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## Beyond the patch: Disturbance affects species abundances in the surrounding community

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## ABSTRACT

The role of disturbance in community ecology has been studied extensively and is thought to free resources and reset successional sequences at the local scale and create heterogeneity at the regional scale. Most studies have investigated effects on either the disturbed patch or on the entire community, but have generally ignored any effect of or on the community surrounding disturbed patches. We used marine fouling communities to examine the effect of a surrounding community on species abundance within a disturbed patch and the effect of a disturbance on species abundance in the surrounding community. We varied both the magnitude and pattern of disturbance on experimental settlement plates. Settlement plates were dominated by a non-native bryozoan, which may have established because of the large amount of initial space available on plates. Percent covers of species within the patch were affected by the surrounding community, confirming previous studies' predictions about edge effects from the surrounding community on dynamics within a patch. Disturbance resulted in lower percent cover in the surrounding community, but there were no differences between magnitudes or spatial patterns of disturbance. Disturbance lowered population growth rates in the surrounding community, possibly by altering the abiotic environment or species interactions. Following disturbance, the recovery of species within a patch may be affected by species in the surrounding community, but the effects of a disturbance can extend beyond the patch and alter abundances in the surrounding community. The dependence of patch dynamics on the surrounding community and the extended effects of disturbance on the surrounding community, suggest an important feedback of disturbance on patch dynamics indirectly via the surrounding community.

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### 1. Introduction

Ecologists have long recognized the role of disturbance in generating non-equilibrium dynamics in communities (Connell, 1978; Petraitis et al., 1989; Sousa, 1984a,b). Disturbance is thought to affect community structure at two scales. At the scale of a disturbed patch, disturbance either influences or resets the successional sequence by reducing the abundance of organisms within the disturbed patch (Berlow, 1997; Petraitis et al., 1989; Sousa, 1979). Recolonization of the patch occurs via recruitment from the regional species pool or growth into the patch from the surrounding community. At a larger, regional scale, disturbance affects the community by freeing resources in different patches at different times, resulting in patch heterogeneity (Leibold and Miller, 2004; Sousa, 1984a).

What links these two spatial scales is the matrix habitat that exists between and surrounds disturbed patches. If patches are considered as oceanic islands or local patches in a metacommunity, the matrix habitat is uninhabitable and need not be considered. However, in many communities, disturbed patches exist within a matrix of similar, but undisturbed habitat, from which recolonization may occur. Although disturbance is predicted to influence structure at the community scale, (e.g. intermediate disturbance leads to increased diversity, Connell, 1978), such predictions stem from studies focused on smaller experimental patches, while the effect of a disturbance on the matrix habitat has seldom been investigated (Berlow, 1997; Miller, 1982; Sousa, 1979, 1984b). The dependence of patch dynamics on the surrounding community (Sousa, 1984a; Petraitis and Dudgeon, 1999), and the possible extended effects of disturbance on the surrounding community, suggests an important feedback of disturbance on patch dynamics indirectly via the surrounding community.

Studies of habitat fragmentation have addressed interactions between patches and the surrounding community, but generally there is little overlap between this work and disturbance studies. Habitat fragmentation studies typically consider a patch of higher quality habitat embedded in a matrix of lower quality habitat and emphasize demographic consequences to populations associated with

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heterogeneity among habitats (Debinski and Holt, 2000; Saunders et al., 1991). Disturbance studies typically focus on a patch affected by disturbance surrounded by a matrix of unaffected habitat and emphasize the aggregate properties of communities and their trajectories through time (Connell, 1978; Sousa, 1979; 1984a,b; Berlow, 1997). The effect of a disturbance on the surrounding undisturbed community has not been addressed directly, but may provide an important link between studies of disturbance and habitat fragmentation and our understanding of disturbance effects at both the patch and the community scale.

Organisms in the surrounding community can affect the community developing within the disturbed patch, particularly around the edges of the patch, where organisms are most likely to interact (e.g., Sousa, 1984a; Petraitis and Dudgeon, 1999). Similarly, prevailing conditions in the patch are likely to affect organisms in the surrounding community. Disturbances increase resource levels adjacent to the surrounding community and, as a result, temporarily decrease competition and increase growth rates (Sousa, 1984b; Wilson and Tilman, 1991). Abiotic conditions, such as light or flow regimes, that are altered by disturbance might affect organisms in the surrounding community (Denny et al., 2003). In cases where a disturbance affects the successional stage of the community (Berlow, 1997; Sousa, 1984b) or results in alternate community states (Petraitis and Latham, 1999), species interactions between the patch and the surrounding community will be altered. Disturbance can affect a patch directly by removing organisms, but may also affect both the patch and surrounding community indirectly, as a result of the feedback between patches and the surrounding community.

The spatial magnitude of a disturbance affects community dynamics within the patch, but may also affect the degree to which the patch and the surrounding community interact (Connell, 1978; Miller, 1982). If a patch is surrounded by plants or invertebrates that can grow into the patch vegetatively, smaller patches are likely to be filled by abundant and more competitive species from the surrounding community that close the patch quickly before other species can recruit. Large patches should interact less with the surrounding community, but rather are likely to be filled by colonizing or refuge species that can take advantage of the available resource before space is filled in by species from the surrounding community (Dudgeon and Petraitis, 2001; Miller, 1982; Petraitis and Latham, 1999; Sousa, 1984b). Large disturbances are also more likely to induce a switch to alternate states within the patch (Petraitis and Latham, 1999; Petraitis and Dudgeon, 1999). As a result, species composition of the patch is likely to be affected by disturbance size, which may alter species interactions between the patch and the surrounding community. Conversely, the degree of edge effects declines exponentially with increasing patch size, resulting in increased independence of dynamics in the patch and the surrounding community (Miller, 1982; Petraitis and Latham, 1999; Sousa, 1984b). However, larger disturbances may free disproportionately more resources and have a greater potential to change abiotic conditions (such as light and flow regimes, Denny et al., 2003) and increase the effect of a disturbance on the surrounding community.

The effect of disturbance magnitude on interactions between the patch and the surrounding community may largely be due to edge effects, which also change as a function of the spatial pattern of a disturbance or the arrangement of multiple patches. An accumulation of small disturbed patches is unique in that it shares the same amount of disturbed area as a large patch, but the accumulated perimeter exposed to edge effects is much larger in the collection of small patches. Distinctly different properties may emerge from the collection of several small disturbances when compared to a larger single disturbance of the same magnitude (Levin, 1992; Miller, 1982). Small patches should close more quickly due to vegetative growth by organisms from the surrounding community, but the recolonization of several such patches is less certain since colonization is potentially

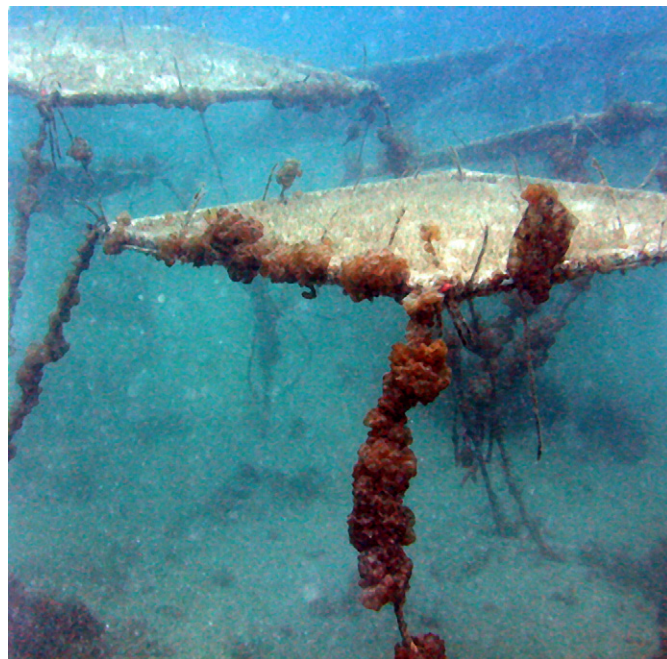


Fig. 1. The settlement plates used in the experiment covered with positively buoyant macroalgae.

limited by growth rates of organisms and supply of propagules. Smaller patches should alter abiotic conditions affecting the surrounding community less than larger patches, but the effect of an accumulation of such patches is uncertain. The effect of a disturbance on both the patch and the surrounding community may depend on both the magnitude and spatial pattern of the disturbance.

Here, we experimentally manipulated marine fouling communities to address three questions concerning interactions between a disturbance, the cleared patch, and the community surrounding the patch. First, we asked if the presence of a surrounding community affects the percent cover of species within a disturbed patch. We compared the percent cover of each species in disturbed patches to those in patches isolated from any surrounding community. Second, we asked if disturbance has an effect on organisms in the community surrounding the disturbed patch. We addressed this question by comparing the percent cover of each species in communities surrounding disturbed patches to communities unexposed to experimental disturbances. Finally, we asked if the spatial scale or pattern of the disturbance had an effect on either of the questions above. Within small, disturbed patches, we expected the percent cover of each species to be more similar to those species in the surrounding community than in large patches, which are less likely to be filled by growth from organisms in the surrounding community. Fouling communities were established on large settlement plates (1 m<sup>2</sup>) that allowed for simulated disturbances varying in spatial scale and pattern. The discrete substrate on which these communities assembled strictly defined the boundaries of the community surrounding a disturbance.

## 2. Methods

The study was conducted at sites near the Wrigley Marine Science Center on Santa Catalina Island, off the coast of southern California. Twelve settlement plates (each 1 m<sup>2</sup>) were deployed at each of three sites: Big Fisherman Cove, Chalk Cliffs, and Chalk Cove. These sites were chosen because each had sandy substrate in which settlement plates could be anchored and nearby natural fouling communities (on rock walls approximately 15–25 m away). The plates were deployed at depths of 8–15 m and arranged in a linear array parallel to the

shoreline, such that each plate was equidistant from the natural fouling community. Each plate was placed at least 1.5 m away from the next unit so that each had equal access to larvae in the water column.

Settlement plates consisted of a 1×1 m piece of Rigid Expanded Polyvinyl Chloride (PVC) sheeting attached to a PVC frame with cable ties. The corners of each frame were attached to the seafloor by polypropylene rope tied between the frame and a sand screw (Fig. 1). The plates were positively-buoyant and floated approximately 1 m above the seafloor. Oodles pool toys (Nomaco, Inc., Tarboro, NC) attached to the plates and positively-buoyant macroalgae settling on the upper surface of the unit kept the units buoyant and suspended in the water column, despite the extra weight on the plates due to invertebrate settlement and sedimentation.

Prior to deploying the settlement plates, disturbance treatments were randomly assigned to underwater locations within the array, with two replicates of each of the six treatments per site. The six treatments varied in the magnitude and spatial pattern of disturbance. The treatments were: (1) control, no disturbance, (2) 400 cm<sup>2</sup> single square clearing, (3) 2400 cm<sup>2</sup> single square clearing, (4) six 400 cm<sup>2</sup> square clearings located randomly on the plate (i.e. a fragmented 2400 cm<sup>2</sup> disturbance), (5) 4800 cm<sup>2</sup> single clearing, (6) twelve 400 cm<sup>2</sup> square clearings located randomly on the plate (i.e. a fragmented 4800 cm<sup>2</sup> disturbance). In treatments (2), (3), and (5), the clearing was placed randomly on the plate by choosing random *x* and *y* coordinates from the upper left corner of the clearing, with at least 10 cm between the clearing and the edge of the plate. In treatments (4) and (6), at least 5 cm of undisturbed area occurred between one or more patches, but two or more patches could be adjacent to one another, creating random shapes of clearings.

The settlement plates were designed to create disturbance by removing a portion of the plate and replacing it *in situ* with a replica of the removed portion. Disturbance regimes were assigned during the construction of the plates. Patches were cut out of the plates and two exact replicas of the removed pieces were created. Replacement patches were cut during plate construction to precisely match the removed patch, thus eliminating any gap between the patch and the remaining plate. Prior to deploying settlement plates, the original patches were reinserted into the empty space in the plates, made to be flush with the surrounding plate, and held in place with cable ties. Disturbances were later initiated *in situ* by removing the pre-cut patch from the plate and replacing it with one of the replicate patches. The clean pieces of PVC sheet mimicked an intense disturbance (i.e. all organisms completely removed) by providing virgin substrate to be colonized. The design of the plates allowed clearings to be imposed with minimal disturbance to organisms in the surrounding community.

Settlement plates were deployed in April 2002 and colonization was allowed to continue until the percent cover of the two most abundant species in the community did not change significantly (determined by a non-significant paired *t*-test between consecutive months for each species). In February 2003, disturbances were imposed. At the time of disturbance, the second of the replicate replacement pieces were deployed at each site (two replicates of each disturbance size). These patches were within 10 m of the other settlement plates, but unlike the other replacement patches, were not free-floating and not embedded within a surrounding community and thus unaffected by surrounding organisms. These isolated patches allowed us to address the first of our questions by comparing isolated patches with those patches embedded in a surrounding community.

The underside of each plate was sampled for the percent cover of each taxon repeatedly each month before and after the experimental disturbance. Poor visibility and picture quality limited sampling during several months following disturbance, limiting the post-disturbance samples to two and seven months after disturbance. Down-facing surfaces tend to have greater invertebrate cover and less macroalgal cover than up-facing surfaces (Irving and Connell, 2002), so we focused on the underside of the plates due to potential

differences in light or nutrient regimes between sites and replicates that might affect photosynthetic organisms that occurred on upper surfaces of plates.

The percent cover of each species was documented *in situ* with digital photographs using a camera attached to a 30 cm×30 cm quadrat—slightly larger than the smallest patch size. Prior to disturbance, four non-overlapping subsamples were taken haphazardly from each settlement plate. Throughout the experiment, the same sampling regime was used in control treatments and in all undisturbed areas (i.e. the surrounding community). In all new patches, the entire patch was documented using non-overlapping subsamples with the same quadrat. The percent basal cover of each conspicuous taxon was determined by image analysis using Optimas (version 6.5, Media Cybernetics, 1999) and calibrated with a ruler present in each image. The percent cover of each species for each settlement plate was estimated from the average of percent cover of the subsamples, using each plate as a statistical replicate.

Three pairs of statistical analyses were performed using JMP (Version 4.0.4, SAS Institute, Inc. 2001). For all analyses, percent cover data were arcsine square-root transformed to improve normality and reduce heteroscedasticity. Since percent cover was largely dominated by two species (see Results), separate analyses were conducted on the percent cover of each of these species. To ensure that there were no initial differences among disturbance treatments, the first pair of analyses (one analysis for each species) compared sites and treatments immediately *before* disturbance, considering site as a random effect in an unrestricted Model III analysis of variance (Quinn and Keough, 2003). The second pair of analyses addressed the first of our questions—does the presence of a surrounding community affect the percent cover of each species within the patch, and does this effect change with disturbance size? These analyses compared three factors [sites (random), disturbance treatments (fixed), and isolated vs. surrounded communities (fixed)] using the percent cover of each species *within* patches seven months after disturbance. The seven month sample was the last sample taken following disturbance and allowed the most time for the community to develop. Since differences in disturbance shapes were only present within surrounding communities and not in the isolated situation, fragmented disturbance treatments were not used in this analysis. The third pair of analyses addressed the second of our questions—does disturbance affect the percent cover of each species in the surrounding community, and does this effect change with disturbance size or spatial pattern? These analyses compared the percent cover of each species in the *surrounding* community two months after disturbance. This was the first month of data available following disturbance and thus likely

**Table 1**

*F*-values from ANOVA and *a priori* contrasts that tested the effect of disturbance treatments and sites on the percent cover of the two dominant species in the community surrounding a disturbance

Effect	<i>df</i>	A. Before disturbance		B. After disturbance	
		<i>C. brunnea</i>	<i>W. subtorquata</i>	<i>C. brunnea</i>	<i>W. subtorquata</i>
Treatment	2,10	1.64	2.07	<b>4.43*</b>	<b>6.16**</b>
Site	5,10	<b>4.86*</b>	<b>23.9**</b>	<b>1.87</b>	<b>7.89**</b>
Treatment×Site	10,18	0.572	1.04	0.482	0.668
Within treatment contrasts					
Control vs. all disturbed	1,10	0.051	3.56	<b>19.2**</b>	<b>26.4**</b>
400 vs. (2400 and 4800)	1,10	1.94	2.78	2.58	0.192
2400 vs. 4800	1,10	0.827	1.40	0.007	3.44
Fragmented vs. non-fragmented	1,10	0.693	0.006	0.281	0.182

\*=<0.05, \*\*=<0.01.

Disturbance has a significant effect on the percent cover of both species (indicated in bold), but neither the size nor spatial pattern affect the percent cover of either species.

**Table 2**

F-values from ANOVA and *a priori* contrasts that tested the effect of site, disturbance treatment, and the presence of a surrounding community on the percent cover of the two dominant species in the disturbed patch

Effect	df	<i>C. brunnea</i>	<i>W. subtorquata</i>
Surrounded/isolated	1,17	<b>11.9**</b>	<b>10.3**</b>
Treatment	2,2	2.81	0.993
Site	1,2	8.83 <sup>†</sup>	10.9 <sup>†</sup>
Treatment × Site	2,17	<b>4.23*</b>	3.13 <sup>†</sup>
<i>Within treatment contrasts</i>			
400 vs. (2400 and 4800)	1,2	5.61	1.21
2400 vs. 4800	1,2	0.006	0.779

<sup>†</sup> < 0.1, \* = < 0.05, \*\* = < 0.01.

The presence of a surrounding community affects the percent cover of both species. Patch size has no effect on the percent cover of either species. Significant effects are indicated in bold. All other interactions were non-significant (*p* > 0.25) and removed from the final model.

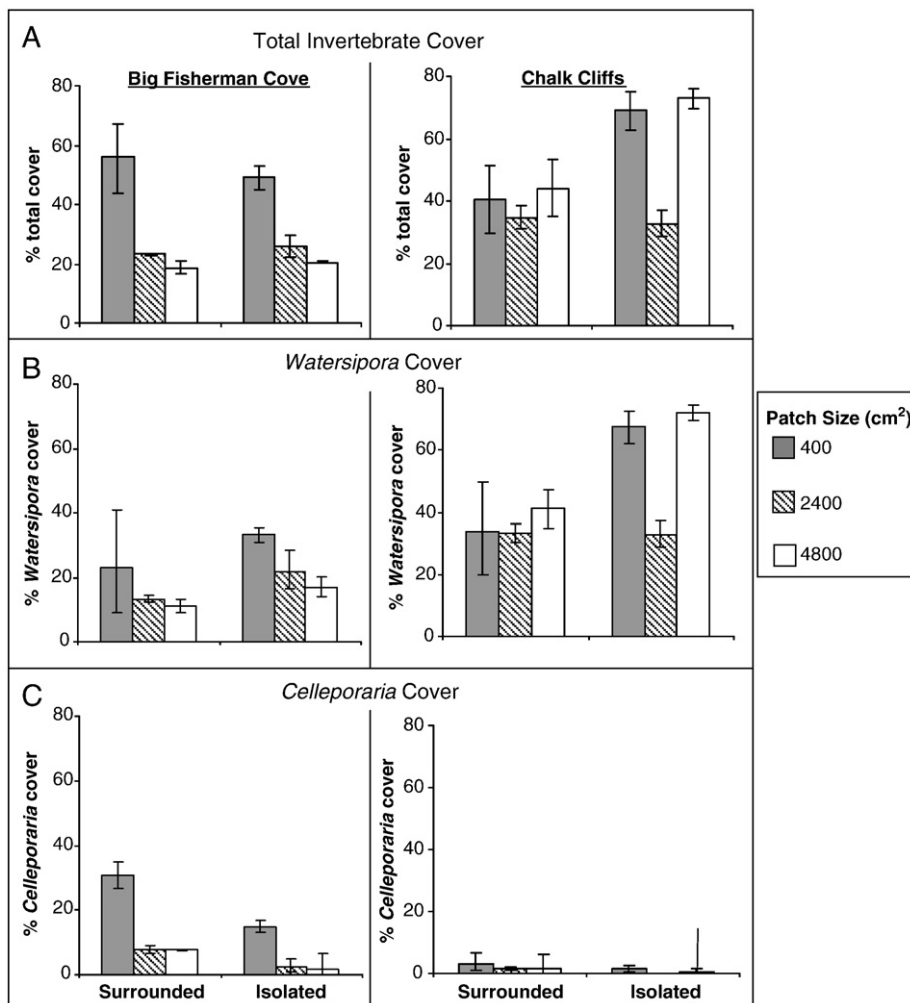
to give the best estimate of the immediate effect of the disturbance on the surrounding community. *A priori* contrasts were used to compare treatment levels: a) no disturbance vs. surrounding a disturbance; b) surrounding a small disturbance vs. surrounding both medium and large disturbances, and c) surrounding medium disturbances vs. surrounding large disturbances; and d) surrounding fragmented vs. surrounding non-fragmented disturbances of the same size, to determine whether spatial pattern of the disturbance had an effect on the surrounding community. With only two replicates per

treatment combination, the power of these analyses was relatively low, and thus provides little support for null results. However, a significant difference between treatments with low power suggests that the effect size of a treatment is, therefore, quite high. To increase the power of detecting treatment effects in this latter analysis, non-significant interaction terms ( $\alpha > 0.25$ ) were removed from the generalized linear model before re-analysis (Quinn and Keough, 2003).

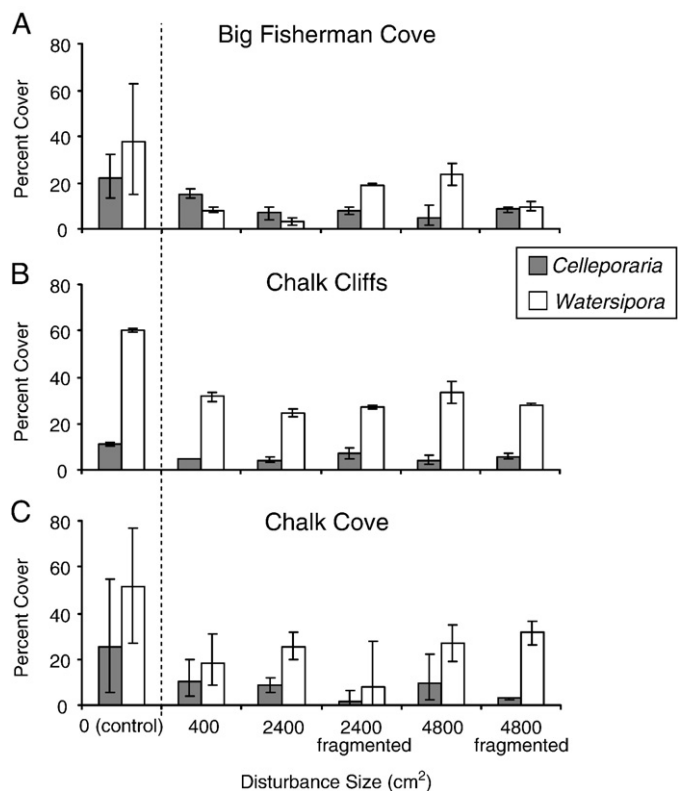
### 3. Results

A low diversity assemblage of bryozoans developed on each of the settlement plates. *Watersipora subtorquata*, an invasive bryozoan native to the western Pacific (Fahey et al., 2002) and *Celleporaria brunnea*, a native encrusting bryozoan, were the two most abundant species in every replicate. Other species occurred rarely on the plates, and in such events, contributed no more than 2% to the percent cover on any plate and no more than 4% overall and so were not used in the analyses. Thus, all analyses focus on the two most abundant species in the community.

Prior to experimental manipulation, plates across all treatments were equivalent in relative percent cover of each species (*W. subtorquata* being most abundant) and this equivalence prevailed at all sites (Table 1). There was, however, a significant difference in the absolute extent of community development among sites prior to disturbance with overall percent cover lowest at Big Fisherman Cove (25.7 ± 2.8%), and similar between Chalk Cove (39.5 ± 3.4%) and Chalk Cliffs (40.8 ± 2.4%).



**Fig. 2.** Percentage A) Total invertebrate cover, B) *W. subtorquata* cover, and C) *C. brunnea* cover (mean ± s.e.) in three patch sizes, within and isolated from a surrounding community at two sites.



**Fig. 3.** Percentage cover (mean $\pm$ s.e.) of the two most abundant species in the community surrounding different magnitudes and spatial patterns of disturbance at three sites. Gray bars are percent cover of *C. brunnea* and white bars are percent cover of *W. subtorquata*. Control (no disturbance) communities are significantly different from the communities surrounding a disturbance.

The presence of a surrounding community affected the percent cover of both species inside a disturbed patch (Table 2, Fig. 1). The presence of a community surrounding a patch reduced the percent cover of *W. subtorquata* in patches but mildly increased the percent cover of *C. brunnea* (Fig. 2). The effect of the surrounding community did not differ among disturbance treatments (non-significant treatment\*in/out interaction, Table 2), nor did patch size have a significant effect on the percent cover of each species within the patch (Table 2). Several replicates of the isolated settlement plates were lost from Chalk Cove following their deployment, so that site was eliminated from this analysis.

Disturbance treatment had a significant effect on the percent cover of both species in the surrounding community two months after disturbance (Table 1). At all sites, the percent cover of both *W. subtorquata* and *C. brunnea* in the surrounding community were lower than the control (Fig. 3). However, the percent cover of each species was not significantly different among surrounding communities of different sizes (Fig. 3): neither patch size, nor pattern, had a significant effect on the surrounding community (Table 1). Percent cover of both species increased in control treatments, but remained stable or increased only slightly in communities surrounding a disturbance (Fig. 3).

#### 4. Discussion

Disturbance affected the percent cover of organisms in the surrounding matrix habitat, despite having no direct effect on the organisms in that habitat. The percent covers of the two most common species increased in the control treatment, but were greatly reduced, relative to the control, in the other treatments (Fig. 3). This study is the first to explicitly address the indirect effect of a disturbance on organisms in the matrix habitat surrounding the disturbed patch.

Further, the percent cover of organisms inside the disturbed patch was affected by the presence of a surrounding community. In this way, our results confirm a general pattern observed in other studies in other systems that demonstrate edge effects on dynamics in the patch (Debinski and Holt, 2000; Petraitis and Dudgeon, 1999; Sousa, 1984b). For example, Sousa (1984a) manipulated disturbance size in the rocky intertidal and suggested that edge effects from the surrounding community affected successional dynamics within the disturbed patch. This study explicitly tested that hypothesis by manipulating the presence or absence of a community surrounding the disturbance. The presence of a surrounding community indeed affected dynamics within the disturbed patch, by decreasing the percent cover of *W. subtorquata*, but increasing the percent cover of *C. brunnea* in the patch.

The disturbance regimes in most experimental studies have examined events of a small spatial scale relative to the size of the community, largely because of the relative ease of experimental manipulation and because their importance is assumed to scale in proportion with their magnitude and frequency of occurrence. However, perturbations on a small spatial scale do not necessarily scale up in a linear fashion, as a result of a non-linear change in edge effects in response to disturbance size. Here, we performed clearings that ranged from medium to large in terms of the percentage of the community directly affected by the disturbance (4% to 48%). Although disturbance affected the percent cover of species in the surrounding community, the effect did not differ with size or spatial pattern of the disturbance (Table 1). If the magnitude of disturbance has any threshold effect on species in the surrounding community (Petraitis and Latham, 1999), it must exist outside of the range of disturbances (400 cm<sup>2</sup>–4800 cm<sup>2</sup>) examined in this study. The spatial scale of this study is small relative to studies examining the effects of disturbances such as fire or hurricanes on communities. The spatial scale is also small relative to the size of natural fouling communities. However, relative to other experiments in fouling communities, the spatial scale is quite large. The smallest disturbance size in this study is two to four times the size of an entire settlement plate typical of most fouling studies (Altman and Whitlatch, 2007; Stachowicz et al., 1999; Sutherland, 1974), so it would not be surprising to find that a threshold effect in disturbance size exists at a smaller size.

The fact that a range of disturbance sizes had similar effects suggests that if a binary threshold exists in this system, it is at the low end of the disturbance size spectrum. All disturbance sizes used in this study adversely affect the two most common species. If fragmentation or spatial pattern of disturbance has any effect on the surrounding community, it is insignificant relative to the effect of the disturbance itself. The increase in percent cover of species in the matrix habitat slowed relative to the control, suggesting that disturbance slowed population growth rates in the surrounding community. If so, then this suggests that the relative strength of local (vegetative growth and recruitment by short-dispersing or “crawl-away” larvae) and regional (recolonization by planktonic larvae) processes are affected by the disturbance as well. Slowed population growth rate means that recolonization from the local surrounding community will occur more slowly. Regional processes are more likely to contribute to community dynamics if local recruitment is slowed. Effects on these processes may have cascading effects throughout the community.

Although we can not discern the mechanism by which growth rates were reduced in the matrix habitat, we can offer three hypotheses. One explanation for the effect of disturbance on species in the surrounding community is that the patterns observed were an artifact of the manipulation. Disturbance may have had a direct effect by physically removing organisms immediately adjacent to the disturbance. To control for this effect, we should have incorporated an additional treatment to control for the manipulation, in which patches were cut and removed from the plate, but then replaced in the same location. We did not conduct such a disturbance control, but evidence

suggests that the artifacts of the manipulation were minimal. If removing a patch removed or injured organisms in the surrounding community, we would have expected this effect to be limited to the perimeter area immediately adjacent to the disturbance. We did not observe any such marked effect in our photographs, but even if such an effect did occur, the perimeter area around the patch contributed little to the total area in the surrounding community. The perimeter around a patch contributes more to the total area around large patches than it does to small patches. The lack of an effect of disturbance size also suggests a relatively unimportant effect of the manipulation. A strong effect of disturbance on the surrounding community suggests the effect of disturbance is in the freeing of new space adjacent to, rather than the removal of organisms within the matrix habitat. However, we are unable to rule out the effect of manipulation artifacts.

A second hypothesis for the decrease in growth in the matrix habitat is that population death rates increased, due to increased rates of dislodgement or predation. The decreased percent cover of organisms in the adjacent patch may have altered the abiotic environment in the surrounding community. Although the flat settlement plates and encrusting bryozoans provided little physical rugosity, *W. subtorquata* typically begins to grow in three dimensions as colonies age (C. terHorst, pers. obs.), resulting in higher rugosity in older populations. Higher rugosity may buffer disturbance due to high flow speeds in the wake of large colonies. The removal of large colonies within the patch could have increased flow-related disturbance in the matrix habitat (Bertness and Grosholz, 1985; Denny et al., 2003), affecting dislodgement rates of attached organisms (Denny, 1994). Predation could also have increased in the surrounding community following disturbance, as the disturbance increased the amount of exposed edges of the surrounding community, affording more feeding opportunities for fish or nudibranchs that might prefer to feed in open patches or around edges.

A third, non-exclusive, hypothesis for the relative decrease in percent cover of organisms in the surrounding community is that population growth rates were reduced due to positive density-dependence (Levitan and McGovern, 2006). Assuming population growth rates in the surrounding community are positively correlated with the density of organisms in the population, the reduction in population sizes in the adjacent patch following disturbance would have resulted in lower population growth rates in the surrounding community. Similarly, recruitment of one species may have been positively correlated with the density of that species, such that higher density of organisms in control communities facilitated the recruitment of more larvae to the settlement plate. If flow regimes were altered in the surrounding community, this could have affected delivery of larvae to the settlement plate (Duggins et al., 1990; Zeldis and Jillett, 1982), or delivery of food to these suspension-feeding organisms (Eckman et al., 1989; Okamura, 1985).

The presence of a community surrounding a disturbed patch significantly affected the percent cover of species in the patch (Fig. 2, Table 2). Two hypotheses might explain this result: a direct effect of the surrounding community on potential settlers or differences in species response to competition. Larvae near the settlement plate may have been filtered from the water column by the surrounding community, resulting in decreased settlement within the disturbed patch relative to an isolated patch (Woodin, 1976). Assuming that larvae are filtered indiscriminately with respect to species identity, this can not explain the increase in percent cover of *C. brunnea*, unless *C. brunnea* larvae are more abundant in the water column than other larvae. This is plausible though, since *C. brunnea* were relatively common and *W. subtorquata* were virtually absent in the natural fouling communities near Santa Catalina Island (C. terHorst, unpublished data).

Second, *W. subtorquata* may respond well when freed from competition. Organisms in isolated patches could only interact with organisms within the patch, where percent cover was relatively low and the primary resource (space, in this case) was abundant. Organisms

in surrounded patches were likely to interact with both organisms in the patch and in the surrounding community, where resources are more limiting, possibly resulting in increased competition. The decrease in *W. subtorquata* cover may have been due to the increased level of competition within these patches surrounded by other organisms. *W. subtorquata* is an invasive species along the west coast of North America (Fairey et al., 2002), but has never been publicly reported in southern California until now. Large disturbed patches were rare in the natural fouling communities near Santa Catalina Island during the study period (C. terHorst, pers. obs.) and may explain the lack of success by *W. subtorquata* in invading these natural communities. If *W. subtorquata* does indeed respond well to such large disturbances, the initial deployment of the settlement plates in this study may explain its abundance in the communities that developed on those plates. *W. subtorquata* facilitates the further settlement of other non-native species (Floerl et al., 2004) and thus disturbance may have additional effects on the community that were not explored in this study.

In this study, we only tested the effect of disturbance during the winter. Although this is the most likely time for disturbance in southern California, due to winter storms, it does not mean that relevant disturbances do not occur in other seasons. Recruitment of different assemblages of species might occur if space is available during different times of the year (Sutherland, 1974) or if the frequency of disturbance were increased (Altman and Whitlatch, 2007). It is also interesting to note that the two species observed in our communities are generally early colonizing species, suggesting that the community observed in this study is an early successional community with lower diversity than that generally observed in the natural fouling community. Similar experiments could be conducted in later successional communities with higher species diversity to determine whether species diversity affects the observed patterns. If different assemblages of species are precluded from later recruitment by these early successional species, then by dampening growth rates of the early successional species, disturbance may act to accelerate succession by facilitating a changeover to later successional species in the surrounding community.

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