



HABITAT DEGRADATION AND SETTLEMENT BEHAVIOR: EFFECTS ON FISH SETTLEMENT, SURVIVAL, AND RECRUITMENT.

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Abstract As coral reefs change in their composition, the dynamics of organisms that depend on them will likely also be affected. Traditionally, marine ecologists have recognized that settlement of fishes (and invertebrates) is tremendously variable in space and time, and changes in coral communities might therefore be expected to operate through effects on settlement. However, recent work demonstrates that density-dependent survival also varies spatially, with high quality sites offering greater recruitment than low quality sites at comparable settler densities. Furthermore, variation in settlement may often be correlated with site quality. As a result, understanding the response of fish populations to changes in coral communities requires that we understand how site quality and settlement interact through larval behavior.

Here, we explore the implications of declines in site quality (e.g., due to the loss of coral habitat) and larval behavior. Specifically, we explore effects of larval site selection (and its dependency on site quality) and larval redirection (the extent to which larvae that would have settled at degraded sites can go on to settle elsewhere). We use data from the six-bar wrasse (*Thalassoma hardwicke*) system in Mo'orea, French Polynesia. We show that under some patterns of larval behavior, settlement, recruitment and survival can actually increase as habitat loss increases. These counter-intuitive results have important implications for informing monitoring studies of reef fish. The results also suggest the need for understanding the relationship between settlement rates and site quality, and for quantifying the extent of larval redirection.

Keywords reef fish, cryptic density dependence, habitat quality, larval redirection, settlement preferences

Introduction

As coral reefs degrade (Wilkinson 2000), the dynamics of organisms that use these reefs for shelter, foraging and reproduction will likely also change (e.g., Booth and Beretta 2002; Jones *et al.* 2004). These faunal responses will be driven, in part, by effects that coral abundance and composition have on demographic rates of the focal populations (i.e., through effects on reproduction, settlement, mortality, and migration). Fishes, which may have very specific requirements for successful settlement and reproduction, may be particularly affected by declines in coral cover and shifts in community composition (Booth and Wellington 1998).

Demographic rates also are likely to be affected by density (Doherty 2002; Osenberg *et al.* 2002a), and if fish density changes in response to coral reef degradation, then these density effects need to be integrated with our knowledge of changes in habitat quality. Importantly, recent studies have further shown that the strength of density-dependent and density-independent demographic rates can vary spatiotemporally and may depend on habitat characteristics, such as coral composition (e.g., Wilson and Osenberg 2002, Shima and Osenberg 2003, Shima *et al.* 2005). To date, most studies of fish responses to changing coral communities have ignored the effects of changing density. Of course, because many reef fishes are site-attached during their benthic life stage and density effects are therefore determined by local neighborhood effects, the effects of density will depend on how fish

distributions (at a local scale) are influenced by shifts in the coral community.

In this paper, we explore how declines in habitat quality (e.g., as mediated by the loss of live coral) affect the settlement, survival and subsequent recruitment of a coral reef fish. We further explore how this response will depend on the settlement behavior of larval fish, specifically whether the larvae exhibit settlement preferences for sites of different quality and whether larvae are able to "redirect" (sensu Osenberg et al. 2002b) their settlement if high quality sites are no longer available (due to habitat loss).

We use the reef fish *Thalassoma hardwicke* (Bennett 1828: the six-bar wrasse), as a model system to explore this question because 1) it settles to and uses live coral habitat during its early benthic life history; 2) post-settlement density-dependent mortality is an important determinant of recruitment; and 3) the strength of this density-dependence varies spatiotemporally and is correlated with coral community attributes (Shima 1999; 2001a; 2001b, Shima and Osenberg 2003, Shima et al. 2005). Although the cause of this heterogeneity in density dependence is not yet known (Shima et al. 2005), here we assume that it is caused by differences in the coral community and thus use our data to simulate the response of six-bar wrasse to shifts in the coral community. Finally, although we motivate our work with the six-bar wrasse system, our approach is fairly general and we hope it will stimulate further work on the interplay of habitat loss, density dependence and larval behavior in a variety of systems.

Materials and methods

The system -

Shima and Osenberg (2003) estimated the strength of density dependent post-settlement mortality using a Beverton-Holt recruitment model (Beverton and Holt 1957; Osenberg et al. 2002a) and data from 480 recruitment events to small patch reefs for *T. hardwicke* on Mo'orea, French Polynesia (17° 30' S, 149° 50' W). The strength of density-dependence was correlated with features of the benthic community on the local patch reef (e.g., coral cover and composition: Shima et al. 2005). The parameter that defines the per capita effect of conspecifics on post-settlement mortality is β -- increases in β indicate increasing effects of density and therefore for a given level of settlement, a site with larger β will yield fewer recruits than a site with β closer to 0. We therefore define habitat quality as $1/\beta$. In this system, there is considerable variation in habitat quality that can be present at the scale of just a few meters to several kilometers (Figure 1).

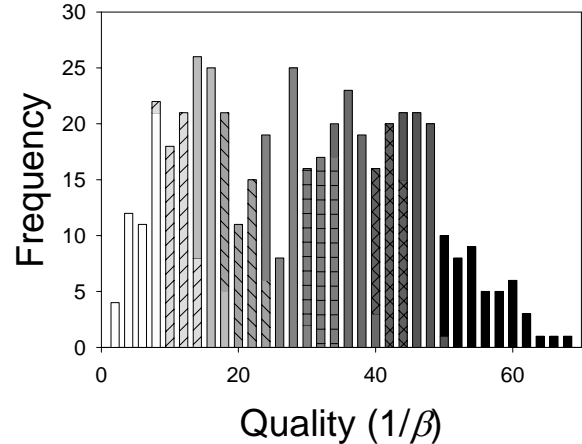


Fig. 1. Frequency distribution of site quality as defined as the reciprocal of the strength of density dependent survival (β) for *Thalassoma hardwicke* in Mo'orea French Polynesia. Higher quality sites yield greater recruitment than lower quality sites at a given density of settlement. The 480 estimates are sorted into groups (denote by different shades) that correspond to 10% of the total distribution. Based on results of Shima and Osenberg (2003).

Simulation of habitat degradation -

Habitat loss. We sorted all 480 recruitment events by site quality ($1/\beta$), assumed that the total sample gave a good description of the range of sites available, and simulated habitat degradation by sequentially eliminating 10% of the sites that were of highest quality. This elimination of 10% of the sites was continued until no sites remained. For each level of habitat loss (0% to 100% by 10% increments), we determined the total settlement and recruitment (i.e., the number of settlers that survived to 90 days) by 1) determining settlement based on site quality (see below) and 2) quantifying recruitment based upon the settlement rate and site quality. Because density-independent losses appear to be minimal in this system (Shima and Osenberg 2003), the Beverton-Holt recruitment function for a local site simplifies to:

$$R = S / (1 + \beta S t) \quad (1)$$

where R is recruitment, S is local settlement, β is the per capita effect of density on survival, and t is the time from settlement to recruitment (in this case, 90 days).

Settlement patterns. Larvae may exhibit preferences for sites of different quality. In the *Thalassoma* system, more larvae settle to sites of higher quality, although the relationship appears to decelerate (Figure 2). Cryptic density dependence (CDD, sensu Shima and Osenberg 2003) occurs whenever settlement increases with site quality. In the pure

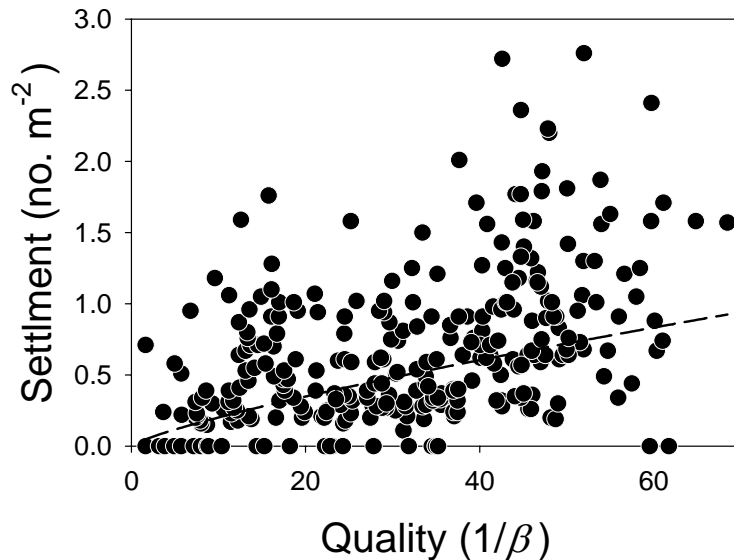


Fig. 2. Settlement intensity in relation to habitat quality, as measured as the reciprocal of the strength of density dependence ($1/\beta$). Settlement and quality are taken from a study of *Thalassoma hardwicke* in Mo'orea, French Polynesia (Shima and Osenberg 2003). The dashed line gives the power function ($Y=aX^b$) with the best fit: $r^2 = 0.14$, $a = 0.033 \pm 0.013$ (SE), $b = 0.79 \pm 0.11$ (SE), which indicates that settlement increases, but at a decelerating rate, as quality increases. Hence, in this system, even though fish settle more to higher quality sites (than lower quality sites), they do so at a rate that is less than expected under the Ideal Free Distribution.

form of CDD, settlement is proportional to habitat quality. This is identical to an Ideal Free Distribution (IFD: Fretwell and Lucas 1970), in which larvae distribute themselves among patch reefs to equalize post-settlement survival: fish that settle to high quality patches do so at sufficiently high density that their expected survival is the same as fish that settle at low densities to sites of low quality. There is evidence from other systems (e.g., Wilson and Osenberg 2002, Holbrook and Schmitt 2003) that the relationship between settlement and site quality may be positive or negative. Thus, we considered 5 forms of settlement pattern (Figure 3): 1) Strongly positive preference (greater than expected under IFD or CDD); 2) Positive preference (as expected under IFD and CDD); 3) weakly positive preference (i.e., weaker than IFD, as is the case for the six-bar wrasse: Fig. 2); 4) random preference (i.e., constant across site quality); and 5) negative preference (proportional to the inverse of site quality).

We also explored the effect of larval "redirection" (sensu Osenberg et al. 2002b): i.e., the ability of larvae that would have settled in habitat that has been lost in other extant habitat. In the absence of larval redirection, habitat loss translates directly into the loss of settlement – larvae that would previously have settled to the degraded site now have nowhere to settle. When larval redirection occurs, the larvae that would have settled into the lost habitat are redistributed among the remaining sites. This will intensify any local process that is density-dependent.

Thus our simulation was a crossed design in which we varied settlement preference (five forms: Figure 3) and larval redirection (two levels: complete redirection vs. none). We quantified settlement and recruitment to all extant sites (i.e., 480 patch reefs

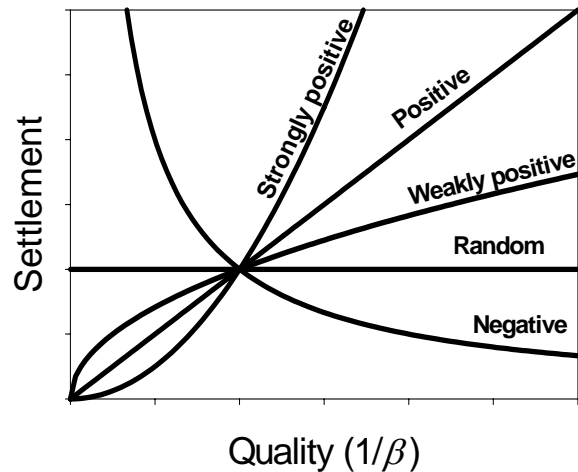


Fig. 3. The five general preference functions explored in the simulation. Settlement was either independent of site quality ("random"), proportional to site quality ("positive" preference, as predicted by an Ideal Free Distribution), increased faster or slower than proportionally to site quality ("strongly" vs. "weakly positive" preference, respectively), or decreased with site quality ("negative" preference). These cases were specifically modeled by assuming that settlement was proportional to quality to the power of -1 (negative), 0 (random), 0.5 (weakly positive), 1 (positive), or 2 (strongly positive).

without habitat loss, or 90%, 80%, etc. of these following the sequential loss of the highest quality sites) under these 10 different preference/redirection scenarios. Settlement in the absence of habitat loss was fixed at the average from our studies (283 fish

per 480 reefs), and decremented due to habitat loss (if there was no larval redirection). These larvae were then allocated to the extant sites as defined by the settlement preference function. Recruitment was then obtained using Eqn. 1 and site-specific estimates of β . We quantified post-settlement survival as the ratio of recruitment to settlement, since survival is a key variable measured in most field studies. Finally, instead of looking at the aggregate of all non-degraded (i.e., extant) sites, we also monitored the 48 worst sites (i.e., the poorest 10% of the 480 sites) and quantified settlement, recruitment and survival to these sites. We did this to mimic a field sampling program that was stratified to focus on a specific type of habitat, as is commonly done in many monitoring designs. Our results apply to any subset of sites, but we chose the worst sites to examine the widest range

of habit loss (these sites were not eliminated until the final 10% of the habitat was destroyed).

Results and Discussion

Regional response without larval redirection -

In the absence of larval redirection (Fig. 4A,B,C), settlement declined as habitat loss increased, although the rate of decline depended on the preference function. When fish settled at random (without respect to site quality), total settlement declined in proportion to the extent of habitat loss (Fig. 4A). If settlement was greatest to lower quality sites (negative preference), the decline was initially slight (because the best sites received fewer settlers) and increased as habitat loss became more pronounced. As preference increased for higher quality sites, the initial loss increased.

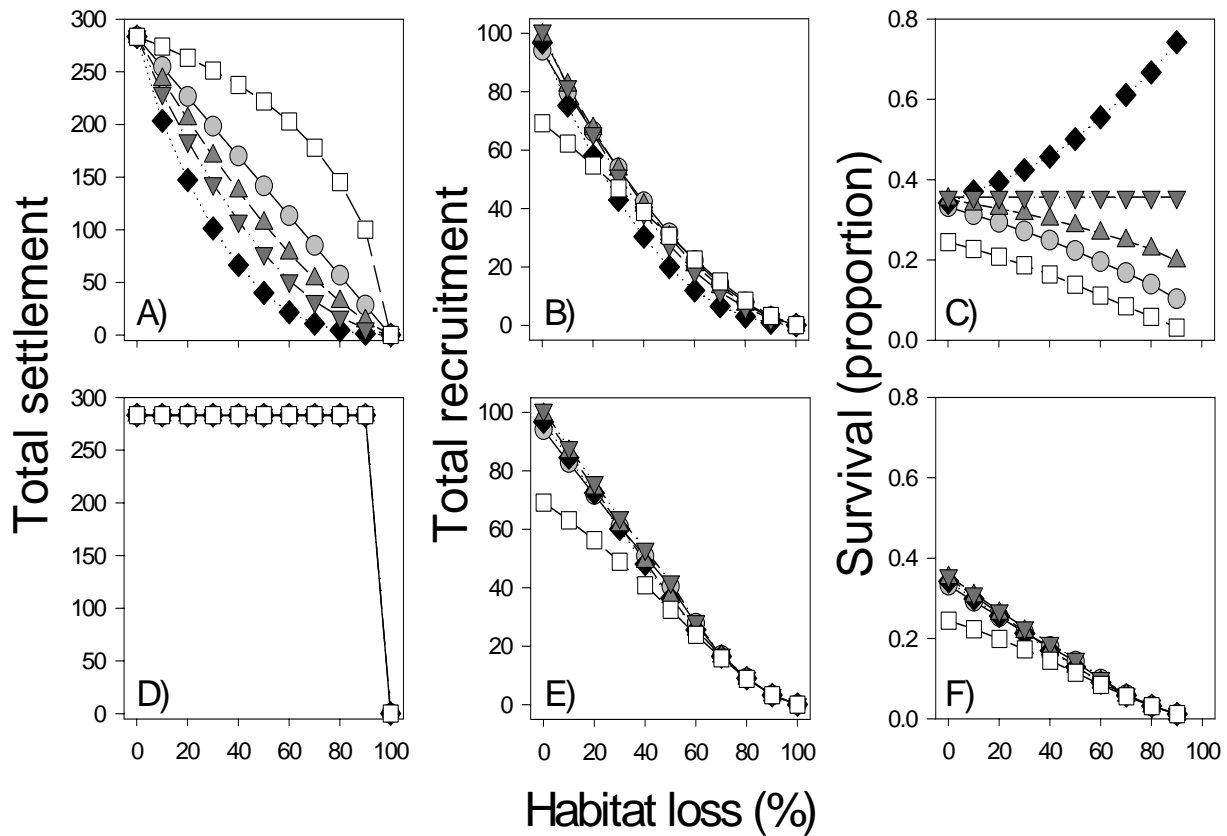


Fig. 4. Effects of habitat loss, settlement preference, and larval redirection on: (A, D) total settlement, (B, E) total recruitment, and (C, F) survival (i.e., proportion of the settlers that survive to recruit). Panels A, B, and C give the results in the absence of larval redirection; panels D, E, and F give the results in the presence of larval redirection. Results are based on all sites that have not been degraded (i.e., lost). Habitat loss was simulated by sequentially removing 10% of the highest quality sites that remained in the regional system (see Fig. 1). The five curves in each panel correspond to the different settlement preference functions and are colored from white to black to indicated increasing preference: strongly positive preference (\blacklozenge), positive preference (i.e., Ideal Free Distribution, dark grey ∇), weakly positive preference (grey \triangle), random preference (light grey \circ), and negative preference (\square).

Recruitment mirrored the general pattern of settlement, although there were relatively few demonstrable effects of the preference function (Fig. 4B). Because settlement declined as habitat loss increased, so too did recruitment. In the absence of habitat loss, there was lower recruitment when fish settled preferentially to low quality sites because densities were concentrated on sites with strong per capita effects of density. Thus, the recruitment from these sites was low compared to the recruitment that would have occurred had those high densities been present on higher quality sites. The limited differences among the remaining preference functions (Fig. 4B) arose because in this particular scenario, settlement rates were sufficiently high to place the system near the asymptote of the Beverton-Holt function: i.e., the system was close to saturation. Reducing the overall input of settlers would increase the disparity among the recruitment response for the different preference functions.

The fraction of settlers that survived to recruit was strongly affected by habitat loss and the preference function (Fig. 4C). Under positive preference (i.e., the Ideal Free Distribution), survival remained constant as habitat was lost. This arose because fish settled to sites of different quality to homogenize their survival despite differences in quality. Because larvae that would have settled to lost habitat are not redirected, the sites that remained yielded the same survival as occurred prior to the habitat loss (because survival is equivalent on all sites at all levels of habitat loss). In contrast, when preference is weakly positive, random or negative, survival declined with habitat loss. This occurred because the highest quality sites were those that provided the highest fractional survival. Settlement to these higher quality sites was not sufficient to reduce survival (through density dependence) relative to the survival that occurred on lower quality sites. The interesting exception occurred when fish exhibited strong preferences for high quality sites: i.e., when they settled at such high densities to the higher quality sites that these sites actually offered lower survival than lower quality sites. As a result, as habitat loss increased, survival actually *increased*!

Regional response with larval redirection -

When larvae were redirected to remaining habitat, a different picture emerged. Total settlement remained high – larvae simply redistributed themselves to the remaining habitats (Fig. 4D). Total recruitment was little affected, because each site was already near saturation – the redirection of larvae to

the remaining sites had little effect on overall recruitment (Fig. 4E). However, this arose because the proportion of settlers that survived to recruit decreased strongly as habitat loss increased (compare Fig. 4F with 4C). Larval redirection concentrated fish on the few remaining sites, intensifying the effects of density, and driving survival to very low levels under all five preference scenarios (Fig. 4F). As a result, the interesting result that arose in the absence of larval redirection when there was positive preference (no change in survival) or strongly positive preference (increasing survival) was completely negated in the presence of larval redirection (compare Figs. 4F and 4C).

Response on a habitat type without larval redirection -

In contrast to quantifying the response of the entire population of sites, we also examined the response on a more limited range of sites (i.e., sites of similar quality): e.g., by sampling sites with a more uniform composition of corals. Such an approach is often taken to increase statistical power and eliminate noise introduced by including a wide range of habitats in a monitoring program. In the absence of larval redirection, there was no change in settlement to these sites as habitat loss increased (until those sites were themselves lost): Fig. 5A. Because settlement was not affected, neither was recruitment (Fig. 5B), nor survival (Fig. 5C). Note that settlement preference did have an effect on settlement, recruitment and survival – when settlers were concentrated on low quality sites (e.g., via negative preference) settlement and recruitment to these low quality sites was greatest, although survival was lowest. As settlement to these low quality sites declined (because preferences became biased towards higher quality sites), settlement and recruitment declined, but survival increased (Figs. 5A,B,C).

However, in the presence of larval redirection different patterns emerged because local density on the focal sites increased as other habitat was lost. As more and more larvae were redirected to the remaining habitat, settlement and recruitment increased, but survival decreased because the increasing density had a negative effect on per capita survival. Thus, as habitat was lost, a sampling program targeting a narrow range of habitat quality (or types) actually found that settlement and recruitment *increased*, potentially hiding the deleterious effects that arose in the environment (which were only revealed by examining survival).

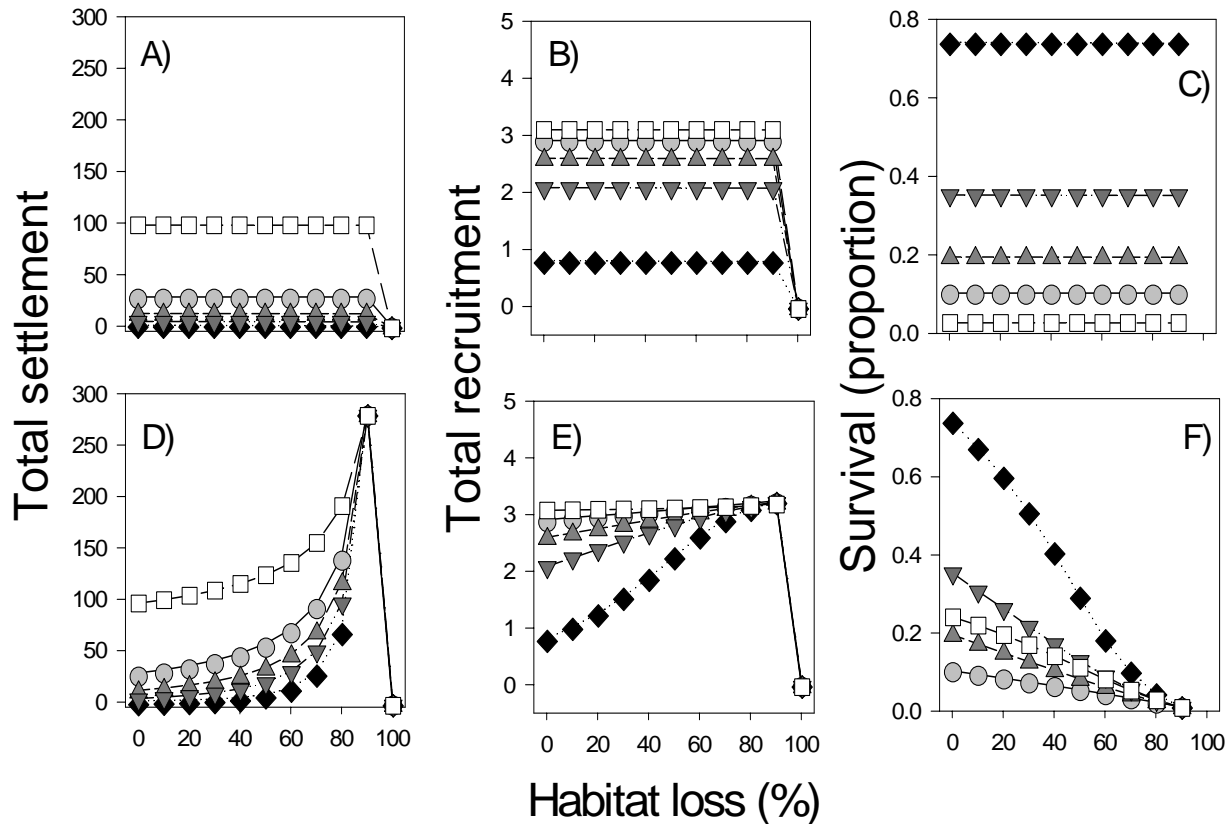


Fig. 5. Effects of habitat loss, settlement preference, and larval redirection on (A, D), total settlement, (B, E) total recruitment, and (C, F) survival (i.e., proportion of the settlers that survive to recruit) for the 48 worst sites (i.e., the final 10% of sites to be lost from the regional system). Habitat loss was simulated by sequentially removing 10% of the highest quality sites that remained in the regional system (see Fig. 1). The five curves in each panel correspond to the different settlement preference functions and are colored from white to black to indicated increasing preference: strongly positive preference (◆), positive preference (i.e., Ideal Free Distribution, dark grey ▽), weakly positive preference (grey △), random preference (light grey O), and negative preference (□).

Implications -

Our analyses implicate the important interplay of settlement behavior (mediated through settlement preferences and larval redirection), density dependent survival, and habitat loss. Because sites may vary in their quality, the habitat that is lost may not be equivalent to the habitat that remains – systems are heterogeneous. Furthermore, because this variation in quality may be mediated through differences in the strength of density-dependence, we cannot simply understand responses to habitat loss by looking at changes in input rates (i.e., settlement) or density-independent survival after settlement. Instead, density-dependence modifies how the remaining habitat will function to either buffer, ameliorate or amplify the effects of habitat degradation and loss.

Unfortunately, we know very little about settlement preferences of fishes (*reviewed by* Booth and Wellington 1998). A wealth of data demonstrates that settlement can vary in space (and time): *reviewed in* Doherty (2002). Marine ecologists often view this dramatic variation in settlement as "random", but it may reflect underlying differences in the quality of sites. Fish larvae are known to possess a wide array of sensory abilities that lead to non-random settlement patterns (e.g., Kingsford et al 2002). Recent work also has documented natural spatial variation in post-settlement survival that is correlated with settlement, although the pattern of this correlation can be either positive or negative (Holbrook and Schmitt 2003, Shima and Osenberg 2003, Wilson 2004). When settlement is disproportionately higher to high quality

sites ("strong preference": Fig. 2), and larval redirection is absent (or sufficiently weak that increased density-dependence does not cancel the effect of settlement preferences), survival of the regional pool of settled fish can actually increase as habitat loss increases (Fig. 4C). Similarly non-intuitive results can arise in the presence of larval redirection when sampling is restricted to a subset of sites (e.g., increasing settlement and recruitment as habitat loss increases: Fig. 5D,E). Thus, care must be taken when interpreting how patterns of settlement, recruitment and survival relate to environmental conditions. Some apparently "positive" effects can arise even when the environment is degrading.

Larval redirection also appears to play a critical role in our results by determining how (or if) the local density of fish changes as settlement habitat is lost. Unfortunately, we know very little about larval redirection or how much different reefs "compete" for larvae. Previous modeling by Osenberg et al. (2002b) also suggested a key role of larval redirection (in the context of the effects of habitat augmentation with artificial reefs), yet we have no empirical data to evaluate this issue. We believe it is a key topic for future field studies that will prove critical in predicting the response of marine populations to habitat alterations.

Acknowledgements

We thank J. Wilson for helpful discussion about cryptic density dependence. This work was funded by the National Science Foundation (OCE-0242312) and an ISAT Linkage Grant from the Royal Society of New Zealand, and is a contribution from the Richard B. Gump South Pacific Research Station.

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