

HABITAT COMPLEXITY MODIFIES POST-SETTLEMENT MORTALITY AND RECRUITMENT DYNAMICS OF A MARINE FISH

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Abstract. For species that have an open population structure, local population size may be strongly influenced by a combination of propagule supply and post-settlement survival. While it is widely recognized that supply of larvae (or recruits) is variable and that variable recruitment may affect the relative contribution of pre- and post-settlement factors, less effort has been made to quantify how variation in the strength of post-settlement mortality (particularly density-dependent mortality) will affect the importance of processes that determine population size. In this study, I examined the effects of habitat complexity on mortality of blue rockfish (*Sebastes mystinus*) within nearshore reefs off central California. I first tested whether variation in habitat complexity (measured as three-dimensional complexity of rocky substrate) affected the magnitude of both density-independent and density-dependent mortality. I then used limitation analysis to quantify how variation in habitat complexity alters the relative influence of recruitment, density-independent mortality, and density-dependent mortality in determining local population size.

Increased habitat complexity was associated with a reduction in both density-independent and density-dependent mortality. At low levels of habitat complexity, limitation analysis revealed that mortality was strong and recruitment had relatively little influence on population size. However, as habitat complexity increased, recruitment became more important. At the highest levels of habitat complexity, limitation by recruitment was substantial, although density-dependent mortality was ultimately the largest constraint on population size. In high-complexity habitats, population dynamics may strongly reflect variation in recruitment even though fluctuations may be dampened by density-dependent mortality.

By affecting both density-independent and density-dependent mortality, variation in habitat complexity may result in qualitative changes in the dynamics of populations. These findings suggest that the relative importance of pre- vs. post-settlement factors may be determined by quantifiable habitat features, rather than ambient recruitment level alone. Because the magnitude of recruitment fluctuations can affect species coexistence and the persistence of populations, habitat-driven changes in population dynamics may have important consequences for both community structure and population viability.

Key words: density dependence; habitat complexity; limitation; mortality; open populations; population regulation; recruit–adult relationships; recruitment limitation; reef fish; rockfish; *Sebastes*; sensitivity.

INTRODUCTION

A central focus in the study of population dynamics is to understand how processes that generate variability in population abundances (e.g., environmental stochasticity, recruitment) are tempered by the stabilizing force of density dependence in demographic rates (Royama 1992). In spatially heterogeneous environments, there is often variation in the magnitude of exogenous forces contributing to population variability (Tilman and Kareiva 1997). There may also be variation in the intensity of endogenous, density-dependent forces that contribute to the regulation of populations (Cappuccino

and Price 1995). Variation in the intensity of density dependence may have important consequences for the dynamics of populations (e.g., Caley et al. 1996, Sinclair and Pech 1996, Bjornstad and Grenfell 2001). However, empirical studies of variation in density dependence are rare and the mechanisms affecting the intensity of density dependence are not well understood. Similarly, the extent to which variable density dependence in demographic rates actually affects variation in population dynamics is unclear and requires that variation in density-dependent rates be evaluated together with other processes that affect population abundance.

Many species have a life cycle in which a sedentary adult stage produces dispersive propagules. The population dynamics of such species may be difficult to predict because mortality and/or dispersal of early developmental stages can decouple local reproduction from local input. For these “open” populations variation in abundance may be largely determined by a

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combination of propagule supply and post-settlement survival (reviewed by Caley et al. 1996, Hixon et al. 2002). The importance of processes that determine the size of open populations has been long debated (e.g., recruitment limitation vs. density dependence). However, the emerging view that the relative importance of pre- vs. post-settlement factors may be dependent on ecological context (Connell 1985, Caley et al. 1996, Schmitt et al. 1999, Menge 2000, Wright and Steinberg 2001) prompts further investigation of the conditions under which pre- or post-settlement factors are most important to population dynamics.

It is widely recognized that supply of larvae (or recruits) is highly variable (Doherty 2002), and that variable recruitment can affect the relative influence of pre- and post-settlement factors on population size (Connell 1985, Gaines and Roughgarden 1985, Schmitt et al. 1999, Menge 2000, Doherty 2002). However, the intensity of post-settlement mortality (including density-dependent mortality) may vary independently of recruitment. Relatively little effort has been made to quantify how variation in the strength of post-settlement mortality will affect the importance of processes that determine population size (e.g., Schmitt and Holbrook 1999, Shima 1999). However, in order to better understand the dynamics of open populations, the overall importance of processes that determine population size should be evaluated in light of what is known about how those processes vary and the range of values that a system is likely to experience (i.e., overall importance should be evaluated with respect to both variation in the recruitment distribution and variation in post-settlement mortality).

Mortality and other demographic rates may be strongly affected by local habitat features such as structural complexity (Crowder and Cooper 1982, Bell et al. 1991, Beukers and Jones 1997). Structurally complex habitats may reduce prey mortality rates by providing refuge space from predators. Refuge availability may also modify density-dependent processes which contribute to population regulation (Jeffries and Lawton 1984, Kareiva and Sahakian 1990, Lynch et al. 1998). Natural heterogeneity in structural complexity or other features of the habitat may therefore lead to fundamental changes in the dynamics of populations. If habitat complexity significantly affects the magnitude of both density-independent and density-dependent mortality, then variation in habitat complexity may play an important role in determining local population dynamics and community structure in open systems (Hixon and Menge 1991, Hixon and Beets 1993, Forrester and Steele 2004).

For open populations, the relationship between population input and the subsequent abundance of older age classes (i.e., the recruitment function) can be described by a simple model and parameterized to provide a theoretical framework in which to assess the relative importance of different ecological processes

(e.g., Schmitt et al. 1999). Such models can be subjected to various forms of sensitivity analysis, in which model parameters are adjusted and their effects on expected population size are compared to evaluate the relative importance of each demographic rate in determining population size. In this study, I used large-scale population surveys to examine the effects of variation in habitat complexity on post-settlement mortality of a temperate reef fish, the blue rockfish (*Sebastes mystinus*; see Plate 1). I then used the cohort-based approach developed by Schmitt et al. (1999) to conduct a limitation analysis to quantify how the effects of recruitment and post-settlement mortality on the local abundance of 1-yr-old blue rockfish varied as a function of habitat complexity.

METHODS

Study species

The blue rockfish is a common species that inhabits nearshore reefs along the west coast of North America. Larvae are released in late winter and spend three to five months in the plankton (Love et al. 2002), potentially dispersing long distances before recruiting to nearshore reefs. Blue rockfish settlement occurs during April–June when most individuals are 3.5–4 cm total length (Love et al. 2002). As young-of-the-year, blue rockfish are tightly associated with reef structure and tagging studies suggest that they display little, if any long distance (>100 m) movement during their first six months within reef habitat (Miller and Geibel 1973). Blue rockfish experience high rates of post-settlement mortality (Adams and Howard 1996, Johnson 2006a) and analysis of size-structured data suggests that local population size is strongly influenced by the number of individuals that survive their first year within reef habitat (D. Johnson, *unpublished data*). Blue rockfish young-of-the-year shelter in the space between rocks and other hard substrates (Love et al. 2002). Greater structural complexity (i.e., increased three-dimensional relief of rocky substrates) may provide blue rockfish with a greater availability of refuge space and may reduce overall mortality rates. In particular, the increase of refuge space associated with increased complexity may alter density-dependent mortality and may therefore have large impacts on population dynamics (Lynch et al. 1998, Forrester and Steele 2004).

Data collection

I used annual, visual-transect surveys of the abundance of blue rockfish to estimate their recruitment and subsequent survivorship during their first year in reef habitat. Fish were counted on discrete, nearshore reefs at sites spanning approximately 250 km of central California coastline. Each reef measured approximately 500 m alongshore \times 70 m wide and supported stands of giant kelp. Surveys were conducted over a period of five years (1999–2004) and were conducted in mid-summer, after the recruitment season for blue rockfish. A total of

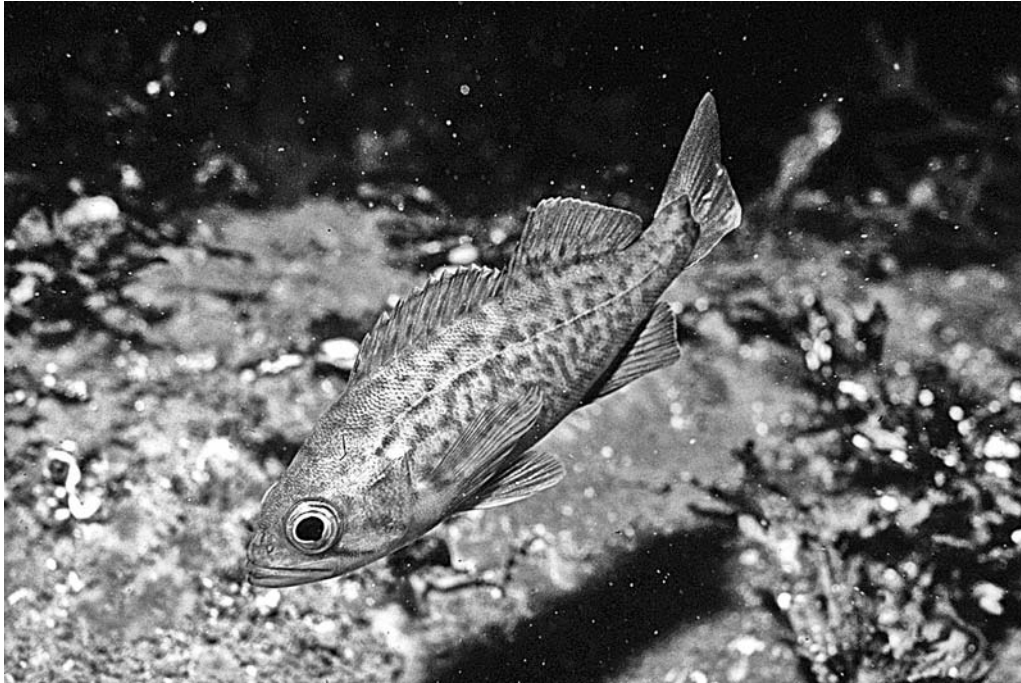


PLATE 1. Young-of-the-year blue rockfish. *Sebastes mystinus*, ~8 cm total length. Photo credit: Steve Lonhart.

23 sites were surveyed, although not every site was sampled each year. On each survey divers counted fish, visually estimated their size, and measured the complexity of the habitat (i.e., three-dimensional relief of the substrate). Fish were enumerated on transects that measured $30 \times 2 \times 2$ m. Counts of fish were conducted by diver pairs such that along each transect one observer counted fish within 2 m of the seafloor and the other observer counted fish in mid-water. The density of fish was expressed as the number of fish in the water above a 30×2 m transect (i.e., [total number of fish observed by both observers]/ 60 m^2). Transects for both fish counts ($n = 24$ transects per site) and substrate measures ($n = 12$ transects per site) were randomly allocated within a stratified sampling design that ensured even coverage of the reef area. Substrate relief was recorded every 0.5 m along each 30-m transect and was measured as the vertical distance between the highest and lowest points of rocky substrate within a 1×0.5 m area. Each observation of substrate relief was categorized into one of four bins (0–0.1 m, >0.1–1 m, >1–2 m, >2 m). For analyses, each observation was counted as the middle or lower point of the interval (0.05, 0.5, 1.5, or 2 m, respectively). Relief values were averaged for each transect and the average relief value for each site was calculated from a total of 12 transects per yearly survey. Relief was calculated as a routine part of the yearly surveys and values were averaged across years to yield an overall value of three-dimensional complexity for each site.

For each year, estimates of the mean density of blue rockfish young-of-the-year (individuals <9.5 cm total length [TL]; hereafter referred to as recruits) at each site were compared to the mean density of 1-yr-olds (10–14 cm TL) estimated at that site the following year. These data were used to estimate mortality of cohorts at each of the sites. All data were used to estimate the recruitment distribution. However, because the analysis of mortality involved estimating a mortality function for each site, I excluded those sites that had fewer than four cohorts. I analyzed data from seven sites that had been monitored for the longest period of time (1999–2004). This approach provided a relatively balanced design to estimate mortality (six sites had mortality estimates for five cohorts and one had estimates for four) and provided the most reliable estimates of the mortality function, given the available data.

Habitat complexity and recruitment dynamics

To examine how habitat complexity affects density-independent and density-dependent mortality, and therefore how habitat complexity may ultimately affect recruitment dynamics, I conducted an analysis in three parts. First, I tested whether mortality was affected by initial density and whether density-independent and density-dependent mortality significantly varied among sites. Next, I estimated mortality coefficients for each site and examined how mortality coefficients varied among sites relative to their level of three-dimensional complexity. Finally, I used the estimated relationship between site complexity and mortality coefficients to

conduct a limitation analysis examining the population-dynamic consequences of variation in habitat complexity.

To explore the effects of habitat complexity on the strength of density-independent and density-dependent mortality, I first expressed annual, per-capita mortality ($-\ln(N_t/N_0)$) as a function of initial density. This relationship can be described by the following equation:

$$-\ln(N_t/N_0) = a + bN_0 + \varepsilon \quad (1)$$

where N_t = density of 1-yr-olds, N_0 = density of recruits, a = estimated intercept parameter, b = estimated slope parameter, and ε = residual error. Note that the intercept and slope parameters in Eq. 1 can be used to estimate parameters for density-independent and density-dependent mortality in a familiar form of the Ricker equation describing cohort survival:

$$N_t = N_0 e^{(-\alpha - \beta N_0)} e^{\varepsilon} \quad (2)$$

where α = density-independent mortality and β = density-dependent mortality. In my analyses, I used a Ricker model to describe the recruitment function. Comparison of model fit indicated that the Ricker model provided a better description of the recruitment function than another common model of density dependence, the Beverton-Holt function (see *Results* section; Appendix A). Although the difference in model fit was not large, the goal of this analysis was to not to precisely describe the form of density dependence, but to examine variation in the intensity of density dependence.

To account for the fact that the data contained multiple observations from several sites, I analyzed proportional mortality ($-\ln(N_t/N_0)$) with a linear, mixed-effects model (S-Plus 6.2; Insightful Corporation, Seattle, Washington, USA). I included initial density as a fixed factor and site as a random factor. This approach allowed me to test whether mortality increased with density and whether the mortality function significantly varied among sites. I used a likelihood ratio test to determine whether a common-slope model was sufficient to describe the data (i.e., only the density-independent component of mortality varied among sites) or whether the data were better described by a model that allowed estimates of both the slope and intercept to vary among sites (i.e., both density-independent and density-dependent mortality varied among sites).

Because the slopes and intercepts significantly varied among sites (see *Results*), I estimated the coefficients of the mortality function for each site. The overall mortality function was calculated from the linear model and the site-specific coefficients were calculated from the linear model and random effect coefficients (using S-Plus 6.2). There was appreciable sampling variability in the estimates of initial density of fish, so the regression coefficients were adjusted to correct for bias associated with error in the predictor variable. First, I estimated sampling error associated with initial density of fish as

the average of the squared standard errors of the fish counts. I then used this estimate of sampling error to generate an unbiased, method-of-moments estimator to correct the values of the slope and intercept of the regressions at each site (Carroll and Ruppert 1996; Appendix B). Once slope and intercept parameters were estimated for each site, they were back-calculated to estimate density-independent and density-dependent mortality in the Ricker equation (Eq. 2). Because Eq. 1 assumes a lognormal error structure and because the best-fit linear model passes through modal values, the mortality coefficients were back-calculated such that they represented the arithmetic average of the Ricker function (Hilborn 1985; Appendix B).

Once mortality coefficients were estimated for each site, I examined how variation in mortality coefficients among sites was related to variation in structural complexity of the sites. I used a MANOVA to test whether the dependent variables (density-independent and density-dependent mortality) significantly changed with substrate relief. Coefficients from the MANOVA model were then used to summarize how the values of density-independent and density-dependent mortality varied with habitat complexity.

Limitation analysis

To further understand how habitat complexity may affect the dynamics of rockfish recruitment, I conducted a set of limitation analyses to quantify the degree to which multiple processes (recruitment, density-independent mortality, and density-dependent mortality) influenced local population size. To describe the relationship between recruits and 1-yr-olds, I used the Ricker equation (Eq. 2) with mortality parameters derived from measures of substrate complexity and the MANOVA model relating substrate complexity to density-independent and density-dependent mortality. Limitation values for each process were calculated as the absolute value of the difference between the density of 1-yr-olds expected when the process under consideration was increased 10% and the density of 1-yr-olds expected when all process are operating at ambient levels (Osenberg and Mittelbach 1996; Appendix C).

Values of limitation will vary with the magnitude of each parameter. Using the general equations for limitation (Appendix C) and estimates of how mortality varied with habitat complexity, I was able to evaluate limitation under a variety of conditions (i.e., at reasonable combinations of recruit density and habitat complexity). To illustrate how recruitment dynamics may change with habitat complexity, I evaluated limitation (expressed as a function of recruit density) for all three processes at three levels of habitat complexity: mean complexity, low complexity (mean relief - 1 SD), and high complexity (mean relief + 1 SD). Both the mean value and standard deviation of substrate relief were calculated from all sites surveyed, not just those with enough data to estimate mortality.

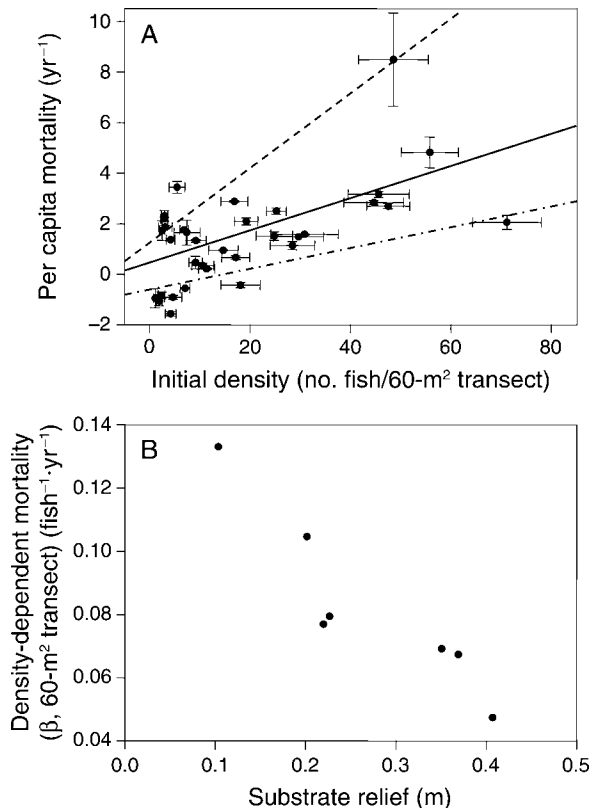


FIG. 1. (A) Density-dependent mortality of blue rockfish. The solid line indicates the best fit mortality function when all sites were considered in a linear, mixed-effects model. Among-site variability in mortality is illustrated by superimposing mortality functions for sites with the lowest (dashed line) and highest (dot-and-dashed line) levels of substrate relief. Error bars indicate \pm SE. (B) Estimated coefficients of density-dependent mortality at each site plotted against habitat complexity (substrate relief).

For each level of habitat complexity, I quantified the overall importance of each process in determining the number of 1-yr-old fish by comparing the limitation functions to the observed recruitment distribution. Recruitment was not correlated with habitat complexity (see *Results*), so I pooled all recruitment observations (collected over time and across a large spatial range) to generate a recruitment distribution that was likely to be representative of the expected distribution of recruitment to any given site. Recruitment observations were collected from the same surveys used to measure mortality. However, there were more observations of recruitment available ($n = 91$ observations) since multiple consecutive surveys were required to reliably measure mortality of cohorts at each site.

The relative importance of each process in determining abundance of 1-yr-olds was quantified by three different measures. First, the frequency at which each of the processes was the most limiting was compared by determining the range of recruit densities over which each process had the greatest values of limitation and

calculating the proportion of recruitment observations that fell within that range. Comparing relative importance based on recruitment observations provides a measure of how often each process is most limiting. This approach is informative, yet it is somewhat unbalanced in that large recruitment events, while infrequent, represent a large number of individuals. As a second, complementary measure of relative importance, I estimated the proportion of individuals that recruited within the range of densities where each process had the highest values of limitation. These two measures can be used to better understand how each process limits population size (i.e., whether particular processes limit population size slightly, but frequently, or whether processes strongly limit population size during rare occasions when recruitment is large). As a final measure of relative importance, hereafter “integrated limitation,” I estimated limitation by each process as an empirically-based integration of the limitation function and the observed recruitment distribution. For each process, I summed the limitation value of that process for all observations in the recruitment distribution. Integrated limitation values for each process were expressed as the proportion of the total of the integrated limitation values for all processes.

RESULTS

Mortality of blue rockfish over their first year was variable, but clearly increased as a function of initial density of recruits (Fig. 1A; Table 1). A linear model of the mortality function was used to estimate parameters of a Ricker equation describing the recruit–1-yr-old relationship. Although other forms of density dependence are possible, the available data were best described by a Ricker model, rather than a Beverton-Holt model that describes an asymptotic recruitment function (Ricker AIC = 74.1, Beverton-Holt AIC = 76.5; Appendix A). I therefore used a Ricker model of density dependence for the rest of my analyses. The linear transformation of the Ricker model provided a good overall description of mortality. However, much of the additional variation in mortality was explained by differences in mortality rates among sites (Fig. 1A). Comparison of linear, mixed-effect models indicated that the data were best described by a model that allowed both the slope and intercept of the mortality function to vary among sites (likelihood ratio test, $P =$

TABLE 1. Model output summarizing the overall effect of initial density on mortality of blue rockfish.

Parameter	Value	SE	df	<i>t</i>	<i>P</i>
Intercept	0.1786	0.372	26	0.48	0.635
Initial density	0.0794	0.0157	26	5.049	<0.0001

Notes: Coefficients are for a linear mixed-effects model with initial density as a fixed effect. Among-site variation was accounted for by allowing the slope and intercept parameters within each site to vary as random effects.

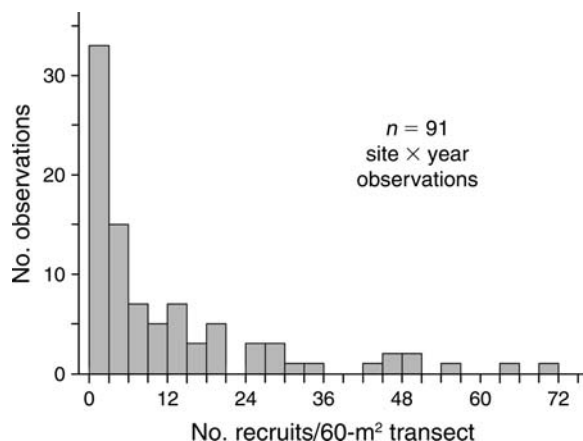


FIG. 2. Distribution of blue rockfish recruitment. Observations were collected over six years at nearshore reefs throughout central California.

0.0397; Appendix D) thus indicating that both density-independent and density-dependent mortality significantly varied among sites.

Although the number of cohorts within each site was limited, visual inspection of the data suggested that the mortality function varied with habitat complexity (Fig. 1B). A formal test based on the error-corrected, back-calculated values of the Ricker equation describing mortality at each site indicated that mortality coefficients significantly varied with habitat complexity (MANOVA, Pillai trace $F_{2,4} = 10.6$, $P = 0.025$) and that both density-independent and density-dependent mortality decreased with increased complexity (linear combinations, $\alpha = 2.145 - 5.409 \times \text{substrate relief}$; $\beta = 0.145 - 0.235 \times \text{substrate relief}$).

Limitation analysis

Data from field surveys suggested that the distribution of the density of recruits was highly skewed, with many observations at relatively low densities (<20 individuals per 60-m² transect) and few observations at high densities (Fig. 2). Recruit density was not correlated with habitat complexity (linear regression, $P = 0.58$, $n = 91$, $r^2 = 0.004$) so recruitment data from all sites were pooled for further analyses. To conduct limitation analyses under varying levels of habitat complexity, I used the output of the MANOVA analysis comparing among-site complexity and mortality to estimate mortality coefficients at three levels of habitat complexity (Table 2).

Comparing the expected recruitment distribution with limitation functions based on mortality at different levels of habitat complexity yielded overall estimates of how important each process is in determining the number of 1-yr-old fish entering the population and how the relative importance of processes may change with habitat complexity (Table 3). In general, density-dependent mortality was most limiting across the widest range of recruitment levels (Fig. 3). However, most

recruitment observations occurred at low densities where recruitment and/or density-independent mortality was the most limiting process (cf. Figs. 2 and 3). At mean complexity levels, the number of recruitment observations that would occur when recruitment was most limiting was slightly higher than the number that would occur when density-dependent mortality was most limiting (Table 3). However, most individuals recruited at densities where density-dependent mortality was the most limiting process, and based on integrated limitation values density-dependent mortality was the largest overall constraint on population size (Table 3). Variation in habitat complexity changed the relative importance of each process. At low complexity levels, density-independent mortality was most frequently limiting, and although most individuals recruited at densities where density-dependent mortality was most limiting, density-independent and density-dependent mortality had very similar constraints on population size (measured by integrated limitation). At high complexity levels, density-independent mortality was never most limiting. Recruitment limitation became more important at high levels of complexity, and most observations occurred at densities where recruitment was most limiting. However, most fish recruited at densities where density-dependent mortality was most limiting and density-dependent mortality still had the largest value for integrated limitation (Table 3).

DISCUSSION

Habitat complexity and recruitment dynamics

By altering rates of density-independent and density-dependent mortality, habitat complexity can have substantial effects on the dynamics of blue rockfish recruitment (i.e., the addition of 1-yr-olds to the population). At low levels of complexity, local population size was most strongly affected by density-independent mortality. Density-dependent mortality was relatively strong and values for limitation by recruitment were low, suggesting that populations in such habitats would likely exhibit little fluctuation in response to variable recruitment. However, as habitat complexity increased, recruitment became more important. At the highest levels of habitat complexity, limitation by recruitment was substantial (integrated

TABLE 2. Effects of habitat complexity (substrate relief) on components of mortality of juvenile blue rockfish.

Habitat complexity	Density independent		Density dependent	
	Mortality (α)	SE	Mortality (β)	SE
Low ($x - \text{SD}$)	0.990	0.121	0.0947	0.0053
Mean (x)	0.598	0.108	0.0777	0.0047
High ($x + \text{SD}$)	0.203	0.143	0.0605	0.0062

Note: Density-independent and density-dependent components of mortality, respectively, correspond to α and β in the Ricker equation describing survival (see Eq. 2).

TABLE 3. Relative importance of three processes determining population size of 1-yr-old blue rockfish: density-independent mortality (DI), density-dependent mortality (DD), and supply of recruits (R).

Process	Mean complexity				Low complexity (mean relief – SD)			
	Limiting range (no. fish/60-m ² transect)	Obs. %	Fish %	Integrated limitation	Limiting range (no. fish/60-m ² transect)	Obs. %	Fish %	Integrated limitation
R	0–4.57	47.3	6.9	29.2	none	0	0	25.3
DI	4.57–7.70	12.1	6.1	28.0	0–10.45	63.7	16.3	37.7
DD	7.70+	40.7	87.0	42.8	10.45+	36.3	83.7	37.0

Notes: Limiting range is the range of recruit densities over which each process had the greatest limitation value. Relative importance was expressed as the percentage of recruitment observations occurring within the limiting range of each process (Obs. %), as the percentage of individuals that recruited at densities where each process was most limiting (Fish %), and as the integrated limitation (i.e., the total limitation values of each process summed over all recruitment observations and expressed as a proportion). Boldface type indicates the greatest value for each column.

limitation = 36.4%), although limitation values for density-dependent mortality were higher (51.1%). In general, limitation values for density-dependent mortality were high because large recruitment events (which have the potential to add many individuals to the population) are strongly reduced by density-dependent mortality. However, even though density-dependent mortality will act to dampen the effects of variable recruitment, in high complexity habitats density-dependent mortality was reduced and population dynamics may still strongly reflect variation in recruitment. Based on the observed recruitment distribution and estimated mortality function, in high complexity habitats approximately 75.8% of the observations (29.6% of the individuals recruiting) occurred at densities where there would be a monotonically increasing relationship between recruitment and number of 1-yr-olds.

Although it is not surprising that habitat complexity affects mortality of fishes (Crowder and Cooper 1982, Beukers and Jones 1997), it is the effects of complexity on both density-independent and density-dependent components of mortality that may lead to qualitative changes in population dynamics. In particular, habitat complexity may have differential effects on density-independent and density-dependent mortality. As hab-

itat complexity increased, both density-independent and density-dependent mortality became weaker. However, the proportional reduction in density-independent mortality was much more severe (see coefficients in Table 2) resulting in a strong decrease in the limitation function. Consequently the relative importance of density-dependent mortality increased with complexity even though the actual magnitude of density-dependent mortality decreased.

Variation in habitat complexity had substantial effects on the variation in the recruit–1-yr-old relationship. However, the analysis was correlative and other factors may contribute to spatial and temporal variation in mortality of reef fishes. Most notably for marine fish, the magnitude of density-dependent mortality may be affected by the abundance of interspecific competitors (Schmitt and Holbrook 1999, Carr et al. 2002) and/or the local density or type of predators (Hixon and Carr 1997, Johnson 2006b). Although the densities of both predators and competitors are likely to be positively correlated with habitat complexity, the available data suggest that increased abundance of predators or competitors results in an increase in the strength of density-dependent mortality for fishes (Schmitt and Holbrook 1999, Carr et al. 2002, Johnson 2006b). In

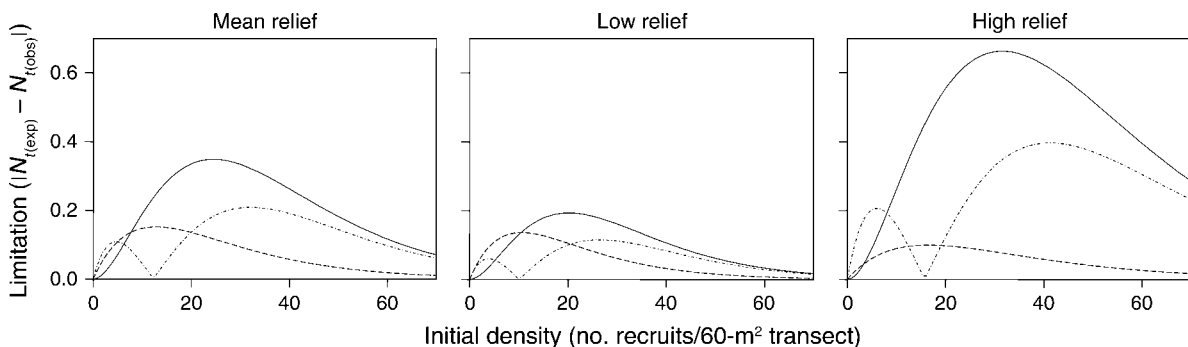


FIG. 3. Limitation of the density of 1-yr-old blue rockfish by three processes: density-independent mortality (dashed lines), density-dependent mortality (solid lines), and recruitment (dot-and-dashed lines). Limitation values are plotted as a function of initial recruit density. $\hat{N}_{t(\text{exp})}$ is the density of 1-yr-olds expected when the process under consideration (density-dependent mortality, density-independent mortality, or recruitment) is increased 10%. $\hat{N}_{t(\text{obs})}$ is the density of 1-yr-olds predicted from the Ricker equation when all processes are operating at ambient levels. Each panel illustrates limitation functions at a different level of habitat complexity (substrate relief): mean, low (mean – SD), and high (mean + SD).

TABLE 3. Extended.

High complexity (mean relief + SD)			
Limiting range (no. fish/60-m ² transect)	Obs. %	Fish %	Integrated limitation
0–12.4	69.2	21.7	36.4
none	0	0	12.5
12.4+	30.8	78.3	51.1

this study, increased habitat complexity decreased the strength of density-dependent mortality. These findings are consistent with experimental studies examining the effects of habitat complexity and prey refuge on the intensity of density-dependent mortality (Forrester and Steele 2004).

Another potential source of bias in this study is the underestimation of initial recruit densities. Data were collected from annual monitoring surveys that were designed to sample many fish species and were conducted in late summer; several weeks after most of the blue rockfish had recruited. The magnitude of recruitment and post-settlement mortality may have been underestimated because of mortality that occurred prior to the surveys. Many small, coral-reef fishes experience extremely high mortality in the short period immediately after settlement. However, blue rockfish settlers are adept swimmers and settle at a relatively large size (3.5–4 cm TL; Love et al. 2002). While there is likely to be some bias, I believe that the survey data used here can provide a reasonable measure of the relative importance of processes that determine abundance. With more accurate estimates of settlement, it is likely that the relative importance of post-settlement mortality would have been greater, since mortality values would be greater. However, the effects of habitat complexity on relative importance would likely be the same unless the effects of habitat complexity on immediate post-settlement mortality are qualitatively different than those reported here. Likewise, the form of density dependence and the choice of recruitment models (e.g., Ricker or Beverton-Holt) may affect the limitation value for each process. Although the choice of models may affect parameter estimates and limitation values, the effects of habitat complexity on recruitment dynamics would be similar and it is unlikely that the use of a different recruitment model would affect the main conclusion of this study.

*Importance of recruitment vs. post-recruitment factors
in determining abundance*

Many studies that have examined the dynamics of open populations suggest that variation in ambient recruitment level largely determines the relative importance of pre- and post-settlement factors (Connell 1985, Gaines and Roughgarden 1985, Jones 1990, Menge 2000). However, this may not always be the case. Variation in post-settlement mortality (particularly

variation in the intensity of density-dependent mortality) may be an important and overlooked factor affecting the relative importance of pre- and post-settlement processes (Shima 1999, Shima and Osenberg 2003). In this study, the structural complexity of the habitat—a demonstrated source of variation in density-dependent mortality (Kareiva and Sahakian 1990, Forrester and Steele 2004, Johnson 2006b) can account for large-scale variation in the dynamics of populations. Moreover, recruitment of blue rockfish was not correlated with habitat complexity, suggesting that the relative importance of pre- vs. post-settlement factors may be determined by a quantifiable habitat feature, rather than ambient recruitment level alone.

Spatial and temporal variation in recruitment dynamics

In this system, habitat complexity had strong effects on post-settlement mortality and exhibited a high degree of spatial variability. This may lead to substantial spatial variation in both the dynamics of blue rockfish and their effect on local communities. In habitats where post-settlement mortality (particularly density-dependent mortality) is relaxed, populations may fluctuate more in response to variable recruitment (Caley et al. 1996). Within such habitats large recruitment events may generate large cohorts that survive to adulthood. Spatial variability in complexity may contribute to source-sink dynamics by determining the degree to which habitats may store reproductive potential in the form of large cohorts of adults (Warner and Chesson 1985). Additionally, recruitment fluctuations may be very important in determining the impact of species on other members of the community (Sale 1982, Gaines and Roughgarden 1987, Connolly and Roughgarden 1999, Chesson 2000).

Variation in habitat complexity may also contribute to temporal variation in recruitment dynamics. For several marine fishes, qualitative changes in recruitment dynamics have been observed in the form of phase transitions in time-series observations of population abundance (reviewed by Duffy-Anderson et al. 2005). Phase transitions are evidenced by changes in the dynamic properties of a system and may include long-term shifts in the strength of density-dependent processes and/or the relative importance of various life history stages to the dynamics of the total population (Ciannelli et al. 2004, 2005). Phase transitions in recruitment and population dynamics may be caused by climate forcing, changes in community structure, or fishery practices (Duffy-Anderson et al. 2005). Changes in habitat complexity may also effect qualitative changes in recruitment dynamics, particularly if biogenic habitat is degraded. Although young-of-the-year blue rockfish primarily associate with rock structure, many fishes with similar life histories inhabit biogenic structures such as corals, macrophytes, or other structure-forming invertebrates. In addition to reducing overall abundance, prolonged reduction in habitat complexity may shift the dynamics of populations from a state where population

size experiences large fluctuations with recruitment to another where recruitment has less influence on abundance. In degraded habitats, cohort size may be kept at a minimum as recruitment fluctuations are strongly dampened by post-settlement mortality. Consequently, population growth and recovery via storage may be restricted in low complexity habitats. Variation in habitat quality, and the resulting effect on local population dynamics should therefore be considered in conservation and management strategies, especially those that are spatially explicit, such as marine protected areas.

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APPENDIX A

Comparison of density-dependent models to describe mortality (*Ecological Archives* E088-101-A1).

APPENDIX B

Methods for calculating density-independent and density-dependent mortality in the Ricker equation (*Ecological Archives* E088-101-A2).

APPENDIX C

Limitation functions for density-independent mortality, density-dependent mortality, and supply of recruits (*Ecological Archives* E088-101-A3).

APPENDIX D

Comparison of linear, mixed-effects models describing among-site variation in mortality of blue rockfish (*Ecological Archives* E088-101-A4).