



Habitat configuration and availability influences the settlement of temperate reef fishes (*Tripterygiidae*)



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ABSTRACT

To survive, most benthic marine organisms must find suitable settlement habitat. For reef fishes, settlement habitat is often structurally complex, spatially heterogeneous, and dynamic. Consequently, successful settlement is likely to be determined by an interaction between larval delivery and behavior, habitat availability, and structural characteristics (e.g., configuration) of the habitat itself. We examined the effects of habitat configuration and availability on the settlement of New Zealand triplefins (*Tripterygiidae*), using a field experiment that comprised three habitat treatments and evaluated effects over naturally varying levels of larval supply. Our results suggest that settler density and total settlement are shaped by both the availability and spatial configuration of habitat patches. Highest total settlement occurred in larger, more clumped habitat patches. Lowest total settlement occurred in more dispersed habitat patches of the same size and smaller isolated patches. The densities of recently settled triplefins were lowest in the dispersed patches, and high in both isolated patches and the clumped patches. We speculate that dispersed patches may comprise a lower quality habitat, and/or provide a weaker settlement trigger for both physical and biological reasons. Clumped patches, on the other hand, may provide a stronger settlement cue via baffling of currents, or may represent a higher quality habitat for recently settled triplefins, triggering higher settlement. Our findings indicate that habitat availability can influence abundance of recently settled fish, but the landscape architecture is an equally important determinant of settlement success for triplefins.

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1. Introduction

A necessary first step in understanding the dynamics of any population is to determine its inputs. For many benthic marine organisms, input of new individuals occurs when pelagic larvae transition to adult habitats through settlement and subsequent recruitment. To settle successfully, many species require structurally complex benthic habitats, which provide foraging sites and refuges from predators. For this reason, habitat availability is debated as a leading cause of density dependent mortality and a constraint on settlement success in reef associated fishes (e.g. Stier and Osenberg, 2010; White and Caselle, 2008). However, the spatial configuration of the landscape may also influence habitat use by fish (Bohnsack et al., 1994), and the interaction between habitat patches and larval behavior may result in enhanced settlement to high quality habitat configurations within a landscape (Breitburg, 1991). A basic assumption is that larvae settle according to the ideal free distribution (IFD, sensu Fretwell and Lucas, 1970), such that higher-quality habitats will support higher densities than lower-quality habitats. If configuration of habitat does not influence its quality, we expect settler density to be

equal across all areas of habitat. A larger habitat patch should support more settlers overall, but the density of settlers would not differ from density in a smaller patch. However, if habitat configuration is a component of habitat quality, then the density of settlers would be highest in areas with favorable habitat configuration. This issue is of central importance to reef fishes, as they can exhibit complex behavioral patterns during settlement (Breitburg, 1991), and their habitats are often heterogeneous at multiple spatial scales (Feary and Clements, 2006; Pérez-Matus and Shima, 2010). Consequently, the existing conceptual framework (i.e., populations are limited by habitat availability) may be insufficient in heterogeneous habitats such as temperate reefs.

Temperate macroalgal reefs are highly dynamic, but relatively little attention has been given to the role of landscape configurations in settlement of fishes in these heterogeneous habitats (but see Deza and Anderson, 2010). Seasonal changes in availability of nutrients (Gerard, 1997), natural disturbances (storms) (Dayton et al., 1992; Ebeling et al., 1985), competitive interactions among benthic species (Schiel, 1988), and top down control by grazing (Ayling, 1981; Schiel, 1990) can all cause dramatic changes in the amount of macroalgae on a reef over time and space. These changes in algal structure can have ramifications throughout the ecosystem (Gaines and Roughgarden, 1987), as macroalgae-associated fishes are known to respond positively to the structural complexity of algal habitats, especially at the time of settlement (Carr, 1989; Pérez-Matus and Shima, 2010; White and Caselle,

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2008). These relationships are strong, and suggest a need for further experimental work on the role of landscape configuration in temperate macroalgal habitats with respect to early life stages.

The interplay between habitat configuration and settlement is of further interest with regards to habitat fragmentation and loss, as well as the use of artificial reefs in mitigation efforts (Grossman et al., 1997). Fragmentation is often cited as a driver of ecological change in marine systems and a leading cause of reduced biodiversity (reviewed in Fahrig, 2003). While there is some evidence of altered ecological interactions in patchy habitats (e.g. edge effects) (Bell et al., 2001; Hovel and Lipcius, 2001; Macreadie et al., 2009), the majority of studies fails to distinguish between the loss of habitat and the changes in landscape structure that typically co-occur in fragmented habitats (but see Bonin et al., 2011; Caley et al., 2001; Deza and Anderson, 2010). This distinction must be made in experiments in order to effectively inform management and mitigate habitat degradation (Fahrig, 2003). A wide variety of responses to landscape architecture has been observed, and the uncertainties underlying settlement success prevent mechanistic understanding of these responses.

In order to address these uncertainties, we asked the following question: how does the availability of settlement habitat and its spatial configuration influence the settlement of triplefins (Family: *Tripterygiidae*) on temperate macroalgal reefs in New Zealand? We used artificial habitat units in a field experiment to test the response of settling triplefins to two spatial configurations and two levels of habitat availability.

Similar to other reef fishes, settlement-stage triplefins use sensory cues to detect settlement habitat (McDermott and Shima, 2006) and settle readily to artificial habitat units (Shima and Swearer, 2009). We assume that settlement-stage individuals can initiate or delay their settlement behavior in response to the distribution and/or strength of cues across the landscape. We predicted that if habitat configuration does not influence habitat quality, then the density of settlers within habitats should be uniform, regardless of the spatial configuration of habitats (i.e. added habitat structure would increase total settlement, but density of settlers per unit of habitat would not change). Alternatively, we predicted that if habitat configuration influences habitat quality, then landscape structure should influence settler density. Specifically, we predicted that the density of recently settled fish per unit of habitat would increase as the quality of habitat increased. If habitat configuration influences habitat quality (for behavioral reasons or otherwise), we predicted that one configuration would receive higher settlement of triplefins given two patches with equivalent amounts of structure and differing arrangements. We did not have an a priori hypothesis concerning which configuration would receive the highest settlement.

2. Methods

2.1. Study species and site

Our experiment focused on the settlement patterns of a group of small reef fishes called triplefins (*Tripterygiidae*), because these are among the most abundant fishes on shallow reefs of New Zealand (Clements, 2003; Feary and Clements, 2006). Most triplefins are strongly habitat associated from the time of settlement (Syms, 1995) through adulthood (Clements, 2003), and there exists a high degree of fine scale variation in habitats used by different species of New Zealand triplefins (Wellenreuther et al., 2007). For triplefins, settlement to poor habitats may result in high post-settlement mortality (Connell and Jones, 1991), which suggests that the configuration of habitat may play a role in settlement success.

We conducted our experiment at Shelly Bay (41°17.8' S, 174°49.2' E), located along the Miramar Peninsula, Wellington Harbor, New Zealand. Shelly Bay is a representative of many of the small bays within Wellington Harbor, and elsewhere in New Zealand, and is characterized by a shallow subtidal reef of boulder, cobble, and rock outcroppings, with a shallow sand flat offshore of the reef (Fig. 1). The boulder and

rock outcroppings host several species of brown macroalgae, which contribute significantly to the reef structure. In Shelly Bay, the dominant species of macroalgae include *Cystophora retroflexa*, *Cystophora torulosa*, and *Carpophyllum maschalocarpum*, which are preferred settlement habitat for some species of triplefins (McDermott and Shima, 2006). Both adult and juvenile triplefins, and specifically the common triplefin, *Forsterygion lapillum*, have been observed in high densities in Shelly Bay (McDermott and Shima, 2006).

2.2. Experimental design

To minimize confounding effects of natural macroalgal structure, we used Standard Monitoring Units for Recruitment of Fish (SMURFs) to quantify spatial and temporal variation in settlement of fishes (Ammann, 2004; see Shima and Swearer, 2009 for details of SMURF construction). To distinguish between effects of habitat availability and configuration, we used SMURFs to construct the following 3 habitat treatments: 1) “clumped”, which comprised three SMURFs attached to moorings spaced 1 m apart, representing a large and relatively continuous patch of habitat (1 m spacing of moorings allowed SMURFs to touch at times, and probably facilitated movement of recruits among SMURFs); 2) “dispersed”, which comprised three SMURFs with moorings spaced 5 m apart, representing a more diffuse patch with the same total amount of settlement habitat (i.e., the two treatments had identical surface area and volume of ‘habitat’); and 3) “solitary”, consisting of a single SMURF, representing a small, isolated patch. We positioned replicates ($n = 3$) of each treatment randomly along a 4–6 m depth contour within Shelly Bay, with each replicate separated from adjacent replicates (and the nearest natural reef) by approximately 20 m (Fig. 1). The goal of this spacing was to (1) sample from a relatively homogeneous larval pool (i.e., we assume larval availability is homogeneous within a given time period), and (2) minimize the potential movement of recruits among independent replicates (Connell and Jones, 1991). Other studies of tagged post-settlement stage triplefins (Shima et al., 2012) suggest that individuals are unlikely to move between SMURFs with this spacing.

We attached each SMURF to an individual mooring line and positioned them approximately 2 m off the sea floor. We conditioned SMURFs in seawater for 1 week prior to the start of sampling to allow biofilms to colonize the substrate. Divers on SCUBA collected all fish from SMURFs every 1–2 weeks using BINCKE nets (Anderson and Carr, 1998) from February 14th–April 11th, 2012. Each site received the same treatment throughout the entire experiment, but the individual SMURFs that made up the treatments were rotated among sites at each sampling date. We sampled all SMURFs within a 3-hour period on the same day and returned all fish to the lab. We then counted and identified all fish to the lowest taxonomic level possible. Mean settlement per SMURF was greater than 1 fish per day during four complete sampling periods (sampling events between February 14th and March 12th); these were included in subsequent statistical analyses.

2.3. Statistical analysis

To distinguish between effects of landscape structure and total habitat area, we conducted two separate analyses of mean daily settlement of triplefins: (1) density of settlers, as calculated per unit of habitat (i.e., individual SMURFs); and (2) calculated per entire sites (i.e., cumulatively, across all SMURFs within each replicate). We considered total settlement to individual sites in addition to density of settlers to provide a complementary test of our predictions (i.e. settlement to an entire habitat patch may tell a different story than density of settlers). For each measure, we calculated daily settlement as the total number of settlers retrieved over the collection period divided by the duration (in days) of SMURF deployment. We did not observe any evidence of an interaction between the effects of treatment and sampling date in preliminary analyses, so we standardized daily settlement to z-scores

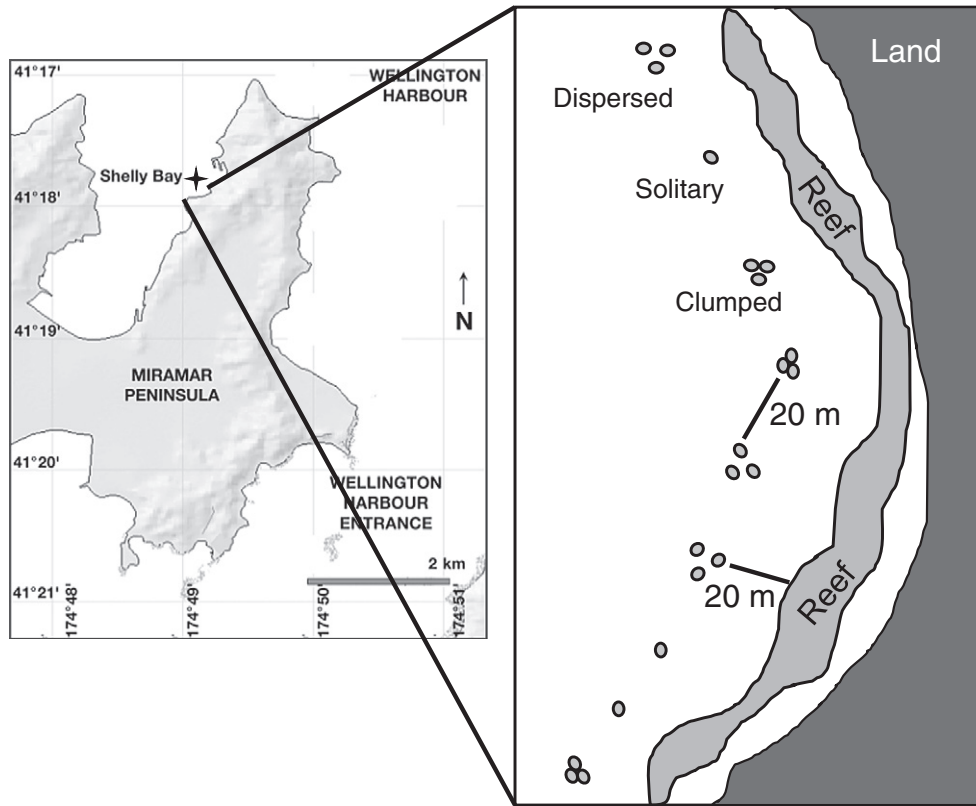


Fig. 1. Shelly Bay, Wellington Harbor, Wellington, New Zealand, with inset of experimental design and site layout (inset not to scale).

for each sampling date (Layman and Winemiller, 2004). This method effectively controlled for temporal variation in larval supply and enabled us to evaluate the effects of experimental treatment using 1-way Analysis of Variance. We conducted separate ANOVAs to evaluate mean daily settlement responses (calculated either per SMURF or per site), and used Tukey's Honestly Significant Difference tests to assess specific differences between treatments (SYSTAT ver. 12, $\alpha = 0.05$).

3. Results

3.1. Triplefin settlement

Over 4000 triplefins were collected, and two distinct settlement pulses were observed on February 14th and March 5th, separated by a period of reduced settlement on February 25th (Fig. 2). At least three species of triplefins were collected (*F. lapillum*, *Forsterygion varium*, and *Forsterygion maryannae*) from SMURFs, though these were not identified to species level (due to their early developmental stage) and were pooled across species for analysis. We believe the majority of the sample is *F. lapillum*. In previous collections, we used the mitochondrial control region to confirm species identities of a subsample of triplefins captured from SMURFs. For those assays, our subsample was not a random sample; instead we targeted individuals that appeared to be morphologically different. Nonetheless, we found that 87.7% of our sample was comprised of *F. lapillum* (Shima, unpublished data).

3.2. Settler density (settlement per SMURF)

We evaluated settler density per unit of habitat (per SMURF per day), and found significant differences in mean density of settlers among treatments ($F_{2,33} = 5.628$, $p = 0.008$, Fig. 3A). Density of settlers was lower in the dispersed treatment than the solitary treatment (Tukey's HSD, $p = 0.046$). The dispersed treatment also had lower

settler density than the clumped treatment (Tukey's HSD, $p = 0.009$). Density of settlers was highest and similar in the solitary and clumped treatments (Tukey's HSD, $p = 0.766$).

3.3. Total settlement (settlement per site)

Individual sites in our experimental array represented relatively isolated habitat patches. The total settlement per site (per day) differed among treatments ($F_{2,33} = 7.851$, $p = 0.002$, Fig. 3B). Total settlement per site was higher in the clumped treatment than both the dispersed treatment (Tukey's HSD, $p = 0.015$) and solitary treatment (Tukey's HSD, $p = 0.002$). The solitary and dispersed treatments were similar and had the lowest settlement overall (Tukey's HSD, $p = 0.708$). Note that total settlement to the dispersed and solitary treatments was

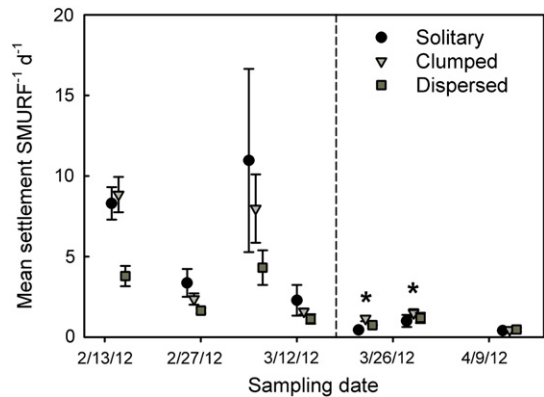


Fig. 2. Mean daily settlement per SMURF over entire sampling period. Symbols are offset to allow specific error bars (1 standard error) to be discerned, with the actual sampling date indicated by the solitary treatment in each grouping. Sampling periods to the right of the dashed line were excluded from analysis, as settlement was <1 fish per day. *Dates excluded due to incomplete sampling.

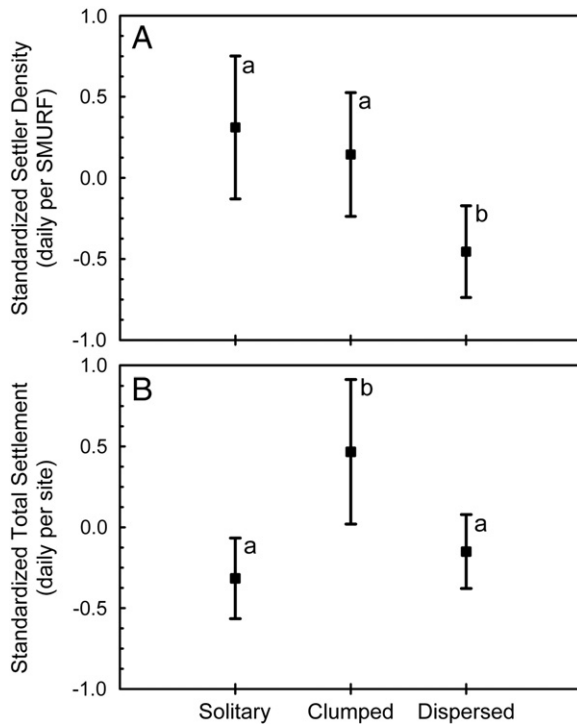


Fig. 3. Standardized daily settlement of triplefins (z-scores, controlling for temporal variability). A. Density of settlers (settlement per SMURF per day); B. Total settlement (settlement per site per day). Bars are 95% confidence intervals. Letter groups denote significant differences with $\alpha = 0.05$.

similar, even though the dispersed treatments contained three times as much habitat structure as solitary treatments.

4. Discussion

Increasing habitat availability appears to increase the total settlement of triplefins at this scale, but habitat configuration modulates this effect. The clumped habitat treatment received the highest total settlement, and the densities of settlers were similar in the solitary and clumped treatments. This suggests that the clumped and solitary treatments were of similar habitat quality. However, we simultaneously observed low settler density and low total settlement to the dispersed treatment, which indicates a more complicated process. If habitat configuration does not influence quality, solitary and dispersed SMURFs should become filled with similar densities of settlers, and clumped and dispersed treatments should have had equal settlement. However, settler density was higher in the solitary treatment than the dispersed treatment, to the extent that total settlement was actually similar between these two treatments, despite the difference in total habitat availability. This suggests the dispersed treatment may be less attractive to settlers (therefore fewer fish settle), or characterized by differences in post-settlement processes. Our prediction that adding additional habitat would increase total settlement of triplefins was not born out in the dispersed treatment, indicating that the configuration of the added habitat structure may determine whether settlement will be enhanced. Below we discuss potential mechanisms which may have contributed to this pattern.

4.1. Pre-settlement processes

The high settlement to the clumped treatment relative to the other treatments is a key result of this study. This pattern may stem from the influence of habitat configuration on larval supply and/or settlement behavior. Specifically, we speculate that the more continuous

structure associated with the clumped treatment may provide a stronger settlement cue to triplefins, both visually and/or chemically. We assumed that settlement cues from solitary SMURFs and clumped SMURFs would be similar because they were comprised of the same type of habitat (SMURFs), but this assumption did not consider the role of physical and behavioral processes. The cluster of three SMURFs in close proximity may have modified current flow (e.g., baffling) more than the other treatments, and thus may have further facilitated settlement of larvae via slowing of flow (Eckman, 1983) and increasing the concentrations of chemical cues around the habitat patch. In this case, settlement in the dispersed treatments may have been reduced if relatively isolated SMURFs provide weaker settlement cues for these reasons. Rather than expand the habitat available to fish, the settlement cues from the dispersed treatment may have been sufficiently weak such that dispersed treatments diluted settlement stage fish between three SMURFs, while solitary treatments essentially concentrated the same number of fish to a single SMURF.

In addition to generating stronger settlement cues via physical processes, we speculate that continuous patches may be of higher quality ecologically, thus triggering a higher proportion of fish to settle. Recruits of multiple species of triplefins have demonstrated fine scale variation in habitat association, which were generally similar to those of adults (Syms, 1995). In particular, *F. lapillum* exhibits preferences for more complex species of macroalgae at the time of settlement (McDermott and Shima, 2006). In this regard, the clumped treatment may have provided better habitat for foraging, as the area between the three SMURFs was somewhat sheltered from currents and predators. Indeed, recently settled triplefins were observed schooling in small groups beneath the clusters of three SMURFs in the clumped treatment, but they would retreat into the SMURF interior as divers approached. In addition, Triplefins defend territories as adults (Feary and Clements, 2006), so it is possible that the species collected here have an innate preference for larger continuous patches that may provide opportunity for future territorial expansion.

4.2. Post-settlement processes

In natural reef habitat, post-settlement processes may differ among habitat configurations. Fragmented (dispersed) habitat configurations have more “edge”, and because some predators frequent habitat edges (Macreadie et al., 2010; Smith et al., 2011), fish in this type of configuration may be more vulnerable to predation. In this way, post-settlement mortality may be higher in dispersed or solitary patches, as settlers compete more strongly for limited refuges. Furthermore, refuges can potentially be shared among juvenile fish over time in larger, more continuous patches, supporting higher densities (White et al., 2010). Alternatively, greater spacing between patches may weaken competition and result in higher post-settlement survival (Bonin et al., 2011). Given our relatively frequent clearing of SMURFs, we believe that post-settlement processes did not play a large role on the patterns of fish abundance that we observed in our study (and hence, we’ve assumed our sampling to be largely indicative of patterns of settlement). However, if post-settlement mortality was an important process in our study, and in particular, if it was highest for the dispersed treatments, then this could have altered the spatial patterns established by settlement processes, to result in lower densities of “recruits” observed for that treatment. If we assume that predation was an important mechanism of (putative) post-settlement mortality in our study, our results would appear to contradict those of other studies of predator behavior from tropical reefs, where transient predators visited aggregated patches of reef habitat more frequently than isolated patches (Overholtzer-McLeod, 2004, 2006).

There is prior evidence that local recruitment of *F. lapillum* is habitat limited (McDermott and Shima, 2006). The high densities of triplefins observed during settlement pulses support the possibility of habitat saturation and density-dependent mortality, especially over the course of

an entire recruitment season. As we did not quantify predation, we cannot determine the magnitude of predator-induced mortality in our system. However we cleared all settlers from SMURFs weekly in an attempt to reduce the potential for these types of post-settlement processes, and patterns we observed held true at both very high and very low magnitudes of settlement.

4.3. Significance

Habitat configuration (e.g. fragmentation) can alter species assemblages and ecological interactions (Anderson and Millar, 2004; Connell and Kingsford, 1998), but recent empirical work suggests fragmentation typically has much weaker effects than habitat loss, which are not consistently positive or negative (e.g. Bonin et al., 2011; Deza and Anderson, 2010; reviewed in Fahrig, 2003). Fishes and marine invertebrates often fail to exhibit consistent patterns of settlement in response to habitat patchiness (Levin, 1993; Sano, 1998), and variable responses to habitat configuration may be due to behavioral tendencies of the species in question and interactions with predators in the system (White et al., 2010). The low settlement of triplefins to our dispersed treatment contrasts with observations of fishes in seagrass habitats (Macreadie et al., 2009, 2010) and on coral reefs (Bohnsack et al., 1994; Bonin et al., 2011), where fish density is often higher in fragmented habitats. However, our findings are consistent with recruitment patterns of kelp bass (*Paralabrax clathratus*) in the Northern Hemisphere, where recruitment is locally enhanced by density of giant kelp (Carr, 1994; White and Caselle, 2008). Our study demonstrates that small-scale landscape architecture, in addition to local habitat availability, can have a significant effect on settlement of triplefins, and potentially other species as well. Future reviews (or a meta-analysis) might help to explain settlement patterns and develop predictive ability by considering behavioral traits (e.g. mobility, territoriality, etc.) of both settling fish and predators in relation to key characteristics of preferred habitats.

The role of habitat limitation has been discussed extensively within the “attraction vs. production” debate (reviewed in Grossman et al., 1997; Pickering and Witmarsh, 1997). The “production” argument assumes that hard-bottom substrate limits fish production (Bohnsack, 1989). The proposed mechanism for enhanced production with increased habitat is often increased recruitment, due to the vulnerability of early life stages to post-settlement mortality (Bohnsack et al., 1994). The “attraction” argument states that additional habitat (e.g. an artificial reef) only concentrates the existing fish in the area due to behavioral preferences (Bohnsack, 1989; Bohnsack et al., 1994). This process of attraction has been applied to larval stages as “propagule redirection” and is hypothesized to cause settlement shadows (Stier and Osenberg, 2010).

In this context, we would have expected settlement shadows to be most obvious in our clumped treatment—because the potential for settlement shadows should decline as the distance between habitat patches increases—but this was not the case. We did observe reduced settlement to the dispersed treatment relative to the solitary treatment, and this finding is somewhat consistent with an experiment conducted by Stier and Osenberg (2010). Small isolated focal coral heads (analogous to our solitary treatment) received higher settlement of fishes than focal coral heads surrounded by a perimeter of additional reef habitat (comparable to our dispersed treatments), but at the scale of the entire reef array, total settlement increased with increasing reef area (Stier and Osenberg, 2010). The authors maintained that adjacent reefs redirected settling fish away from focal reefs, supporting the propagule redirection hypothesis, but at larger scales the addition of reef habitat increased recruitment success, supporting the production hypothesis. In our study, increasing habitat area in the clumped treatment increased total settlement, but increasing habitat in the dispersed treatment did not increase total settlement. We expected stronger settlement shadow effects in the clumped treatment, so our results suggest that favorable habitat configuration may override any potential settlement shadows,

or that the scale of our habitat treatments may not have been large or dense enough to generate settlement shadows. Based on the high density of settlers observed throughout our study, it is possible that there is low potential for settlement shadows in this system.

A caveat of our study is that we only manipulated habitat configuration at one level of habitat structure (three SMURFs arrayed in two different ways), and when we examined the effect of additional habitat, we increased the spatial extent of the habitat (as opposed to adding habitat via increased structural complexity within the same space). In order to more completely address the interaction between habitat availability and configuration, future experiments could construct additional treatments that include varying amounts of habitat structure in the same volume of space (SMURFs can be built with varying amounts of material within). A fully crossed orthogonal design examining a low complexity habitat and high complexity habitat, in both clumped and dispersed configurations, could provide further detail on the role of landscape structure and settlement of triplefins. Nonetheless, our treatments are ecologically relevant in the context of reef dynamics, as common sources of change in reef structure (e.g. large storms, urchin outbreaks) often completely remove large sections algal habitat from the reef, rather than evenly decreasing the complexity of algal structure (Dayton et al., 1992).

Our habitat units and treatments were designed with the structure of the natural reef habitat in mind, and the mechanisms suggested here (current baffling, habitat preferences, etc.) should also apply at larger scales. With careful consideration of these mechanisms (Steele and Forrester, 2005), and the variation that is present in the system (Hunsicker et al., 2011) it is possible to apply our results to the scale of a small reef system. While we observed habitat dependent settlement on small scales, and there is evidence that localized processes do scale up (Steele and Forrester, 2005) so long as we account for both the total habitat density as well as the spatial variance in the habitat density (representing the dispersion of the reef patches) (Hunsicker et al., 2011). It would be necessary to identify the functional response to the spatial variance, which may be non-linear (Hunsicker et al., 2011). We only manipulated spatial variance at two levels, but natural reef habitat could be manipulated at multiple spatial scales and levels of spatial variance to determine whether triplefin response to habitat configuration is repeated in natural substrates, and to determine if there is a threshold level of spatial variance that controls habitat quality.

5. Conclusions

Adding habitat increased total settlement of triplefins in our treatments, but only when the habitat patches were clumped. Thus, the local configuration of habitat is important in the settlement of these fishes, and more continuous patches appear to be of higher quality to settlement stage larvae. While the total amount of habitat plays a role in total settlement at larger scales, the landscape architecture is also a key determinant of settlement. Specifically, more continuous habitat patches with higher potential for movement and foraging within the patch may increase production of recruits or may be strongly attractive to larvae, or both, although post-settlement processes may ultimately determine how fish populations respond to increased recruitment success.

The scale at which habitat architecture is assessed can have strong effects on interpretation. When considering density of settlers, the small, isolated habitat treatment actually received higher density of settlers than the larger, dispersed habitat, and was similar to the clumped patch. However, when total settlement to the entire habitat patch was considered, it became clear that increasing the total amount of available habitat in the clumped configuration increased settlement of triplefins. This should be considered when attempting to scale-up results. As ontogenetic shifts in microhabitat use have been documented in triplefins (McDermott and Shima, 2006), future directions include an examination of how adults and juveniles interact with landscape configuration,

and an investigation of how post-settlement processes (e.g. density dependent mortality) and fish performance vary with habitat characteristics. Triplefins make up a substantial portion of the vertebrate biomass and fish diversity on rocky reefs in New Zealand, and provide significant trophic links within the food web. Understanding the interaction between spatial characteristics of reef habitat and recruitment of triplefins allows us to better predict how these system may respond to disturbances which alter reef structure, and may help inform the design and placement of marine reserves aimed at protecting diverse and productive reef ecosystems.

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