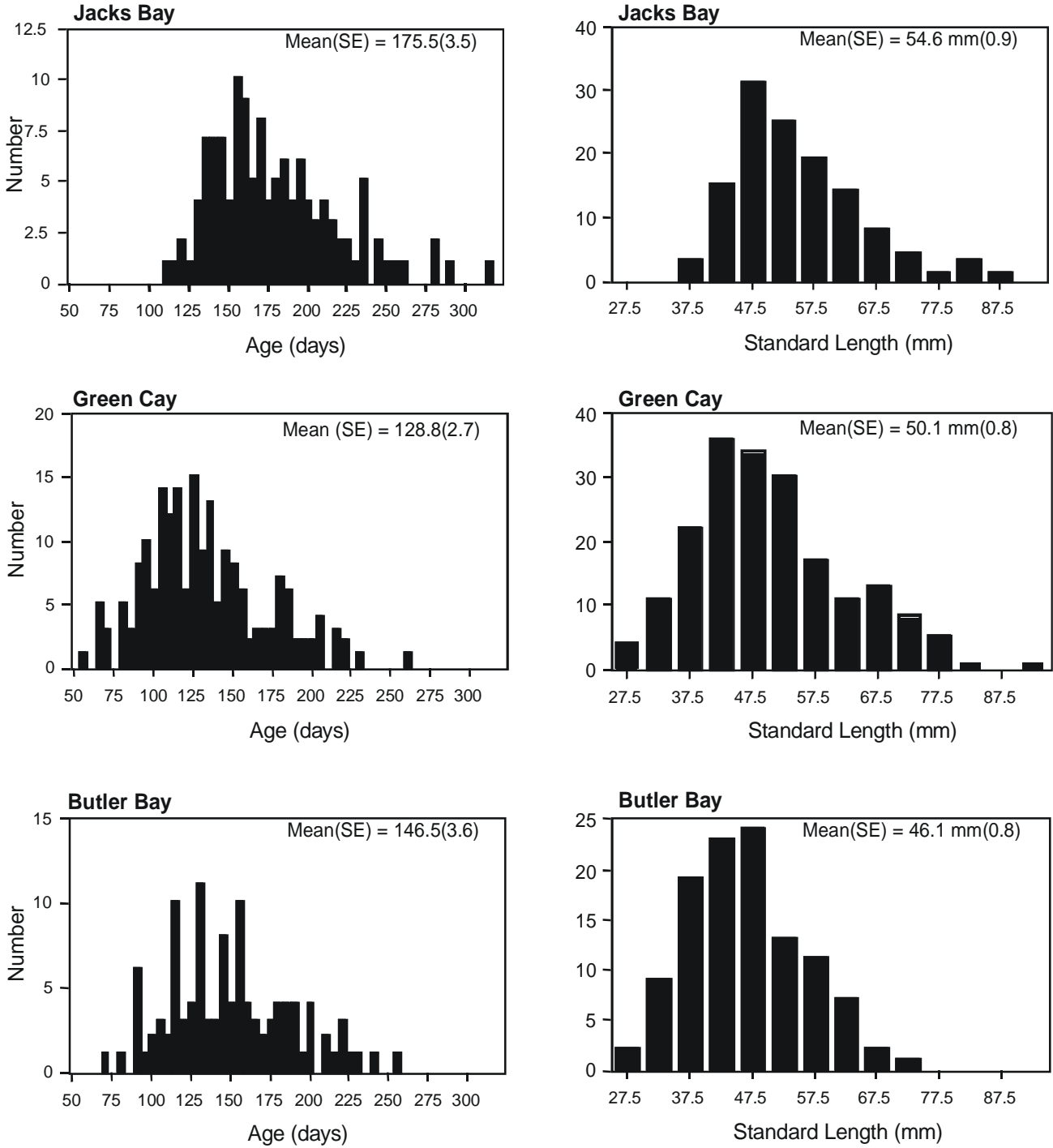
Figure 4. Size and age structure for adult *T. bifasciatum* collected from three sites around St. Croix in 1992. Each bar is the midpoints of 5 mm length or 5 day age classes.

Differences in density can alter patterns of growth, which may influence the timing of maturation and ultimately affect fecundity of entire populations. Intraspecific competitive interactions can influence the number of juvenile coral-reef fish maturing through density-dependent effects on maturation time (Jones 1987b, Forrester 1990, Booth 1995). These results are consistent for freshwater fish as well. Growth, maturation, and egg production were reduced for female poeciliids in high-density treatments (Weeks 1993). For the sedentary slimy sculpin in lake Ontario, female length was negatively correlated with density (Owens and Noguchi 1998). In addition, the size-fecundity relationship itself was influenced by density. As a result, females in the high-density populations produced up to 50% fewer eggs than similarly sized females in low density populations. Most previous studies have investigated variation in fecundity through a growth rate mechanism, yet for bluehead wrasse mortality appears to ultimately have more influence on size structure and population output.

While the disparity between recruitment and eventual adult size structure and production among sites in St. Croix is striking, the patterns alone do not indicate the source of the differences. Both the mean and the maximum sizes were smaller at Butler Bay than the other sites, yet the growth rates at the sites did not differ significantly. Thus density-dependent effects on growth are unlikely to be the explanation for the lack of large, highly fecund individuals at Butler Bay. In contrast, the mortality rate at Butler Bay is significantly higher, and related to recruitment intensity (Caselle 1999), suggesting that large individuals are rare because few fish live to reach large size. The average fish at Butler Bay is almost 5 mm smaller and 17 days younger than at Green Cay, and 10 mm smaller and 20 days younger than at Jacks Bay. In addition, the difference in length between the largest individuals at Butler Bay and the other two sites is 20 mm (Maximum SL: BB = 71 mm, GC = T90 mm, JB = 89 mm). Given that intense recruitment can trigger density-dependent processes that in turn have a perverse effect on production, what factors lead to spatial differences in recruitment? Our past work has shown that recruitment varies by an order of magnitude around St. Croix, and oceanographic features largely determine the spatial patterns and magnitude of recruitment. High recruitment to Butler Bay occurs when persistent convergent features are present in the lee of the island (Harlan et al. 2002). We have also shown that at times when recruitment is highest at the west end of the island (Butler Bay), the majority of larvae are the result of local production and retention (Swearer et al. 1999). Conversely, at the eastern island site (Jacks Bay), recruitment is a result of production from upstream sources (Swearer et al. 1999). These patterns are consistent over time, and the consistently high recruitment at the downstream sites results in consistently greater density-dependent mortality rates. The result of this mortality is the differences in size structure we observed at the sites.

Differences in the size distribution of individuals have major consequences for local populations. Since fecundity is positively related to size in female bluehead wrasse, as well as most other fish (Bagenal 1978), the reproductive output of populations composed of smaller fish can potentially be much lower than populations composed of larger individuals (Schultz and Warner 1991). Reduced reproductive output can arise as a simple consequence of a smaller breeding population (fewer mature fish), but may also occur as a result of a population being composed of smaller, less fecund individuals. The strength of any effect might vary if population density affects the fecundity-size relationship or other factors such as fertilization success. For bluehead wrasse, there is no evidence for such density-dependent effects on individual fecundity or fertilization success (Schultz and Warner 1991), however the potential effects should not be overlooked. Spawning frequency is also likely to affect egg production. Spawning frequency of female bluehead wrasse is related to their size and not to population density: large females spawn two out of every three days whereas smaller females spawn one out of every two to three days (Schultz and Warner 1991). This was not calculated in our production estimates, but in this case such size-related differences in spawning rate will magnify the large differences in reproductive output at the sites. Other species may show the opposite pattern, with spawning frequency reduced at high density. In summary, the conspicuous lack of large individuals at Butler Bay relative to the other two sites has potentially large consequences on reproductive output.

In terms of marine reserve location, sites predicted to have high retention and recruitment may not always be the highest production sites due to density-dependent processes, as was shown here. One message from this study is that high recruitment rates into a population do not *necessarily* correspond to eventual high production rates, so that recruitment "hotspots" are not automatically the best sites for reserve placement. Certainly, high recruitment will enhance the sustainability of local populations, especially if that recruitment is the result of local retention of production. However, the major objective of some marine reserve designs is to enhance larval production within the reserve and thus increase recruitment into

non-reserve areas (e.g., for fisheries replacement). In this case, it is important to consider other demographic responses to protection that may affect local production. Of course, recruitment can be extremely variable in time and space, as can demographic rates. This study summarized data from a single year, and although the spatial patterns and density of recruitment in St. Croix show little interannual variability over the relatively short term (see Caselle 1997, Swearer et al. 1999), this may not be the norm for other systems.

Society will only accept marine reserves as an effective conservation and fisheries management tool if the perceived benefits (increased density and biomass) inside reserves begin to occur on relatively short time scales. In light of recent evidence (Halpern in press) that density, biomass and diversity increase rapidly to mean levels and then stay constant inside reserves, future reserves are under greater pressure to perform rapidly toward meeting management goals. We have argued that the strength of local recruitment and the effects of density dependence must be considered in the design and placement of marine reserves. Yet the rate of density augmentation is likely to depend on propagule supply. Rates of increase following reserve establishment will be much less in low recruitment areas than high recruitment and retention areas (Roberts 2000). Reserves are often evaluated on the basis of the change in density or biomass from before to after reserve establishment. A greater absolute change is often seen as a sign of reserve effectiveness. Although low recruitment areas may be more successful in the long-run (once densities equilibrate) due to the effects of density dependence on mortality, growth, and production, supply-limited areas may be deemed less effective in the short-term as rates of biomass increase are less than that exhibited by high recruitment sites.

If we are interested in using marine reserves as a long-term sustainable fisheries management tool, our findings that high recruitment and retention areas potentially export fewer young to surrounding areas open to fishing are relevant. In the continuing debate over reserves for biodiversity vs. reserves for fisheries management, it is important to consider the relative values of self-recruitment and larval export in reserve design.

ACKNOWLEDGMENTS

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