

Adult avoidance behavior leads to ontogenetic shifts in habitat use of an intertidal fish

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ABSTRACT: Spatial distributions of organisms result from a complex interplay of processes, including habitat selection as well as species interactions, and it remains a continual challenge to disentangle the relative importance of such effects. I investigated how habitat variation and conspecific interactions influence the abundance and distribution of different life history stages of the intertidal fish *Oligocottus snyderi*. I first examined the role of priority recruitment effects and found that prior recruitment had no effect on subsequent *O. snyderi* recruitment. I then examined how habitat variation influences adult and recruit abundances by manipulating surfgrass *Phyllospadix* spp. cover in tide pools, a habitat attribute that positively covaries with both *O. snyderi* life history stages. Surprisingly, whereas *O. snyderi* adults showed the expected negative response to surfgrass removal, the recruit response was positive. Additional experiments investigated whether these contrasting results were due to an ontogenetic change in habitat preference or to negative interactions between adults and recruits. Direct manipulation of adult abundance in the field determined that *O. snyderi* recruit abundance increases when adult abundance decreases. Laboratory studies indicated that although *O. snyderi* recruits have little to no preference for surfgrass cover, they do exhibit a strong negative reaction to conspecific adults and adjust their distributions accordingly. This combination of field and laboratory studies suggests that the ontogenetic habitat shift of *O. snyderi* is actually a result of negative interactions between size classes, such that recruits settle into sub-optimal tide pools in order to avoid interacting with adults.

KEY WORDS: Habitat variation · Conspecific interactions · Intraspecific competition · Aggregation · Recruitment · *Oligocottus snyderi*

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INTRODUCTION

Habitat selection is a complex behavioral process where organisms determine which habitats to reside in based on several characteristics that may influence their fitness, including physical aspects of the habitat and interactions with other organisms (Sutherland 1996). The complexity of this process is manifested in the trade-offs that individuals are subject to under different conditions, as habitats which provide benefits such as increased resources may also incur costs such as increased susceptibility to predation (Lima & Dill 1990, Werner & Anholt 1993, Holbrook & Schmitt

2002). The process of habitat selection is made even more complicated because habitat requirements and preferences, as well as susceptibility to predation, are likely to change throughout their lives. For many taxa, such variation in resource use and susceptibility to predation is primarily dependent on individual body size, and for species that undergo substantial changes in body size, the optimal habitat is likely to change as a function of ontogenetic stage (Werner & Gilliam 1984, Diehl & Eklöv 1995).

Animals should preferentially settle into habitats that have high 'intrinsic quality,' i.e. those habitats that have features that enhance the growth, survivor-

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ship, or reproduction of individuals (Muller et al. 1997). Spatial variation in habitat quality, such as resource levels or refuges from predators and parasites, can provide direct cues to potential settlers and subsequently lead to spatial structuring in populations (Muller et al. 1997). However, such spatial structuring in populations can also be caused by conspecific aggregation behaviors and may only be indirectly or even unrelated to habitat quality. In fact, in some cases conspecific aggregation behaviors can be so strong as to lead to aggregation within lower-quality habitats even if higher-quality habitats exist within the same landscape (Stamps & Krishnan 2005). In a similar vein, negative interactions from conspecifics could lead to repulsion regardless of habitat quality (Diehl & Eklöv 1995). Even though both habitat quality variation and interactions with conspecifics can influence the settlement patterns of new recruits into populations, there is still little consensus as to which of these 2 factors is generally most important in determining population spatial structure (Muller et al. 1997).

In addition to habitat quality and social factors, the distribution of individuals in a population can also be influenced by other factors such as predation pressure that can cause direct mortality or induce behavioral modifications in prey (Creel & Christianson 2008). For prey, non-lethal effects of predators can be more important than direct mortality inflicted by predators (Preisser et al. 2005). Indeed, among various behavioral responses to predation risk are changes in habitat use and aggregation (Creel & Christianson 2008). Theory on predator and prey space use has mainly focused on situations where multiple patches that vary in shelter or resource levels are available for both predators and prey, using the ideal free distribution approach to study 3 trophic levels (predators, prey, and a basal resource: Hammond et al. 2007). A general qualitative prediction from many of these types of models is that if predators pose a significant predation risk, then the number of prey in a high resource patch will be lower than expected given resource availability per se. Clearly the potential for predation can cause indirect effects in the habitat selection process, requiring more complex experimental designs to fully understand the relative importance of various factors contributing to habitat selection and spatial population structure. Determining which factors are most important in structuring populations becomes even more difficult in those organisms where cannibalism occurs – as the conspecifics utilizing the same resources (and potentially providing cues to resource

quality) can also pose a substantial predation threat (Fagan & Odell 1996, Persson et al. 2000). In fact, once thought to be rare, cannibalism is now generally accepted as a widespread process (Ohlberger et al. 2012), likely to be even more common in organisms with an open population structure where relatedness among individuals is low (such as for many marine organisms: Caley et al. 1996). By extension, then, negative interactions among conspecifics such as cannibalism could have non-lethal effects on distribution similar to predation and could lead to lower recruitment in a patch than expected purely based on habitat quality.

I studied a system of intertidal tidepool fish in which questions of habitat needs are further complicated by intraspecific interactions both within and among life history stages. To date, relatively little work has been done in marine systems that links the relative influence of habitat variation, ontogenetic shifts in habitat preference, conspecific interactions, and predation on structuring populations in their natural habitat. Specifically, I investigated the effects of the presence of conspecifics on the subsequent recruitment patterns of the fluffy sculpin *Oligocottus snyderi* in the face of habitat quality variation. I conducted experiments both in the field and in the laboratory to: (1) determine whether spatial variation in resident recruit abundance affects subsequent conspecific recruitment, (2) examine whether both adults and recruits exhibit the same response to variation in tidepool cover, (3) determine if spatial variation in adult abundance influences subsequent conspecific recruitment, and (4) examine the behavioral responses of recruits in relation to variation in tidepool cover and conspecific adult presence. In doing so, I describe how patterns of recruitment are the result of interactions between the distribution of high-quality habitat and the presence of resident adults resulting from a behavioral avoidance of young sculpins to intraspecific predation.

MATERIALS AND METHODS

Study system

Oligocottus snyderi is the most common constituent of the intertidal fish assemblage found in tidepools in the low to mid-intertidal zones of rocky intertidal sites along the coast of central California, USA (Yoshiyama 1981, Ritter 2009). After hatching, *O. snyderi* larvae spend ~1 mo in the plankton before settling into tidepool habitat during their recruitment

season from March to August (Pfister 1996, Ritter & Preisler 2006). Individuals inhabit tide pools for the remainder of their lives, reaching ~1.5 yr of age (Washington et al. 1984, Freeman et al. 1985), and are resident in the same tidepool or set of pools for months at a time (Yoshiyama et al. 1992, Knope et al. 2017, A. Ritter pers. obs.). *O. snyderi* reside in a very heterogeneous environment, with substantial natural variation occurring in the physical (size, depth, etc.) and biological (e.g. abundance of other organisms) characteristics of tidepools. Adults and recruits are closely associated with surfgrass and other forms of cover (Ritter 2008) that may provide structural refuge from predation by shore birds and larger fishes, or minimize temperature fluctuations and UV exposure in tidepools during low tides (Nakamura 1976a, Zamzow 2003, Shelton 2010). However, adults tend to be more abundant in larger pools, whereas recruits are more abundant in smaller, shallower pools (Ritter 2008). Considering their strong tidepool fidelity and ease of capture and marking (Yoshiyama et al. 1992, Knope et al. 2017), as well as their naturally heterogeneous environment, *O. snyderi* provide a model system in which to investigate the interactive effects of habitat-related and intraspecific interaction-related processes in a natural setting.

Field data collection

Several field experiments were conducted at Scott Creek and Pigeon Point, 2 intertidal sites 18.5 and 41.5 km north of Santa Cruz, California. Sampling of fish was done with dipnets once water had been drained from tidepools using 3.8 l buckets, and species, size (standard length, SL, in millimeters), and source pool of each captured fish was recorded. In some experiments, individual fish were marked with a small subcutaneous injection of elastomer (Northwest Marine Technology) using a 3/10 cc gauge needle. The abundance of recruits and adults was estimated as the number of individuals that were ≤ 25 or > 36 mm SL, respectively. Individuals between these size ranges were most likely older recruits from earlier in the same year or previous years and were therefore excluded from the other 2 categories because of this ambiguity. However, these individuals were marked and treated as adults in all experiments. The experimental design used throughout this study reflects the constraints due to working in a tidepool system; indeed, as it was not possible to find enough tidepools with similar physical (depth, volume) and biological (species diversity, surfgrass)

characteristics at a given site to conduct fully orthogonal experimental designs, the majority of the investigations in this study involve comparisons over time (repeated measures within a season as well as comparisons across seasons).

Effects of resident recruits on recruitment

To determine if prior recruitment levels influence the abundance of subsequent recruits, I experimentally manipulated the abundance of recruits at Pigeon Point in 2001 and conducted a series of follow-up surveys in 2002. In 2001, I chose 10 tidepools which occurred within the low to mid-intertidal zone on 2 adjacent intertidal benches, which were similar in physical characteristics (e.g. volume, surface area, and depth), as well as in proportion of surfgrass or algal cover (A. Ritter pers. obs.). I randomly allocated each pool to either a recruit removal treatment (5 pools), in which I removed prior recruits both initially and throughout the duration of the study, or a control (5 pools), wherein prior recruits were left intact and subsequent recruits were allowed to accumulate naturally. Since I was explicitly investigating recruit-recruit effects, I removed individuals > 25 mm SL from all 10 pools throughout the duration of the experiment (as juvenile and/or adult presence may also influence subsequent recruitment). I marked all captured fish to indicate the type of treatment pool they originated from, and transplanted any fish from removal treatments into different pools over 100 m away from experimental pools. This distance was effective as a removal in contrast to other studies on *O. maculosus* (Yoshiyama et al. 1992, Knope et al. 2017), as only 2 re-encounters occurred through the duration of the experiment, both the same adult *O. snyderi*. I censused these 10 pools and continued to maintain the treatments twice monthly from May to mid-July 2001. For each census, I recorded the number of *O. snyderi* per pool and determined the status of each fish (new recruit, prior recruit, or adult) based on size and elastomer marks.

Based on the 2001 experiment, there was evidence that recruitment patterns varied non-randomly across pools. To test whether this recruitment variation across tidepools was consistent even when priority effects are eliminated, in 2002 I gave all 10 pools the same treatment of recruit removal (and adult removal) and measured how subsequent recruitment covaried across tidepools. I censused these pools and maintained the removal treatment twice monthly from May to mid-July 2002. All fish collected in the

2002 censuses were removed from the site and used in laboratory experiments described below. Censuses in 2002 were conducted using the methods as in 2001, but in this case all fish were identified as either new recruits or newly migrated adults.

To determine whether the abundance of *O. snyderi* varied between each of the treatments in this and all subsequent field experiments in this manuscript, I analyzed the data with a linear mixed effects model (LMEM), using restricted maximum likelihood to obtain estimates of model parameters (Littell et al. 1991). Cross-correlations between sampling occasions at different lags indicated that the data were temporally autocorrelated, so the appropriate covariance structure (unstructured, compound symmetric, and first-order autoregressive, including Kenward-Rogers denominator degrees of freedom correction for first-order autoregressive covariance structure) was incorporated into each model (determined by comparisons of models using Akaike's information criterion and Schwarz's Bayesian information criterion). The units of replication (pools) were specified as the repeated measures subjects. Implicitly incorporated into this LMEM are both whole-plot error (i.e. γ , or the pool error) and sub-plot error (the residual), as well as both fixed (Treatment, Period, Time(Period)) and random factors (as both pool covariance and ϵ , the normally distributed independent sampling error, are random factors). For each analysis using an LMEM, the response variable was normalized using an $x^{0.25}$ (fourth-root) transformation which provided the best match to normality by visual inspection of the frequency distribution. The specific model structure that I used for the recruit removal experiment was: Abundance = μ + Treatment + Time + Year + Treatment \times Time + Treatment \times Year + Treatment \times Time \times Year + γ + ϵ , where the term 'Treatment' refers to whether or not the pool was allotted to the recruit removal or control treatment in 2001, 'Time' refers to which census the data were collected in (to account for within-season temporal variation), and 'Year' refers to 2001 or 2002 (to distinguish between habitat vs. recruit-recruit effects). Note that although the recruit abundance manipulation treatment was not in effect in 2002, the inclusion of the 2001 treatment (recruit removal or control) as a fixed factor in the model allows an assessment of whether or not any treatment effect detected in 2001 was truly due to the different treatments or a spurious result due to non-random recruitment variation across the pools allotted to each treatment group.

Effect of surfgrass variation on recruitment and adult abundance

In 2002, I experimentally manipulated surfgrass cover in tidepools to explore how its presence or absence may influence the abundance of adults and recruits (simulating natural variation in tidepool surfgrass cover at this site). Within the low to mid-intertidal zone on one large intertidal bench at Scott Creek, I chose 11 tidepools that were similar in surface area, volume, and tidal height, and all of which had initial levels of surfgrass *Phyllospadix torreyi* cover near 100% (and little to no algal cover). I estimated baseline abundance levels of *O. snyderi* in these pools through monthly censuses from January to March 2002. I then randomly allocated each of the 11 pools to either of 2 treatments: surfgrass removal (5 pools) or surfgrass control (6 pools). In surfgrass removal pools I used grass shears to trim surfgrass plants back to the rhizome, allowing the *P. torreyi* plants to recover over time. After implementing the surfgrass manipulation treatment (intentionally timed to coincide with the peak period in the annual recruitment of *O. snyderi*: Ritter & Preisler 2006), I continued monthly censuses of recruit and adult abundance in both surfgrass removal and control pools from April to July 2002. I marked all captured fish (recruits, subadults, adults) before returning them to their original pools, so that the abundance of new recruits could be determined for subsequent sampling occasions (note that the results of the first experiment in this study indicate that there are no priority effects among prior and subsequent recruits).

I analyzed the data for recruits and adults separately using a repeated-measures LMEM with the following model structure: Abundance = μ + Treatment + Period + Time(Period) + Treatment \times Period + Treatment \times Time(Period) + γ + ϵ , where the term 'Period' refers to when the data were collected relative to the manipulation (i.e. from before or after surfgrass removal), and the factor 'Time' is nested within the factor 'Period,' as data were collected multiple times prior to and after the manipulation. *A priori* orthogonal contrasts were also specified to compare the abundance of adults and of recruits across treatments, both before and after surfgrass manipulations were conducted.

Effect of adults on recruitment

In 2003, I conducted an adult removal experiment in the same set of pools originally used in the surfgrass manipulation experiment. The goals for this experi-

ment were 2-fold: (1) to determine how the abundance of recruits varied with the abundance of adults (while holding surfgrass cover constant), and (2) discriminating between the relative influence of adult abundance versus surfgrass cover on recruit abundance (by qualitatively comparing the results of the 2003 adult removal experiment to the 2002 surfgrass removal experiment). For this experiment, I conducted the adult removal treatment in the 5 pools which had exhibited higher numbers of adults in the previous surfgrass removal experiment (surfgrass control pools; 1 of the 6 original control pools was randomly dropped to facilitate field sampling), and I maintained the adult control treatment in the 5 pools which had exhibited lower numbers of adults in the previous experiment (surfgrass removal pools). If adult abundance is the main factor determining recruit abundance, then recruitment levels should be reversed based on those detected in the 2002 surfgrass treatments. I first estimated baseline abundance levels of *O. snyderi* through twice-monthly censuses from January to February 2003, before any manipulations were conducted. I then implemented and maintained the adult removal and control treatments through twice-monthly censuses from March to July 2003 (again intentionally timed to coincide with substantial recruitment of *O. snyderi*). For each census, I marked all fish before returning them to their original pools (except for adults from adult removal treatment pools, which were completely removed from the site), so that the abundance of new recruits and adults could be estimated. I did not remove recruits from these pools, as the recruit manipulation experiment described above showed no priority effects (see 'Results; Effects of prior recruits on recruitment').

To determine whether the abundance of *O. snyderi* recruits and adults varied between the adult removal and the control treatment, I analyzed the data with a repeated-measures LMEM using the same model structure as described above for the surfgrass experiment, except that in this case the term 'Period' refers to when the data were collected relative to the adult manipulation. *A priori* orthogonal contrasts were also specified to determine whether or not the abundance patterns varied between the treatment and control pools both before and after the adult abundance manipulations were conducted. Finally, to assess the relative importance of adult presence vs. surfgrass presence on *O. snyderi* recruitment patterns, qualitative contrasts were made between recruit abundance patterns generated in this experiment to those generated in the surfgrass removal experiment conducted in the same set of pools in 2002.

Behavioral response of recruits to adult presence

To further examine if the response of recruits to the surfgrass manipulation was driven by habitat preference or recruit–adult interactions, I conducted a set of laboratory experiments examining recruit behavior while simulating conditions from the surfgrass and adult abundance manipulation experiments conducted in the field. The first experiment tested whether recruits will behaviorally adjust their distribution based on the presence of adults. Ten recently collected *O. snyderi* recruits (14–15 mm SL) were released into each of 12 aquaria (20 l each) with a central divider of plastic mesh permeable to recruits but not to adults. This number was chosen to simulate *O. snyderi* recruit densities often seen in pools of similar volume as aquaria (A. F. Ritter pers. obs). After a 24 h acclimation period, 1 adult *O. snyderi* was released into 1 side of 8 of the 12 aquaria. I then recorded the number of recruits located in either side of the aquarium for both the treatment (adult addition; $n = 8$ aquaria) and control (no adults added; $n = 4$ aquaria) aquaria at 15 min intervals for 3 h (12 censuses total).

In the second experiment, 5 of the same experimental aquaria as described above (including the recruit-permeable central divider) were used, except that this time habitat characteristics were included to mimic the conditions in the field-based surfgrass manipulation experiment: surfgrass plants either whole or trimmed (to the rhizome) were placed on each side of the experimental aquaria. Ten recently collected *O. snyderi* recruits (14–15 mm SL) were then released into each aquarium and allowed to acclimate over a 24 h period. I then recorded the distribution of recruits in each aquarium relative to the 2 habitat treatments (with vs. without surfgrass cover), and subsequently introduced 1 *O. snyderi* adult (≤ 50 mm SL) into the high surfgrass cover treatment side of each aquarium (simulating results found in field experiments, where *O. snyderi* adult abundance was greater in pools with surfgrass cover). After 0.5 h (based on timing of recruit responses observed in first lab experiment), I recorded the final distribution of recruits relative to the presence or absence of an adult (combined with surfgrass cover vs. no cover).

For the first laboratory experiment, to determine whether the ratio of the number of recruits on the adult introduction side versus the adult-free side differed between the adult addition treatment and the control (where both sides were adult-free), I analyzed the data using an LMEM, except in this case the units of replication (aquaria) were specified as

the repeated measures subjects (rather than pools as for the field experiments). The model structure used was: Ratio of Abundance = μ + Treatment + Time + Period + Treatment \times Time + γ + ϵ . Finally, to test whether there was a difference in recruit abundance among surfgrass levels both before and after the introduction of an adult in the second laboratory experiment, I analyzed the untransformed data, as they were approximately normal on the distribution of recruits with an intercept-only analysis of variance (testing the null hypothesis that the difference among treatment groups is not significantly different from 0).

RESULTS

Effect of prior recruits on recruitment

The abundance of recruits varied among censuses but differentially across years (Table 1, Year \times Time). However, recruit abundance between the treatment levels did not vary substantially between years or among censuses (Table 1; no treatment effect or treatment interaction with year or time). Indeed, the pools assigned to either of the 2001 treatment groups (recruit removal or control) had similar recruit abundance patterns in both years, even though all of the pools were treated as recruit removal pools in 2002 (Table 1). Adult abundance patterns did not vary between recruit removal and recruit control treatments (Treatment: $F_{1,8} = 0.02$, $p = 0.8972$, Treatment \times Year: $F_{1,8} = 0.00$, $p = 0.9639$, Treatment \times Time: $F_{5,40} = 1.00$, $p = 0.4309$, Treatment \times Year \times Time: $F_{4,32} = 0.95$, $p = 0.4502$).

Table 1. Results from the mixed effects model analyzing the *Oligocottus snyderi* recruit patterns from the recruitment manipulation experiment at Pigeon Point, California. 'Treatment' was either recruit and adult removal or adult removal only. Recruit abundance data were $x^{0.25}$ transformed. Covariance structure used in model: compound symmetric. Degrees of freedom (df) are reported as numerator followed by denominator df

Effect	df	F	p
Year	1,8	24.76	0.0011
Time	5,40	6.88	0.0001
Year \times Time	4,32	3.05	0.0307
Treatment	1,8	0.09	0.7776
Year \times Treatment	1,8	0.98	0.3512
Time \times Treatment	5,40	0.49	0.7845
Year \times Time \times Treatment	4,32	0.04	0.9962

Effect of surfgrass on recruitment and adult abundance

Oligocottus snyderi adult abundance was strongly affected by the surfgrass treatment; there were no differences among treatments before the manipulation, whereas after the manipulation adult abundance was lower in surfgrass removal pools than in surfgrass control pools (Table 2: Treatment \times Period, Fig. 1a). Although *O. snyderi* adult abundance declined in surfgrass removal pools just after the

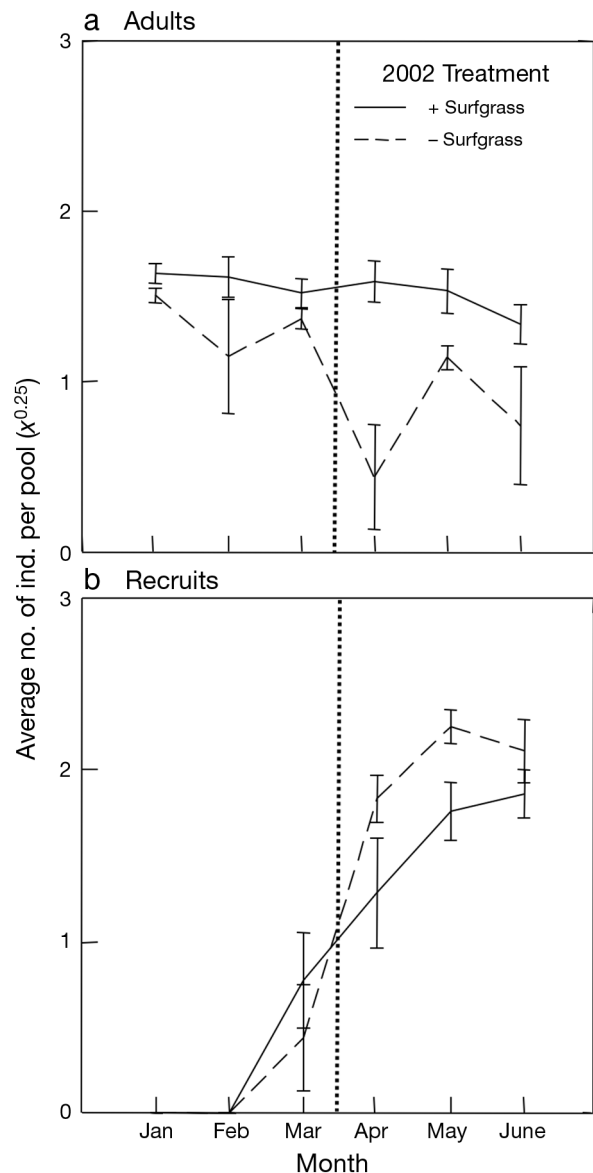


Fig. 1. Patterns of *Oligocottus snyderi* (a) adult and (b) recruit abundance (\pm SEM from raw data) in the surfgrass removal experiment both before and after the surfgrass manipulation treatments were initiated (indicated by the vertical dotted line)

Table 2. Results from the mixed effects model analyzing the *Oligocottus snyderi* adult and recruit abundance patterns in the surfgrass removal experiment at Scott Creek, California. 'Treatment' was either surfgrass control or surfgrass removal. 'Period' refers to when the data were collected relative to the manipulation (i.e. before or after surfgrass removal), and the factor 'Time' is nested within Period, as data were collected multiple times prior to and after the manipulation. Covariance structure used in model: compound symmetric. Degrees of freedom (df) are reported as numerator followed by denominator df

Effect	df	Adults		Recruits	
		F	p	F	p
Treatment	1,9	13.76	0.0049	7.57	0.0224
Period	1,9	18.15	0.0021	104.79	<0.0001
Treatment × Period	1,9	8.74	0.0160	12.36	0.0066
Time (Period)	4,34	2.22	0.0877	4.38	0.0058
Treatment × Time (Period)	4,34	2.55	0.0571	0.81	0.5269
Contrasts – Surfgrass control vs. removal					
Before treatments (Months 1–3)	1,9	2.75	0.1317	0.01	0.9171
After treatments (Months 4–6)	1,9	21.70	0.0012	18.49	0.0020

manipulation was conducted, it began to increase back to pre-manipulation levels as surfgrass levels recovered (Table 2: Treatment × Time (Period), Fig. 1a). Despite a tendency towards differences in adult abundance among treatment pools even before manipulations were implemented (Table 2: Treatment effect), substantial differences in adult abundance between the treatments were only evident after the surfgrass manipulations were conducted (Table 2: Contrasts).

A difference in recruit abundance was evident after but not prior to implementation of the surfgrass manipulations (Table 2: Treatment × Period, Fig. 1b). After the surfgrass treatments were conducted, the recruitment levels of *O. snyderi* were greater in surfgrass removal pools relative to control pools (Table 2: Contrasts, Fig. 1b). There was also substantial variation in recruitment among sampling occasions within each period (Table 2: Time(Period)). Overall, the patterns that recruits showed in relationship to surfgrass treatment were opposite to those detected in adults (Fig. 1b): recruits were less abundant in surfgrass control pools (where adults tended to be more abundant), and more abundant in surfgrass removal pools (where adults tended to be less abundant).

Effect of adults on recruitment

Prior to the adult manipulations, there was no difference in abundance of *O. snyderi* adults between the pools allotted to each treatment group (contrast among treatments before adult manipulations: $F_{1,8} = 0.06$, $p = 0.8137$). After the treatments were conducted, there was a strong difference in adult abun-

dance between adult removal and control treatments (contrast among treatments after adult manipulations: $F_{1,8} = 8.42$, $p = 0.0199$). Overall, *O. snyderi* adults declined in abundance in adult removal pools only once the adult removal treatments were begun (Treatment × Period: $F_{1,8} = 10.94$, $p = 0.0107$), indicating that the adult removal treatment was effective. For *O. snyderi* recruits, abundance did not differ between the treatment groups before the adult manipulations were conducted, whereas once the adult removals had begun recruit abundance increased in adult removal pools relative to adult control pools (Table 3: Contrasts, Fig. 2). Considerable temporal variability in recruitment among the 2 periods (Table 3: Period) and among sampling occasions within periods (Table 3: Time(Period)) makes an interaction between treatment and period difficult to detect. Nevertheless, there was an overall effect of adult treatment on recruitment levels (Table 3: Treatment).

Because the same 10 tidepools used in this 2003 adult manipulation experiment were also used in the surfgrass manipulation experiment in 2002, it is pos-

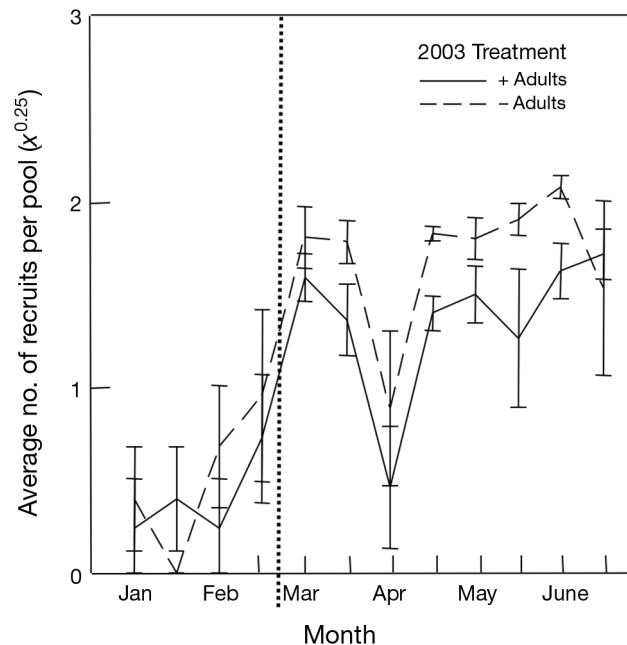


Fig. 2. Patterns of *Oligocottus snyderi* recruit abundance (\pm SEM from raw data) in each treatment both before and after the adult abundance manipulation treatments were initiated (indicated by the vertical dotted line)

Table 3. Results from the mixed effects model analyzing the *Oligocottus snyderi* recruit patterns in the adult abundance experiment at Scott Creek, California. 'Treatment' was either adult control or adult removal. 'Period' refers to when the data were collected relative to the adult manipulation (i.e. before or after removal), and the factor 'Time' is nested within Period, as data were collected multiple times prior to and after the manipulation. Covariance structure used in model: first-order autoregressive. Degrees of freedom (df) are reported as numerator followed by denominator df; denominator df are Kenward-Rogers corrected (uncorrected df in parentheses)

Effect	df	F	p
Treatment	1, 23.1(8)	3.63	0.0694
Period	1, 33.6(8)	85.70	<0.0001
Treatment×Period	1, 33.6(8)	0.96	0.3351
Time (Period)	10, 77.4(80)	4.94	<0.0001
Treatment×Time (Period)	10, 77.4(80)	0.99	0.4580
Contrasts – Adult control vs. adult removal			
Before treatments (Times 1–4)	1, 30.3(8)	0.32	0.5751
After treatments (Times 5–12)	1, 23.5(8)	5.72	0.0251

sible to compare qualitatively how recruit abundance varied across the 2 years and by the 2 treatment types (Fig. 3). In 2002, the surfgrass removal treatment led to lower *O. snyderi* adult abundance relative to the surfgrass control pools (Fig. 3a), whereas the 2003 adult control treatment, conducted in the same set of pools, resulted in a greater *O. snyderi* adult abundance relative to the adult removal pools (Fig. 3c). Overall, the adult manipulation experiment was successful at reversing the 2002 patterns of adult abundance across the treatment pools, and the recruit abundance patterns in 2003 were also reversed relative to the 2002 recruit abundance patterns (Fig. 3b,d). For example, recruit abundance in

2002 was greater in surfgrass removal pools relative to surfgrass control pools (Fig. 3b), whereas in 2003 the same pools had lower recruit abundance under the adult control treatment relative to the adult removal treatment (Fig. 3d). In both years, the abundance of recruits varied negatively with the abundance of adults, within the same tidepools and regardless of the level of surfgrass cover.

Behavioral response of recruits to adults

In the first laboratory experiment, the initial distribution of recruits between the 2 sides of each aquarium was relatively even in both the control and the treatment aquaria (ratio ≈ 1.0 ; Fig. 4a). After an adult was introduced into 1 side of the treatment aquaria, the ratio of recruits on the adult-absent side versus the adult-present side rapidly increased and stabilized at a higher level relative to the control aquaria,

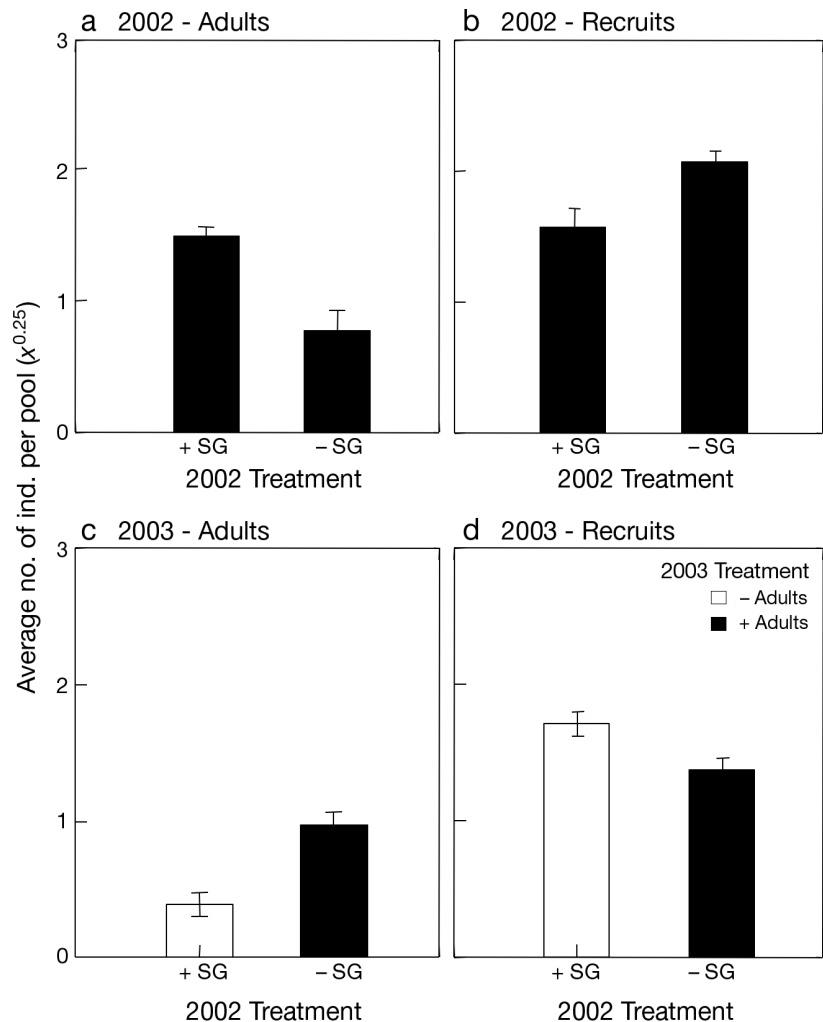


Fig. 3. Abundance patterns (\pm SEM from data) in surfgrass removal/adult abundance manipulation pools for *Oligocottus snyderi* (a) adults and (b) recruits in 2002 and for *O. snyderi* (c) adults and (d) recruits in 2003. The surfgrass manipulations (indicated by '+SG' for surfgrass control, and '-SG' for surfgrass removal) were conducted in 2002, and the adult abundance manipulations were conducted in the same pools in 2003 (note that surfgrass levels were not actually manipulated in 2003)

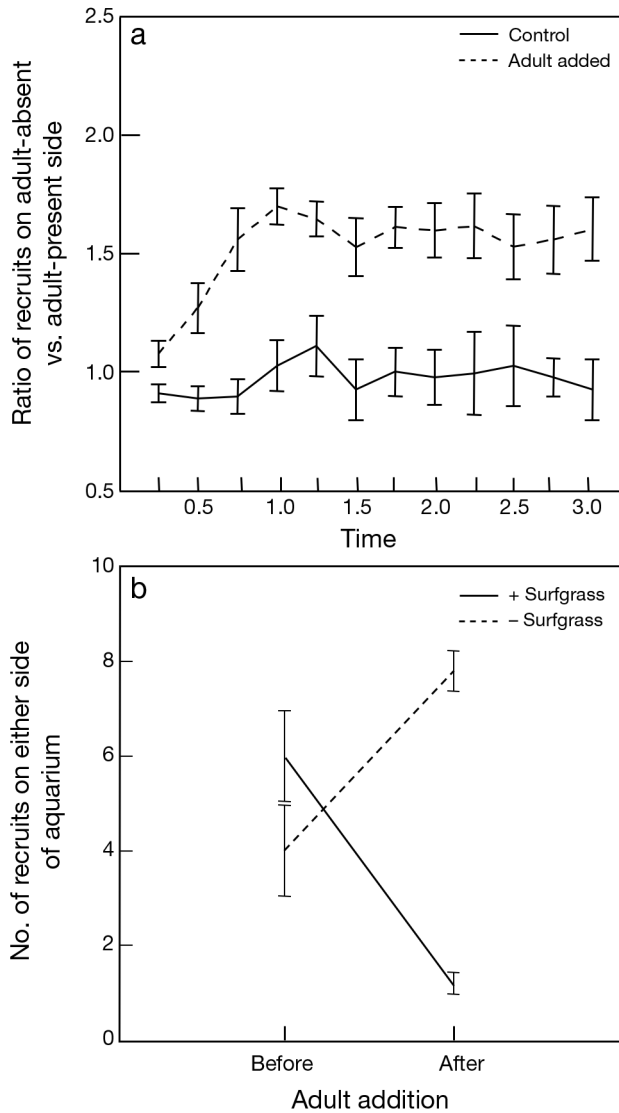


Fig. 4. Lab experiments. (a) *Oligocottus snyderi* recruit distribution estimated as the ratio of the number of recruits on the 'adult-absent' vs. the 'adult-present' side of each aquarium (\pm SEM from raw data; note that controls had no adult introductions). x-axis indicates time elapsed since introduction of adult to aquarium (in hours). (b) Ratio of the abundance of recruits (\pm SEM from raw data) relative to surfgrass level in the absence and presence of an adult

which maintained a near even ratio of recruits between the 2 sides (treatment: $F_{1,10.1(10)} = 19.92$, $p = 0.0012$, uncorrected degrees of freedom in parentheses). Although there was variability in the recruit ratio over time for both treatment and control aquaria, there was still an overall effect of adult presence on the distribution of recruits (Time: $F_{11,90.8(110)} = 2.80$, $p = 0.0035$; Treatment \times Time: $F_{11,90.8(110)} = 1.47$, $p = 0.1577$). In those aquaria where an adult was present, most of the recruits initially moved away

(within 0.5–1 h) and then remained away from the adult-present side of the aquarium for the duration of the study (Fig. 4a). In the second laboratory experiment, recruits initially showed no preference for surfgrass cover relative to no cover ($F_{1,4} = 1.43$, $p = 0.2980$; Fig. 4b). Once an adult was added to the surfgrass cover portion of each aquarium, recruits became more abundant in the side of the aquaria lacking surfgrass cover ($F_{1,4} = 167.54$, $p = 0.0002$; Fig. 4b). A comparison of the relative recruit abundance across surfgrass treatments after an adult was added indicates that despite no strong preference for surfgrass cover, recruits demonstrated a clear preference to be away from adults (Fig. 4b). For both laboratory experiments, I directly observed a few cannibalism events in those aquaria into which adults were introduced (e.g. note slight decrease in the number of total recruits after adult introduction in Fig. 4b).

DISCUSSION

Species–habitat associations can be the result of multiple processes including not only species-specific habitat preferences and physical tolerances, but also direct and indirect interactions within and among life history stages. In this study, I conducted a comprehensive investigation of the factors responsible for determining variation in the distribution of 2 life history stages of an intertidal sculpin, *Oligocottus snyderi*, using a combination of experiments in their natural habitat as well as within a laboratory setting. I found that the distribution and habitat association of recently settled sculpins were in fact a result of the interaction between 2 different processes, namely responses to habitat heterogeneity and interactions among conspecifics. The amount of cover found in tidepools, in this case provided by surfgrass, had a direct positive effect on the abundance of *O. snyderi* adults. The surprising results from the surfgrass manipulation experiment were that the abundance of *O. snyderi* recruits actually increased in surfgrass removal pools. Further experimentation in the field and in the laboratory determined that the positive response of *O. snyderi* recruits to reduced surfgrass cover was an indirect effect: recruits were actually responding positively to a decrease in the abundance of *O. snyderi* adults. This negative intraspecific relationship is driven by adult aggression towards recruits, and subsequent adult-avoidance behavior by recruits.

The differential responses of the adult and recruit life history stages of *O. snyderi* to variation in surf-

grass cover could result from a variety of different factors. For example, there could be a positive interaction between recruits, such as recruitment facilitation (Caley et al. 1996), which overrides any recruit preference for surfgrass. Although unlikely, if there had been higher initial recruit densities in pools allotted to the surfgrass removal treatment, or if prior recruits were more visible in pools without surfgrass, subsequent recruitment facilitation could lead to an increase in recruit abundance in the surfgrass removal pools that is not directly related to surfgrass cover. However, the experimental investigation of recruit–recruit interactions indicated that no such positive interaction occurs among *O. snyderi* recruits. Another possibility is that although *O. snyderi* adults have a preference for surfgrass cover (Nakamura 1976b), the habitat preference of *O. snyderi* recruits is actually different from that of the adults. Some dissimilarities between the distributions of adults and recruits of the same intertidal fish species have been recorded in past studies, such as recruits occurring at slightly higher or lower tidal heights (Pierce & Pierson 1990, Davis 2001, Szabo 2002), or in pools that are slightly smaller in size (Rickhus 1981). Previous research on *O. snyderi* indicated that the distribution of recruits closely matched the adult distribution (i.e. both had positive density associations with surfgrass/algal tidepool cover), the main difference being that recruits also tended to be more abundant in pools that were shallower or smaller in size (Ritter 2008). The results of the surfgrass manipulation experiment and the laboratory experiments indicate that these slight ontogenetic differences between the distributions of *O. snyderi* adults and recruits is more likely driven by negative interactions between these 2 life history stages rather than differences in habitat preference.

Finally, differential habitat use among life history stages may be an indirect result of negative intraspecific interactions, such as aggression or the threat of cannibalism by adults towards recruits. In classical predator–prey systems, it has been demonstrated that even without direct predation events, the presence of predators alone can strongly influence prey habitat use (Hammond et al. 2007, Creel & Christianson 2008), and there is evidence that the threat of cannibalism can have similar effects on the habitat use of smaller conspecifics in closed populations of freshwater fish (Diehl & Eklöv 1995, Persson & Eklöv 1995). For tidepool fishes such as *O. snyderi*, there is anecdotal evidence of intraspecific aggression (Yoshiyama 1981, Pfister 1995, Rojas & Ojeda 2010), but only a few studies have experimentally examined

intracohort aggression (albeit only in laboratory settings: Hernandez et al. 2002, Szabo 2002, Arakaki & Tokeshi 2012). I examined the effect that varying adult abundance has on subsequent recruitment levels by conducting an adult abundance manipulation experiment in their natural habitat. The results of this field experiment indicated that even a slight decrease in the abundance of adults led to a corresponding increase in recruit abundance in the same tidepools, suggesting that the abundance of adults is a stronger determinant of recruitment levels than variation in the amount of surfgrass cover. Furthermore, the laboratory experiments in this study revealed that recruits will strongly bias their distribution away from adults, a behavior that may be assisted by the ability of intertidal sculpins to chemically detect conspecifics, particularly other injured individuals (Hugie et al. 2010). In fact, in a few of the experimental replicates the total number of recruits actually decreased during the duration of the experiment due to predation of recruits by adults. Even if actual cannibalism occurs infrequently in the field (based on gut content studies of intertidal cottids: Yoshiyama 1980, Freeman et al. 1985), the combination of aggressive behavior and potential cannibalism from adults is likely to be a strong deterrent for recruits. Indeed, escape behavior of juveniles in response to agonistic behavior from intraspecific adults has been predicted to be an even stronger determinant of juvenile spatial distributions and ontogenetic habitat shifts than cannibalism itself (Martin et al. 2013).

This study elucidates the mechanisms that are likely determinants of ontogenetic differences in the distributions of intertidal fishes—a combination of agonistic interactions between life history stages and habitat preference in the context of a heterogeneous environment. Interestingly, the difference in the habitat use of different size classes of *O. snyderi* found in this study are as would be predicted by predator–prey theory: juveniles (in this case the potential prey) become more abundant in less optimal habitat relative to adults (the potential predators). In fact, previous studies of *O. snyderi* suggest that mortality may increase in tidepools that have less surfgrass cover (Ritter 2008). It is indeed likely that tidepools with less surfgrass cover or of smaller size are a less optimal habitat, as *O. snyderi* are very sensitive to variation in both temperature and UV exposure (Zamzow 2003), and tidepools have been shown to vary substantially in both variables relative to the amount of surfgrass cover (Shelton 2010). Several studies in both terrestrial and aquatic systems

have also found that interactions between life history stages within a species can profoundly influence habitat use patterns (freshwater salamanders: Rudolf 2006; freshwater fish: Persson & Eklöv 1995, Biro et al. 2003; migrating passerines: Bearhop et al. 2004). However, very few studies have demonstrated that the combined effects of habitat heterogeneity and negative intraspecific interactions, specifically avoidance behavior of smaller individuals due to aggression from larger conspecifics, can determine spatial structuring even in completely natural settings. Even fewer studies of these processes have been conducted in marine systems, where due to the prevalence of open-population structure and likely low relatedness among individuals, cannibalism may be more likely to occur and may be an even more important factor structuring populations. The threat of cannibalism alone can influence not only prey populations but also community structure (Rudolf 2007, Crumrine 2010), suggesting a strong need for further investigation of these phenomena in marine organisms if we are to better understand community dynamics in marine systems.

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