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Larval exposure to shared oceanography does not cause spatially correlated recruitment in kelp forest fishes

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ABSTRACT: In organisms that have a life history phase whose dispersal is influenced by abiotic forcing, if individuals of different species are simultaneously exposed to the same forcing, spatially correlated settlement patterns may result. Such correlated recruitment patterns may affect population and community dynamics. The extent to which settlement or recruitment is spatially correlated among species, however, is not well known. We evaluated this phenomenon among 8 common kelp forest fishes at 8 large reefs spread over 30 km of the coast of Santa Catalina Island, California. In addition to testing for correlated recruitment, we also evaluated the influences of predation and habitat quality on spatial patterns of recruitment. Fish and habitat attributes were surveyed along transects 7 times during 2008. Using these repeated surveys, we also estimated the mortality rate of the prey species that settled most consistently (*Oxyjulis californica*) and evaluated if mortality was related to recruit density, predator density, or habitat attributes. Spatial patterns of recruitment of the 8 study species were seldom correlated. Recruitment of all species was related to one or more attributes of the habitat, with giant kelp abundance being the most widespread predictor of recruitment. Mortality of *O. californica* recruits was density-dependent and declined with increasing canopy cover of giant kelp, but was unrelated to predator density. Our results indicate that physical forcing of larval delivery did not generate spatially correlated patterns of recruitment in a suite of temperate-reef fishes.

KEY WORDS: *Macrocystis* · *Oxyjulis californica* · Reef fishes · Predator–prey interactions · Habitat · Settlement · Density dependence · California

INTRODUCTION

Many marine organisms have a life history phase whose dispersal can be directed by abiotic factors, such as ocean currents at large scales, and oceanographic features, such as tidal bores and coastal upwelling, at smaller scales. Exposure of different species to the same physical factors affecting their dispersal can lead to spatial correlations among species in their settlement (the number of larvae settling to benthic habitat) and recruitment (the number of young juveniles accumulated in a population). For species that interact, such as predators and prey, such spatially correlated input can alter population dynamics (White 2008, Wieters et al. 2008). Thus, understanding the extent to which settlement or recruitment of interacting species is correlated over space is necessary for accurate models of population and metacommunity dynamics, and potentially for spatially explicit management strategies.

A study by White (2007) revealed that a predator–prey pair of coral-reef fish species had spatially correlated patterns of recruitment around a Caribbean Island. For this pair of species, the correlated patterns of recruitment influenced the dynamics of the prey species because density-dependent mortality was more intense at high recruitment sites. White (2007) speculated that such patterns of spatially correlated recruitment might be widespread in organisms whose dispersive phase is exposed to the same abiotic forcing.

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While it seems logical that abiotic forcing of dispersal might lead to spatially correlated patterns of settlement and recruitment, few studies have attempted to quantify such patterns. Here we do so with a suite of common kelp forest fishes. Planktonic larvae of marine organisms can potentially be dispersed long distances, largely by the actions of ocean currents, and can be further influenced at various spatial scales by other physical features, such as tidal bores (Findlay & Allen 2002), sub-mesoscale and mesoscale eddies (Limouzy-Paris et al. 1997, Nishimoto & Washburn 2002), and coastal upwelling events (Roughgarden et al. 1988, Wing et al. 1998). The timing, magnitude, and spatial pattern of reproduction, as well as pelagic larval duration and larval behavior can further affect dispersal potential of marine fishes (Robertson et al. 1993, Leis et al. 1996, Sponaugle & Cowen 1997, Paris & Cowen 2004, Cowen & Sponaugle 2009). For spatially correlated recruitment among species to occur as a result of shared exposure to physical forcing of dispersal, the physical drivers of dispersal must be spatially and temporally persistent, or eggs and larvae of different species must enter the plankton at the same times and places and remain in the pelagic realm for the same length of time. Moreover, for correlated recruitment to result from shared patterns of larval delivery, settlement choices by larvae and movement and mortality after settlement must not obscure the original patterns of larval delivery.

We tested for spatially correlated recruitment at the relatively large spatial scale of 8 large (>1000 m^2), rocky reefs spread over ~30 km of the coastline of Santa Catalina Island, California: a spatial scale similar to that at which White (2007) observed spatially correlated recruitment between a predator and its prey (St. Croix is ~35 km long). At the 8 study reefs, over the course of the majority of a settlement season, we tested for spatial correlations (1) in the recruitment of 8 common species including the dominant predator in the system, and (2) in the densities of these species as older, young-of-year (YOY). We expected to see more and stronger correlations among YOY densities than among younger recent settlers (i.e. recruits) if post-dispersal processes play a more important role in generating correlations among densities of the study species, e.g. if habitat quality modifies the risk of mortality (Steele 1999, Anderson 2001) similarly for different species. (3) We investigated predator densities and habitat quality as possible causes of variation in recruit and YOY densities. Lastly, (4) we tested the effects of predators, habitat, and population density on mortality rates of prey to understand the causes of spatial patterns of recruitment.

MATERIALS AND METHODS

Study system

We studied patterns of recruitment of a suite of rocky reef fishes at Santa Catalina Island, California, USA (33° 27′ N, 118° 29′ W), in the Southern California Bight. During this study, the rocky reefs at Catalina supported dense populations of giant kelp *Macrocystis pyrifera*, although populations of this macroalga are very dynamic (Dayton et al. 1999). We studied 8 common species of fish found on rocky reefs and kelp forests in Southern and Baja California: kelp bass *Paralabrax clathratus*, rock wrasse *Halichoeres semicinctus*, señorita *Oxyjulis californica*, blacksmith *Chromis punctipinnis*, giant kelpfish *Heterostichus rostratus*, kelp perch *Brachyistius frenatus*, bluebanded goby *Lythrypnus dalli*, and blackeye goby *Rhinogobiops nicholsii*. All of the study species except kelp perch have a pelagic larval stage that lasts for 24 to 90 d (Table 1). Kelp perch were studied because their lack of a larval stage made it possible for us to determine whether correlated recruitment patterns might be caused by factors other than shared larval delivery, such as shared responses to habitat features.

The kelp bass is the dominant predator of small fishes on the rocky reefs at Catalina, making up ~90% of all piscivorous fishes at the island's reefs (Steele 1998). Kelp bass prey upon all of the study species, including recently settled conspecifics (Carr 1991). Predation by kelp bass has been shown to regulate populations of their prey, including bluebanded gobies, blackeye gobies, and kelp perch (Steele 1997a, Anderson 2001).

Young of the 8 study species appear on reefs at Catalina Island between spring and fall. The spawning seasons, larval durations, sizes at settlement or parturition, time of settlement or parturition, and maximum sizes and ages vary somewhat among species (Table 1). All of the study species are relatively sedentary after settlement, generally spending the rest of their lives on a single large reef (Hartney 1996, Lowe et al. 2003), such as each of our study sites.

Sampling design

Each of the 8 large reefs, separated by at least 1.5 km and spread along ~30 km of the northeast-facing, leeward side of Catalina (Fig. 1), were surveyed 7 times between June and December 2008, a time that encompassed the peak recruitment period of all of the study species. The first 6 surveys took

Table 1. Aspects of the life history of the 8 study species. Time of settlement or parturition is based on observations of young fish made during this study. Fish surveys were conducted from June to December 2008. Sizes: total (TL) or standard (SL) length. NK: not known

Species (Family)	Spawning season	Larval duration (d)	Time of settlement or birth	Size at settlement or birth (mm)	Max. size (mm)	Max. age (yr)
Paralabrax clathratus (Serranidae)	Summer[a]	~30[h]	Aug–Oct	10 (TL)[g,j]	720 (TL)[m]	33[m]
Rhinogobiops nicholsii (Gobiidae)	Late winter to fall[b,c]	60–90[b]	Jun–Dec	15–29 (SL)[b,c]	90 (SL)[b]	5[b,d]
Lythrypnus dalli (Gobiidae)	Spring to fall[b,d]	60–90[b]	Jul–Dec	9–11 (SL)[k]	50 (SL)[b]	2[k]
Oxyjulis californica (Labridae)	Spring to late fall[e]	36–43[h]	Jun–Dec	10 (TL)[l]	250 (TL)[n]	4[e]
Halichoeres semicinctus (Labridae)	Late spring to fall[e]	24–36[h]	Aug–Dec	10 (TL)[l]	380 (TL)[n]	14[e]
Chromis punctipinnis (Pomacentridae)	Late spring to fall[e]	32–38[i]	Jul–Dec	10 (TL)[l]	320 (TL)[o]	NK
Heterostichus rostratus (Clinidae)	Late winter to spring[e]	37[e]	Jun–Aug	20 (TL)[l]	610 (TL)[n]	4[e]
Brachyistius frenatus (Embiotocidae)	Fall to winter[f]	0	Jun–Aug	20 (TL)[l]	220 (TL)[n]	3[p]

[a]Erisman & Allen (2006); [b]Steele (1997b); [c]Wiley (1973); [d]Wiley (1976); [e]Shanks & Eckert (2005); [f]Love (1991); [g]Butler et al. (1982); [h]Victor (1986); [i]Wellington & Victor (1989); [j]Cordes & Allen (1997); [k]Behrents (1983); [l]authors' (pers. obs.); [m]Love et al. (1996); [n]Eschmeyer et al. (1983); [o]Johansson (2004); [p]Anderson (1994)

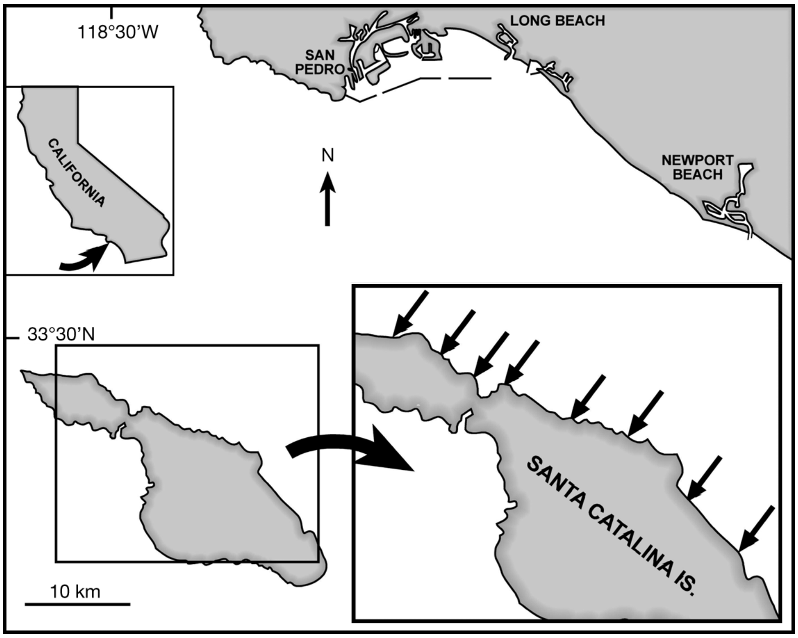

Fig. 1. Approximate locations of 8 study sites (inset: arrows) at Santa Catalina Island. Site names from West to East: Lorenzo's, Little Geiger, Lionhead, Big Fisherman Cove, Ripper's Cove, Little Gibraltar, Hen Rock, Frog Rock

place every ~2 to 4 wk between early-June and late-September, and the final survey was completed in late-November–early-December.

Although chosen for their general similarity, the 8 reefs differed somewhat in size, minimum and maximum depths, and types of habitat that characterized them (e.g. amount of giant kelp, presence of large boulders). Some sites were on a fairly steep slope from the shoreline down to 15–18 m in depth, whereas others were fairly homogeneous in depth. The inner-reef area at all sites was typically dominated by macrophytes other than giant kelp, such as *Eisenia arborea*, *Sargassum* spp., and surfgrass (*Phyllospadix* sp.), whereas giant kelp dominated the middle-reef area out to the deepest outer edge of the reef.

Fish and habitat were surveyed along 30 m long band transects by SCUBA divers. Transects were systematically distributed into 9 areas at each study site. The 9 areas were approximately evenly spaced throughout the reef, with each reef divided into 3 sections (west, middle, and east), each containing 3 zones: reef edge, middle, and inner. In each of these 9 areas, 3 transects were completed, one at each of 3 depth strata: benthic, mid-water, and kelp canopy (1 to 2 m below surface). Thus, fishes were surveyed along 27 transects at each of the 8 sites. Different transect dimensions were used for small (≤100 mm) and larger fishes: 30 m long × 1 m wide × 1 m high for small fishes and 30 × 2 × 1 m for larger fishes. Transects were completed only when underwater visibility was ≥3 m.

Small fishes were counted during every survey, whereas larger fishes were counted during every other survey. The length of each fish was estimated visually and recorded into 5 mm size bins for small fish (≤5 cm), 1 cm size bins for larger fish (5 to 50 cm), and into a single size bin of >50 cm for the largest fishes. These visual size estimations were tightly correlated with actual sizes (r = 0.87) and were unbiased (Krug 2009). The 2 species of gobies were counted within 27 quadrats of 1 m^2 at each site; 3 quadrats were evenly spaced along each of the 9 benthic transects.

To test whether recruit densities were related to habitat attributes, we quantified habitat attributes by conducting surveys of benthic macroalgae and substrate type along the nine 30 m long benthic transects at each of the 8 sites, once in June and once in September 2008. The number of giant kelp individuals, giant kelp stipes, *Eisenia arborea* individuals, and the percent cover of base and surface substrate were quantified along these transects. Numbers of giant kelp individuals and stipes, and *E. arborea* individuals were counted within a 1 m wide swath along each benthic transect. Percent cover of giant kelp canopy was also recorded along each canopy transect during every survey by noting the presence of giant kelp above each meter mark along the 30 m canopy transect.

Base and surface substrate type were recorded at one random point within each meter along the benthic transects at each site. Base substratum was recorded as sand, cobble (<10 cm), small (10–30 cm), medium (30–75 cm) and large (>75 cm) boulder, or sheet rock. Surface substratum was categorized as either bare substratum or live cover. If the surface substratum was bare, it was recorded as just described; whereas live cover was recorded as the algae *Sargassum* spp., *Dictyota/Dictyopteris* spp., *Zonaria* spp., *Corallina* spp., *Macrocystis pyrifera*, 'other brown algae,' or 'other' (anything not in the previous groups, e.g. coralline algae, bryozoans).

Data analysis

To test the hypothesis that shared oceanography causes shared patterns of recruitment of the study species, we tested for spatial correlations in their recruitment rates. We tested recruitment rates averaged over all time periods, as well as recruitment rates at each sampling period for species that were actively recruiting. We defined active recruitment periods as those in which recruits were detected at the majority of study sites. For all analyses, recruit densities per transect were transformed to $\log(x + 1)$ to approximate normal distributions. We also used the same methods to test for spatial correlations among densities of YOY stage fish recorded during the final survey. With so many tests of correlation, there was an increased probability of a 'false positive', i.e. a Type I error. We viewed this increased probability as an acceptable tradeoff to maintain reasonable statistical power given that logistics limited us to only 8 study sites (i.e. n = 8 in all tests). For readers who do not share our view, we indicate which p-values would be statistically significant based on sequential Bonferroni corrections.

We also evaluated whether habitat characteristics and predator densities at each site predicted recruitment to them. Habitat variation was first summarized with principal components analysis (PCA). PCA of the correlation matrix of transformed mean data of the 16 habitat variables was performed in PRIMER 6 (Clarke & Gorley 2006). Prior to conducting the PCA, count data (densities of giant kelp stipes and plants, density of *Eisenia arborea* plants) were $\log(x)$ transformed, and percent covers (substrate cover, benthic substrate, giant kelp canopy cover) were arcsine-square-root transformed. These data were then normalized by subtracting the mean and dividing by the standard deviation because different habitat attributes were measured in different units (counts or percent cover). The first 4 principal components (PCs) explained a majority (~70%) of the variation in habitat; therefore they were used for subsequent correlative analyses.

Before testing whether habitat variation among sites predicted recruitment, we first tested whether habitat attributes differed significantly among the 8 sites. To do so, we used multivariate analysis of variance (MANOVA) to test for differences among sites in the first 4 PCs. A significant MANOVA was followed by a series of univariate ANOVAs conducted on each PC to further investigate differences in habitat attributes among sites. A significant ANOVA on PC2, which primarily summarized attributes of giant kelp, was followed with separate ANOVAs testing differences among sites in giant kelp canopy cover, number of giant kelp plants, and number of giant kelp stipes because giant kelp abundance and density influence recruitment and survival (Carr 1989, 1994, Anderson 1994, 2001).

Prior to testing whether predator density at each site predicted recruitment, we first evaluated whether predator density differed among the 8 study sites with ANOVA. Study sites were divided into 3 zones (nearshore, middle, and reef edge), and so we used 2-way ANOVA models in which site was treated as a random factor and zone as a fixed factor. Based on our prior work, we defined predator abundance as the density of kelp bass >100 mm total length (TL). Densities were $\log(x)$-transformed to meet normality and homoscedasticity assumptions.

We used linear regression to evaluate the influence of habitat and predator density on recruitment and YOY density. Average recruit densities and YOY densities were regressed against predator density (ordinary linear regression), the scores of PCAs summarizing habitat (multiple regression), and the 3 measures of giant kelp abundance (canopy cover, density of stipes, density of plants; multiple regression). We analyzed these 3 measures of kelp abundance in addition to and separately from the PC scores, because each affects recruitment or survival of some of the study species (Anderson 1994, 2001, Carr 1994). Because the kelp data were used in both of the 2 multiple regression models (either on their own or as summarized by PC scores), we provide Bonferroni-corrected α levels to aid in the interpretation of the statistical results. As the measure of kelp canopy cover, we used the average over all 7 surveys to reduce the potential influence of inter-observer variation and day-to-day variation caused by current speed and tide height. Recruit densities were the average number of fish from times when each species was actively recruiting.

We tested whether mortality rates of recruits differed among cohorts settling during different time periods or among sites; and whether any differences among sites were related to either the abundance of predators, habitat attributes, or the average abundance of recruits. Mortality rates were estimated from the decline in density of cohorts through time. Only one species, señorita, settled frequently enough and in sufficient numbers for this approach to be used with multiple cohorts. For this species, we were able to estimate mortality rates of 4 separate cohorts. We used analysis of covariance (ANCOVA) to test whether the mortality rate (the slope of the relationship between density and time) differed among cohorts or sites. ANCOVA models included the covariate 'number of days after peak cohort density' and the factors site and cohort. Non-significant interaction terms involving the covariate were removed sequentially starting with the highest-order interactions (Winer et al. 1991).

Because mortality rate did not differ among recruit cohorts at a site, we averaged mortality rates of cohorts of señorita at a site and tested whether the average mortality rate at a site was related to the abundance of predators, habitat attributes, or average recruit density. We used separate linear regressions of mortality rate on predator density and recruit densities. Multiple regression analyses were used to test for effects of habitat on mortality rates by regressing them on 3 measures of giant kelp abundance (i.e. canopy cover, density of stipes, density of plants); and separately on the first 4 PCs derived from PCA.

RESULTS

Spatial correlations in recruitment among species

Spatially correlated recruitment was not widespread among our study species. When recruitment was averaged over all time periods, only a single species pair (señorita and rock wrasse) out of 28 possible pairs had spatially correlated recruitment (Table 2). When comparing recruitment during each time period that species pairs were observed actively recruiting, spatially correlated recruitment occurred between several species pairs, although such correlations were relatively uncommon (9 of 72 possible pairwise comparisons) and included one negative correlation (Table 3). No pair of species had consistently correlated recruitment across the different periods surveyed.

Spatial correlations in densities were not much more evident at the YOY stage, which we measured in early winter. Of 28 possible pairwise correlations, 4 were statistically significant, with 2 pairs positively correlated and 2 negatively correlated (Table 2). Densities of YOY kelp bass and rock wrasse, and rock wrasse and señorita were positively correlated. Densities of YOY kelp bass and blacksmith, and blacksmith and rock wrasse were negatively correlated.

Differences in predator density and habitat attributes among sites

The mean number of kelp bass large enough (>100 mm TL) to eat small fishes differed significantly among sites (ANOVA: $F_{7,144} = 6.35$, $p < 0.001$) and ranged from an average (±SE) of 2.78 ± 0.09 to 6.61 ± 1.04 per transect (30 m^3). Habitat attributes varied among sites as well. Four PCs explained 69% of the variation in habitat attributes among sites (25.5, 17.7, 14.7, and 10.9%, respectively). PC1 was most strongly related to the percent cover of 'other brown algae' and 'other' (positively correlated) and sand (negatively correlated). PC2 primarily represented giant kelp abundance (canopy cover, density of stipes and plants; positively correlated), bare rock (positively correlated), and sand (negatively correlated). PC3 mainly represented cobble (positively

Table 2. Correlation coefficients from tests of spatially correlated recruitment of (A) recently settled fishes and of (B) older young-of-year (YOY) at the 8 study sites. Recruitment: number of fish per 30 m^3 (or m^2 for gobies) averaged over all times when each species was actively recruiting for (A) or densities of YOY during the last survey of year for (B). Densities were log(x + 1)-transformed for the analysis (n = 8). *p ≤ 0.05, ** p ≤ 0.01. None of the correlations were statistically significant if sequential Bonferroni corrections were applied to each table. GK: giant kelpfish *Heterostichus rostratus*; S: señorita *Oxyjulis californica*; B: blacksmith *Chromis punctipinnis*; RW: rock wrasse *Halichoeres semicinctus*; KB: kelp bass *Paralabrax clathratus*; BBG: bluebanded goby *Lythrypnus dalli*; BEG: blackeye goby *Rhinogobiops nicholsii*; KP: kelp perch

Species	GK	S	B	RW	KB	BBG	BEG	KP
(A) Recent recruits								
GK	1.000							
S	–0.026	1.000						
B	–0.232	0.367	1.000					
RW	–0.027	0.710*	0.260	1.000				
KB	–0.112	0.205	–0.240	0.357	1.000			
BBG	–0.341	0.364	0.159	–0.070	–0.067	1.000		
BEG	0.479	–0.466	–0.625	–0.530	–0.101	–0.023	1.000	
KP	0.350	–0.362	–0.543	0.069	0.628	–0.456	0.511	1.000
(B) YOY								
GK	1.000							
S	–0.429	1.000						
B	–0.441	0.753*	1.000					
RW	0.305	–0.560	–0.819*	1.000				
KB	0.306	–0.609	–0.900**	0.772*	1.000			
BBG	–0.012	–0.077	–0.086	–0.197	0.240	1.000		
BEG	–0.494	0.578	0.646	–0.637	–0.377	0.195	1.000	
KP	–0.521	0.096	–0.163	–0.005	–0.013	0.113	–0.140	1.000

correlated), and PC4 mainly represented sheetrock, giant kelp, and the density of *Eisenia* plants (positively correlated), and medium boulders (negatively correlated). Scores from all 4 PCs differed significantly among sites (MANOVA: Pillai's trace = 2.09, $F_{28,192}$ = 7.47, p < 0.001; univariate ANOVA on each PC: $F_{7,48}$ > 6.90, p < 0.001 for all 4 PCs). The average percent cover of giant kelp canopy and density of kelp stipes varied among sites (ANOVA: $F_{7,144}$ = 13.24, p < 0.001; $F_{7,24}$ = 8.74, p < 0.001, respectively), but number of kelp plants did not (ANOVA: $F_{7,24}$ = 2.18, p = 0.07).

Effects of predators and habitat on spatial patterns of recruitment

We found no evidence that site-to-site variation in predator density affected recruitment of recently settled fishes, whereas habitat attributes did. Recruitment of only one species was related to the density of predatory kelp bass (>100 mm TL), and this relationship in recently born kelp perch was positive (Table 4). Mean recruitment of all species, except kelp perch, was significantly related to one or more PC axes; however relationships with PC axes and the direction of the relationships varied among species (Table 4). Densities of recently recruited giant kelpfish and blacksmith were positively related to the PC1 axis, whereas kelp bass and blackeye gobies were negatively related to PC1. Blacksmith and blackeye gobies were positively related to PC2, whereas señorita, rock wrasse and kelp bass were negatively related to PC2. Giant kelpfish was also positively related to PCs 3 and 4, and bluebanded and blackeye gobies were negatively related to PC4.

Evaluating the effects of giant kelp attributes on recruitment in more detail than provided by the PCs revealed that recruitment of half of the study species was significantly related to 2 of the 3 measures of giant kelp abundance (Table 4). Densities of giant kelpfish recruits and recently born kelp perch were positively related to the density of giant kelp plants, whereas recruitment of kelp bass was negatively related to the density of giant kelp plants. Recruitment of giant kelpfish was negatively related to the percent cover of giant kelp canopy, whereas recruitment of blackeye gobies was positively related to the percent cover of giant kelp canopy.

By the YOY stage, there was stronger evidence of negative effects of predators, and weaker evidence of effects of habitat variation. Densities of YOY of the 2 most abundant mid-water prey species, blacksmith and señorita were negatively

Table 3. Correlation coefficients from tests of spatially correlated recruitment of all study species during periods when each species was actively recruiting. Data: average number of fish per 30 m^3 (m^2 for gobies) at each site, which were $\log(x + 1)$-transformed for analyses (n = 8). *$p \leq 0.05$, **$p \leq 0.01$. None of the correlations were statistically significant if a sequential Bonferroni correction was applied across all 72 comparisons. —: species was not actively recruiting. See Table 2 for definitions

Species	GK	S	B	RW	KB	BBG	BEG	KP
Time 1								
GK	1.000							
S	0.508	1.000						
B	—	—	1.000					
RW	—	—	—	1.000				
KB	—	—	—	—	1.000			
BBG	−0.190	−0.377	—	—	—	1.000		
BEG	−0.104	−0.344	—	—	—	−0.101	1.000	
KP	0.087	−0.613	—	—	—	−0.148	0.639	1.000
Time 2								
GK	1.000							
S	0.466	1.000						
B	—	—	1.000					
RW	—	—	—	1.000				
KB	—	—	—	—	1.000			
BBG	−0.391	−0.453	—	—	—	1.000		
BEG	−0.322	−0.117	—	—	—	−0.075	1.000	
KP	0.527	0.562	—	—	—	−0.285	−0.371	1.000
Time 3								
GK	1.000							
S	−0.400	1.000						
B	—	—	1.000					
RW	—	—	—	1.000				
KB	—	—	—	—	1.000			
BBG	0.141	−0.070	—	—	—	1.000		
BEG	0.373	−0.155	—	—	—	0.748*	1.000	
KP	—	—	—	—	—	—	—	1.000
Time 4								
GK	1.000							
S	−0.205	1.000						
B	—	—	1.000					
RW	—	—	—	1.000				
KB	—	—	—	—	1.000			
BBG	−0.275	0.353	—	—	—	1.000		
BEG	−0.567	−0.052	—	—	—	0.208	1.000	
KP	—	—	—	—	—	—	—	1.000
Time 5								
GK	1.000							
S	—	1.000						
B	—	0.733*	1.000					
RW	—	0.385	0.333	1.000				
KB	—	0.556	0.713*	0.715*	1.000			
BBG	—	−0.018	−0.518	−0.311	−0.584	1.000		
BEG	—	−0.308	−0.639	−0.595	−0.595	0.703*	1.000	
KP	—	—	—	—	—	—	—	1.000
Time 6								
GK	1.000							
S	—	1.000						
B	—	0.179	1.000					
RW	—	0.573	0.022	1.000				
KB	—	−0.723*	−0.551	−0.278	1.000			
BBG	—	0.457	0.399	−0.324	−0.548	1.000		
BEG	—	0.100	0.792*	0.076	−0.264	0.000	1.000	
KP	—	—	—	—	—	—	—	1.000
Time 7								
GK	1.000							
S	—	1.000						
B	—	0.664	1.000					
RW	—	−0.075	−0.315	1.000				
KB	—	−0.061	−0.320	0.711*	1.000			
BBG	—	0.436	0.698*	−0.366	0.046	1.000		
BEG	—	—	—	—	—	—	1.000	
KP	—	—	—	—	—	—	—	1.000

Table 4. Associations of densities of (A) recruits and (B) young-of-year (YOY) of 8 reef fish species with habitat attributes and predator density. Direction (+/–) of the association and statistical significance (p-values) are from 2 multiple regression models, (1) one with 3 measures of giant kelp *Macrocystis pyrifera* abundance and (2) another with 4 principal components (PC) summarizing all measured forms of habitat variation; and (3) one simple linear regression with predator density. Replication is at site level, i.e. n = 8 study sites in each regression. p < 0.05 in **bold**. If a Bonferroni correction is applied to the 2 multiple regression models because data used in them overlap, p = 0.025 is adjusted α level for significance. See Table 2 for definitions

Species	Kelp attributes			Habitat PCs				Predator density
	Canopy	No. of stipes	No. of plants	PC1	PC2	PC3	PC4	
(A) Recruits								
GK	– 0.052	– 0.104	+ **0.018**	+ **0.016**	+ 0.905	+ **<0.001**	+ **0.018**	+ 0.337
S	– 0.267	– 0.794	– 0.585	+ 0.648	– **0.018**	– 0.709	+ 0.717	– 0.229
B	– 0.387	– 0.809	+ 0.361	+ **<0.001**	+ **0.035**	– 0.455	– 0.136	– 0.422
RW	– 0.634	– 0.086	– 0.477	+ 0.182	– **0.009**	+ 0.165	+ 0.083	– 0.296
KB	+ 0.721	+ 0.206	– **0.023**	– **0.001**	– **0.018**	+ 0.228	+ 0.395	+ 0.576
BBG	+ 0.458	– 0.961	– 0.927	– 0.790	– 0.237	– 0.989	+ **0.001**	– 0.231
BEG	+ **0.018**	– 0.292	+ 0.339	– **<0.001**	+ 0.051	+ 0.566	– **0.015**	+ 0.091
KP	+ 0.088	– 0.276	+ **0.012**	– 0.068	+ 0.068	– 0.705	+ 0.101	+ **0.012**
(B) YOY								
GK	+ 0.089	– 0.101	+ **0.048**	– 0.255	+ 0.084	+ 0.549	+ 0.392	– 0.717
S	+ 0.108	– 0.489	– 0.156	– 0.141	– 0.247	– 0.858	+ 0.973	– **0.008**
B	+ 0.178	– 0.553	– 0.457	– 0.369	– 0.367	– 0.562	– 0.140	– **0.047**
RW	+ 0.307	– 0.629	+ 0.564	– **0.049**	+ 0.763	+ 0.555	+ **0.001**	+ 0.400
KB	+ **0.042**	+ 0.850	– 0.116	– **<0.001**	– 0.092	+ 0.393	+ 0.854	+ 0.213
BBG	+ 0.713	+ 0.399	– 0.840	– 0.185	+ 0.108	+ 0.586	– **0.011**	– 0.722
BEG	+ 0.511	+ 0.227	– 0.174	– 0.350	+ 0.981	– 0.172	– 0.189	– 0.086
KP	+ 0.823	+ 0.173	– 0.085	+ 0.874	– 0.504	– **0.021**	+ 0.959	– 0.591

related to the density of predatory kelp bass at a site (Table 4). Many of the significant relationships between recruitment and habitat as summarized by PCs no longer existed by the YOY stage (Table 4). Densities of YOY giant kelpfish, señorita, and blacksmith were no longer significantly related to any PC axis. YOY rock wrasse density was no longer significantly related to PC2, though they were positively related to PC1 and negatively related to PC4. At the YOY stage, kelp bass density continued to be negatively related to PC1, but it was no longer related to PC2. Densities of YOY bluebanded gobies continued to be negatively related to PC4. Densities of YOY blackeye gobies were no longer related to any PC axis. Densities of YOY kelp perch were related to PC3, whereas densities of younger recruits of this species had not been related to any PC axis.

Likewise, many of the significant relationships between recruitment and giant kelp abundance no longer existed, although densities of YOY giant kelpfish and kelp bass were still significantly related to some measurement of giant kelp abundance (Table 4). The positive relationship between giant kelpfish and the density of giant kelp plants persisted into the YOY stage; however YOY of this species were no longer significantly negatively related to the percent cover of giant kelp canopy. Densities of YOY kelp bass were no longer negatively related to the density of giant kelp plants, but they were positively related to the percent cover of giant kelp canopy. Kelp perch at the YOY stage were no longer significantly related to the density of giant kelp plants, and YOY blackeye gobies were no longer significantly related to the percent cover of giant kelp canopy.

Table 5. *Oxyjulis californica*. Results of ANCOVA testing for effects of site, cohort, and covariate number of days on density of señorita *O. californica* recruits. Non-significant ($p > 0.25$) interactions with the covariate were dropped sequentially. Data were $\log(x + 1)$-transformed

Source	Type III SS	df	MS	*F*	p
Site (S)	9.22	7	1.32	8.24	<0.001
No. of days (D)	34.47	1	34.47	215.54	<0.001
Cohort (C)	7.08	3	2.36	14.76	<0.001
S × D	5.25	7	0.75	4.69	<0.001
S × C	3.59	21	0.17	1.07	0.38
C × D	5.39	3	1.80	11.23	<0.001
Error	246.46	1541	0.185		
S × D × C	1.86	21	0.09	0.55	0.95
Error	244.60	1520	0.16		

Table 6. *Oxyjulis californica.* Summary statistics for 2 multiple regressions of mortality of señorita *O. californica* against habitat variables: one against 3 measures of giant kelp *Macrocystis pyrifera* abundance, the other against principal components (PC) 1–4 scores. Replication was at the level of site, i.e. n = 8 sites

	Standardized coefficient	*t*	p
Giant kelp abundance			
Canopy	–0.761	–3.014	0.039
No. of stipes	0.010	0.036	0.973
No. of plants	–0.312	–1.295	0.265
Principal component scores			
PC1	0.436	1.735	0.181
PC2	–0.591	–2.726	0.072
PC3	0.572	2.812	0.067
PC4	0.245	1.387	0.260

Effects of predators and habitat on mortality rates of recruits

Mortality rates were estimated for 4 cohorts of señorita by following the decay of density of each cohort through time at each site. Mortality rates differed among the 4 cohorts, and this pattern of differences among cohorts was consistent among sites (Table 5). Mortality rates of recently recruited señorita (averaged over the 4 cohorts) also varied among sites (Table 5). There was no relationship, however, between mean mortality rates of señorita and density of predatory kelp bass at a site ($r^2 = 0.14$, $p = 0.36$; Fig. 2A); whereas mortality rate was negatively related to kelp canopy cover ($p = 0.04$; Table 6, Fig. 2B), despite the lack of any relationships between mortality rate and habitat characteristics as summarized by the 4 PCs (Table 6). Mortality was also density dependent, increasing with average density of recruit señorita at a site ($r^2 = 0.75$, $p = 0.005$; Fig. 2C).

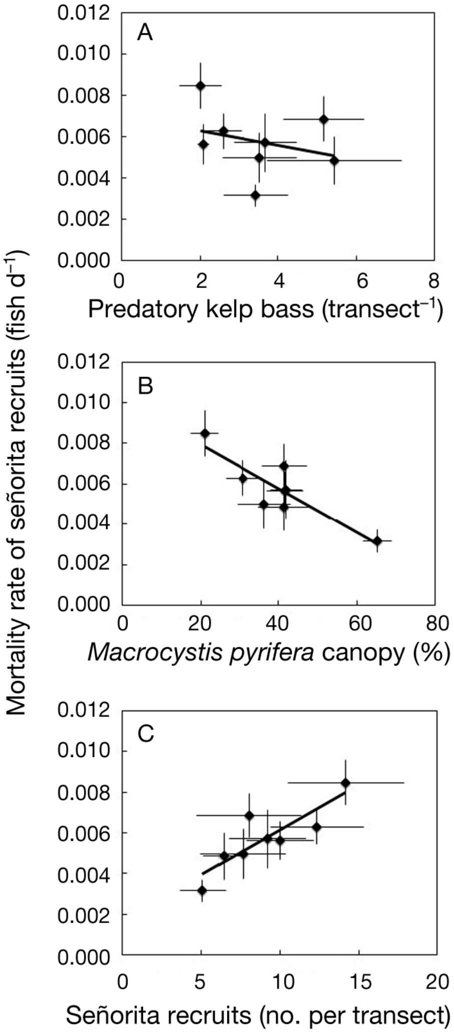

Fig. 2. *Oxyjulis californica*. Relationships between mortality rate (no. of fish lost d^{-1}) of señorita *O. californica* recruits and (A) density of predatory kelp bass, (B) mean percent cover of giant kelp canopy, and (C) density of señorita recruits at the 8 study sites. Data: mean ± SE

DISCUSSION

The results of this study indicate that recruitment of a suite of rocky reef fishes was not consistently correlated in space. We found some relatively strong positive correlations in recruitment of certain species pairs, but these correlations were not consistently present over time, nor were they statistically significant if more stringent critical p-values that controlled for family-wise Type I error rate were applied. These findings indicate that physical forcing of larval delivery by oceanographic features did not generate spatially correlated recruitment of reef fishes at sites spanning the northern side of Santa Catalina Island. While our findings contrast with those of White (2007) for the pair of species he studied around St. Croix, an island in the Caribbean similar in size to Catalina Island, they are consistent with a study by Tolimieri et al. (1998), which failed to find consistent spatially correlated patterns of recruitment among 14 species of fishes around 3 Caribbean islands including St. Croix.

There are several possible reasons why spatially correlated recruitment was not more prevalent among the 8 species we studied at Santa Catalina Island. These reasons fall into 2 general classes: those that operate prior to settlement and those that act at or after settlement. Delivery of larvae may not be spatially correlated, or if it is, correlated spatial patterns of delivery from shared physical forcing may be disrupted by settlement choices of larvae or by postsettlement movements or mortality.

For correlated larval delivery to occur, the oceanographic features that drive dispersal of larvae must either be stable over time, or larvae of different species must be in the pelagic realm at the same time and place. The correlated recruitment detected by White (2007) around the island of St. Croix is likely the result of stable oceanographic features around St. Croix, which include a convergence zone along the northwestern edge of the island. This consistent feature has been suggested to cause the consistent spatial patterns of recruitment observed in reef fishes on the northern side of the island (Hamilton et al. 2006). We suspect that the uneven distribution and low number (4) of sites around St. Croix in the study by Tolimieri et al. (1998) rendered that study incapable of detecting this consistent pattern of recruitment at this island.

The oceanographic features around Santa Catalina Island seem to be more dynamic than those around St. Croix, and this difference may result in uncorrelated spatial patterns of larval delivery and recruitment around Catalina. Within each of our study species, spatial patterns of recruitment were not generally consistent over time (Krug 2009), implying that spatial patterns of larval delivery may be inconsistent over time. Although there are some persistent oceanographic features around Catalina Island, notably a persistent mesoscale cyclonic eddy off the southeastern end of the island (Dong et al. 2009), along the portion of the island that we studied, the oceanographic features appear to be more dynamic. For example, using the Regional Oceanic Modeling System (ROMS), Dong & McWilliams (2007) documented over a period of just several days a series of submesoscale cyclonic eddies that formed and moved along the northwestern (leeward) side of the island, where we conducted our study. These eddies were sometimes associated with upwelling events. Furthermore, a warm, wind-induced island wake caused by island shielding has been documented on the eastern, leeward side of Catalina Island (Caldeira & Marchesiello 2002, Caldeira et al. 2005). These wakes add to the dynamism of the oceanography around the island, as they would be expected to change with wind velocity and direction. With temporally variable oceanographic features like those noted along the leeward side of Catalina Island, even if larval reef fishes acted as passive particles, it seems likely that their delivery to reefs along this side of the island would be uncorrelated among species if they had different larval durations. Pelagic larval durations varied among our study species, which is fairly typical (e.g. Wellington & Victor 1989, Shanks et al. 2003), making it likely that settling larvae would have been exposed to different oceanography by virtue of having spent different amounts of time in the pelagic realm.

Moreover, larvae of many marine species are not passive particles (Leis et al. 1996, Stobutzki & Bellwood 1997), which could also decouple delivery of different species. For example, larvae of different fish species have characteristic depth distributions and are found at different distances from shore (Leis 1991, Cowen & Castro 1994), which would presumably expose them to different oceanographic features (Cowen 2002). Furthermore, the timing and location of reproduction could influence larval dispersal if eggs or larvae are released at different times of day or at different locations, thereby subjecting them to different oceanographic features (Cowen & Sponaugle 2009).

On the other hand, it is possible that oceanography may in fact cause correlated delivery of larvae of different species to sites around Catalina Island, but this pattern might be disrupted by various processes occurring at or after settlement, causing a disconnect between patterns of larval delivery and patterns of recruitment. Larvae of many marine organisms make choices about where to settle (e.g. Crisp 1967, Sweatman 1983, Raimondi 1988), and more recent evidence indicates that these small-scale choices can affect larger-scale patterns of distribution (Forrester et al. 2008). After settlement, movements and mortality could decouple recruitment patterns from patterns of larval delivery (e.g. Shulman & Ogden 1987, Moksnes et al. 2003). Given that our study sites were large and relatively isolated from other reefs, and our study species move little after settling, post-settlement movements are unlikely to have modified settlement patterns much in the present study; post-settlement mortality, however, may have.

Predation is the main proximate cause of post-settlement mortality in temperate and tropical reef fishes (Hixon 1991, Steele & Forrester 2002, Almany & Webster 2006), and it reduces recruitment and disrupts settlement patterns (Carr & Hixon 1995, Steele & Forrester 2002). At first glance, we found little evidence that predation affected the spatial patterns of recruitment of our study species: recruit densities were not negatively correlated with predator densities. Moreover, the mortality rate of the one species we were able to estimate it for (señorita) was not related to predator densities. But recruitment patterns of all species and mortality rate of señorita were related to habitat variables. We suspect that these correlations with habitat were at least partially caused by habitat characteristics ameliorating predation intensity, as has been found in experiments on several of the study species (Carr 1991, Steele 1999, Anderson 2001). By the end of the settlement season, the role of predators became more apparent, with densities of YOY of the 2 most abundant prey species being negatively related to predator density.

Predation was likely the cause of the density-dependent mortality we found in señorita, as it is in other reef fishes (Hixon & Carr 1997, Forrester & Steele 2000). Even at the relatively large (30 km) spatial scale of our study, by the YOY stage, this density-dependent mortality disrupted initial differences in density among sites that had been established at the time of recruitment. This result is similar to that of White (2007).

Spatially correlated recruitment may be more an exception than the rule, but only more studies can reveal the veracity of this conclusion. Stable oceanographic features, such as those found around the island of St. Croix (Hamilton et al. 2006) are probably a prerequisite for spatially correlated delivery of larvae of different species. Where such correlations occur among interacting species, it will be important to incorporate them into attempts at understanding spatial population and community dynamics.

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