

CONCORDANCE BETWEEN SHORT-TERM EXPERIMENTS AND LONG-TERM CENSUSES IN TIDE POOL FISHES

CATHERINE A. PFISTER¹

Department of Ecology and Evolution, 1101 East 57th Street, University of Chicago, Chicago, Illinois 60637 USA

Abstract. Sixteen years of annual censuses (1990–2005) of an assemblage of tide pool sculpins at Tatoosh Island, Washington, USA, revealed relative constancy in the numbers of recruits and adults. However, the dominant species as a recruit (*Clinocottus globiceps*) was always replaced numerically as an adult by another species (*Oligocottus maculosus*). When mechanisms of coexistence were evaluated, little support was found for either a lottery model, because competitive interactions are hierarchical, or a storage-effect model of coexistence, because the relative ranking of recruitment varied little among years and did not covary among species with environmental variables such as ocean temperature, upwelling indices, or an estimator of ocean productivity (oyster condition index). There was also little evidence of niche partitioning based on habitat affinities. Additionally, predation-mediated coexistence had little support, given that the competitive dominant did not have the greatest rates of mortality. Instead, a competition–colonization trade-off may contribute to the coexistence of these species, where *C. globiceps* always recruits in the greatest numbers, while *O. maculosus* dominates the adult assemblage via competitive processes. The importance of post-recruitment processes in this assemblage is further suggested by some negative associations among species, the presence of density dependence, some habitat affinities, and previously published experimental work that demonstrated the competitive dominance of *O. maculosus* over *C. globiceps*.

Key words: *coexistence; competition–colonization trade-off; complex life cycles; El Niño; intertidal fishes; long-term data; ocean condition indices; recruitment variation; sculpins; upwelling.*

INTRODUCTION

In organisms with life cycles in which the young and adults occupy different habitats, an enduring question has been the extent to which processes that influence one stage affect the dynamics of the other (Frogner 1980, Roughgarden et al. 1988, Caley et al. 1996). In benthic marine systems, this is an especially relevant question because propagules of many taxa spend time in the plankton during which they experience environmental conditions that are distinct from those of the adult. There are many instances where events in the early life history result in high variability in the abundance of young (Hjort 1914, Caffey 1985, Gaines and Bertness 1992, Doherty and Fowler 1994, Davis and Levin 2002). As a result, the recruitment of new individuals to the established adult population can be highly variable and driven by environmental factors. If adult population numbers are highly sensitive to the supply of young, then adult populations can also fluctuate with recruitment variation (Doherty and Fowler 1994). If, on the other hand, adult population numbers are more sensitive to processes that affect adult survivorship, then the contribution of recruitment fluctuations will be lessened.

Indeed, occasional years of recruitment failure affect the abundance of longer-lived species very little (Paine 2002).

Here I report the results of 16 years of quantifying the abundance of recruits and adults in a guild of tide pool fishes. This study complements previous experimental manipulations of species abundances that showed a competitive hierarchy (Pfister 1995, 1999) and demographic studies demonstrating differential growth and survivorship of these species (Pfister 1996, 1997). I now present long-term data to quantify the variability in recruit and adult numbers, to understand the processes that may underlie the translation of recruitment patterns to adult dynamics, and to identify the possible mechanisms of coexistence in these fishes.

There is a diversity of coexistence mechanisms, and they are challenging to differentiate empirically. All require that one know how species affect resources and how they are affected by enemies, disturbance agents, and environmental variables (Amaresekare 2003). Differential population responses to events early in the life history potentially have great implications for species coexistence via competition. Possible mechanisms of coexistence in an assemblage of interacting and competing species increase if recruitment events vary among species. First, if species are equivalent competitors, then small differences in the timing or magnitude of recruitment can be important in a lottery model (Sale 1977,

Manuscript received 3 November 2005; revised 21 April 2006; accepted 2 May 2006. Corresponding Editor: M. A. Hixon.

¹ E-mail: cpfister@uchicago.edu

1978, Munday 2004). A second coexistence mechanism is the storage effect, where the covariance between competition and the environment allows a species at low density to accrue individuals in an area that is favorable either in space or time (Warner and Chesson 1985, Chesson 2003). However, if competitive rankings are unchanged by the environment, then a storage effect is unlikely. Other mechanisms of coexistence that may be relevant to this group of fishes include niche partitioning via tide pool habitat preferences and predator-mediated coexistence, where the superior competitor is affected the most by predation. A final mechanism, and the one for which there was the most support, is a competition–colonization trade-off where the inferior competitor has a higher rate of colonization (Tilman 1994). Note, however, that the demonstration of a competition–colonization trade-off is not sufficient itself to contribute to coexistence (Levine and Rees 2002), and key features necessary for the trade-off to contribute to coexistence are in strong asymmetric competition with displacement competition, where a competitively dominant species can displace another species from an occupied site (Yu and Wilson 2001, Levine and Rees 2002, Amaresekare 2003, Kisdi and Geritz 2003).

Here I show that recruit and adult numbers are relatively constant over time and that recruitment was relatively insensitive to variability in environmental parameters. In contrast, there was abundant evidence that post recruitment events greatly modified species composition and the adult community. I evaluate likely mechanisms of coexistence in this assemblage and show that a competition–colonization trade-off is a possible mechanism in this system.

METHODS

Study system

Intertidal sculpins (Family Cottidae, Order Scorpaeniformes) occupy mostly rocky tide pools areas from Alaska to California (Hart 1973), mostly occurring in tide pools. They have been shown to have high site fidelity and are capable of returning to home tide pools when displaced over a scale of hundreds of meters (Yoshiyama et al. 1992; *personal observation*). They have relatively small body size compared with other sculpins and are capable of reproducing at standard lengths of only 35 mm. Demersal eggs are laid during the winter months. Larvae are 4–6 mm in length and may spend 30–60 days in the water column (Washington et al. 1984) before recruiting back into nearshore areas during the late spring and summer months (*personal observation*).

Annual census data for a guild of tide pool sculpins were collected on Tatoosh Island (48°24' N, 124°44' W), 0.6 km off the northwest corner of Washington State, USA. Tatoosh Island is a complex of islets approximately 6 ha in area, and all studied tide pools were exposed to wave swells year-round. The tide pools used in this study varied in volume over two orders of magnitude, ranging from 13 to 1000 L, and the

abundance of fish was positively correlated with tide pool size (Pfister 1995). I deliberately chose tide pools over a narrow tide range (1.4–2.3 m above mean lower low water [MLLW]) to minimize the chance that pools were too high and could not support a fish fauna year-round or that pools were so low that they did not constitute insular habitat for the fishes. The dominant species in the pools at Tatoosh Island are the common tide pool sculpin (*Oligocottus maculosus*), the mosshead sculpin (*Clinocottus globiceps*), and the calico sculpin (*C. embryum*). Although other sculpin species were occasionally encountered (*O. snyderi*, *C. acuticeps*, *Artedius lateralis*), they were not abundant enough for quantitative analysis. Sculpins comprise in excess of 90% of the fish in these tide pools.

Censusing

Thirteen tide pools on Tatoosh Island were censused annually from 1990 to 2005 (with the exception of 1999). To census, the pool was partially drained, and then a small quantity of the fish anesthetic Quinaldine (Sigma-Aldrich, St. Louis, Missouri, USA) was added and mixed. When no more fishes were caught after repeated searching, the pool was emptied and refilled with untainted water. All fishes were measured (to standard length [SL]) and the gender was determined when possible. Fish were returned to the pool after censusing. All censuses were done during June and early July, when fish recruitment was greatest (Pfister 1996). Based on extensive tagging studies, I determined that individuals ≤ 35 -mm SL in June were young-of-the-year and were designated as “recruits” (Pfister 1996). The exception to this criterion were censuses of *C. globiceps* that were done in July, when 40-mm SL was used as the cut-off for designation as a recruit due to the relatively rapid growth of this species.

Environmental correlates

I asked whether the abundance of recruits was related to any oceanic environmental variables, in particular whether there were among-species differences in the relationship between abundance and environmental variables. Species-specific correlates to environmental variables might indicate the potential for competitive relationships among these species to vary through time. I asked whether sea surface temperature (SST) or upwelling patterns at the closest offshore automated buoy operated by the National Buoy Data Center (Cape Elizabeth Buoy, number 46041, 47°34' N, 124°75' W) correlated with recruit abundance by taking the mean SST and upwelling index for April, May, and June, the period preceding my censuses when larvae were likely to be in the plankton. Another indicator of oceanic conditions is the oyster condition index (OCI) that has been estimated monthly at four sites at Willapa Bay Washington for five decades by the Washington Department of Fish and Wildlife, Olympia, Washington. The OCI provides a monthly index of the ratio of oyster

tissue to shell material and should thus provide an estimate of phytoplankton productivity; the OCI has been found to correlate with El Niño-Southern Oscillation (ENSO) events (Schoener and Tufts 1987) and, thus, I thought that it would provide a biologically based indicator of ocean conditions. I again used a mean of April–June estimates to correlate with fish recruitment estimates and used the average of two sites (Stony Point at 46°68' N, 123°91' W; Parcel A at 46°50' N, 124°03' W) where transplanted oysters were monitored.

Differences in habitat preferences among species could be an indicator of niche partitioning. Thus, I asked whether there were habitat correlates for both the numbers of recruits and adults. The habitat variables I examined were pool volume (estimated using the colorimetric method described in Pfister 1995) and the eight most abundant habitat types: mussels (*Mytilus californianus*), the sea anemones *Anthopleura elegantissima* and *A. xanthogrammica*, the seagrass *Phyllospadix* (*P. scouleri* and *P. serratulus* were combined), red foliose algae (a grouping that was predominantly *Odonthalia* spp., *Neorhodomela* spp., *Microcladia* spp., and *Prionitis* spp.), gravel and crustose coralline algae, or articulated coralline algae. The latter two groupings were taxonomically complex, and species were not identified. Nonetheless, based on what is known about the taxonomy at Tatoosh Island, the crustose forms were likely *Pseudolithophyllum whidbeyense*, *Lithothamnion phymatodeum*, and *Lithophyllum impressum*, while the articulated forms were probably comprised of *Corallina vancouveriensis*, *Calliarthron tuberosum*, and *Bossiella* spp. (R. T. Paine, *personal communication*). The resulting data were structured such that there are repeated observations of habitat composition for each pool. To accommodate this hierarchical data structure with repeated observations through time on the same tide pool, I used linear mixed-effects models (Pinheiro and Bates 2000) in R (R Development Core Team 2005) to consider both fixed (all habitat variables) and random effects (the tide pools), while asking whether there were correlations through time. To normalize the residuals and provide a density estimate per tide pool, the abundance of each species ($\text{species}_i + 1$) was divided by the tide pool volume and then log-transformed. All percent cover data were arcsine square-root transformed prior to analysis. Habitat variables that explained a significant amount of the variation in species abundance were determined with a stepwise regression model (AIC based) fitted with MLE (maximum likelihood estimation). I asked whether the best-fitting model was significantly different from a model that included no habitat variables (null model) with a likelihood ratio test (LRT). For the best-fitting model, I also used a LRT to ask whether including a temporal autocorrelation structure within the data (at a lag of one year) improved the model fit. The final models for each species were re-fit using restricted maximum likelihood methods to obtain less biased parameter estimates.

Temporal patterns in species composition

Temporal patterns in species composition can reveal whether the abundance relationships among species are constant or dynamic. I asked whether there were long-term trends in species composition by quantifying community differences through time in two ways. In the first, I estimated Euclidean distances in fish composition as a function of yearly lags using the methodology of Collins et al. (2000). I regressed the Euclidean distance on the lag in years to ask if there was a significant trend to the abundance patterns for recruits and adults separately. Because there are fewer samples at greater time lags, I used the square root of the time lag as suggested by Collins et al. (2000). Although there are other metrics of dissimilarity, I used the Euclidean distance because it emphasizes change in the abundant species, which seems to be appropriate for this system of only three dominant species. I estimated significance values for the regression coefficient of time lag vs. Euclidean distance by generating coefficients from resampling the population data 1000 times. I also performed an ordination of the data, using principal components analysis (JMP software; SAS Institute 2003) to determine if there was a pattern to the censuses through time.

I used two additional metrics of community composition combined with permutation tests to ask whether annual vectors of change in this community were unidirectional and predictable, based on the composition of recruits (sensu Fulton and Harcombe 2002). The city block distance metric (CBD), also referred to as Manhattan (Faith et al. 1987), differs from Euclidean dissimilarity metrics because the differences are not squared, thus de-emphasizing the largest differences and allowing for negative values such that

$$\text{CBD}_{i,j} = \sum |x_{i,j} - x_{j,k}|.$$

The CBD is the dissimilarity between vectors of species abundance i and j for all k species. I was specifically interested in asking whether the vectors of change for recruits at time t to adults at time $t + 1$ were correlated with the composition of recruits at time t . I thus constructed two dissimilarity matrices using CBDs: one for the dissimilarity between recruits at time t and recruits at time $t + n$, and another for the estimated change in recruits at time t to adults at time $t + 1$ over the time period n . A positive correlation between these two dissimilarity matrices would indicate that years with comparable recruitment composition would yield vectors of change to the adult community that were also more similar. Fulton and Harcombe (2002) postulate that a strong correlation between this state vector matrix and change vector matrix indicates a system with relatively predictable dynamics. I used nonparametric Spearman's correlation coefficient to quantify the correlation between the two CBD estimates. I also asked whether the CBD estimates I observed from a

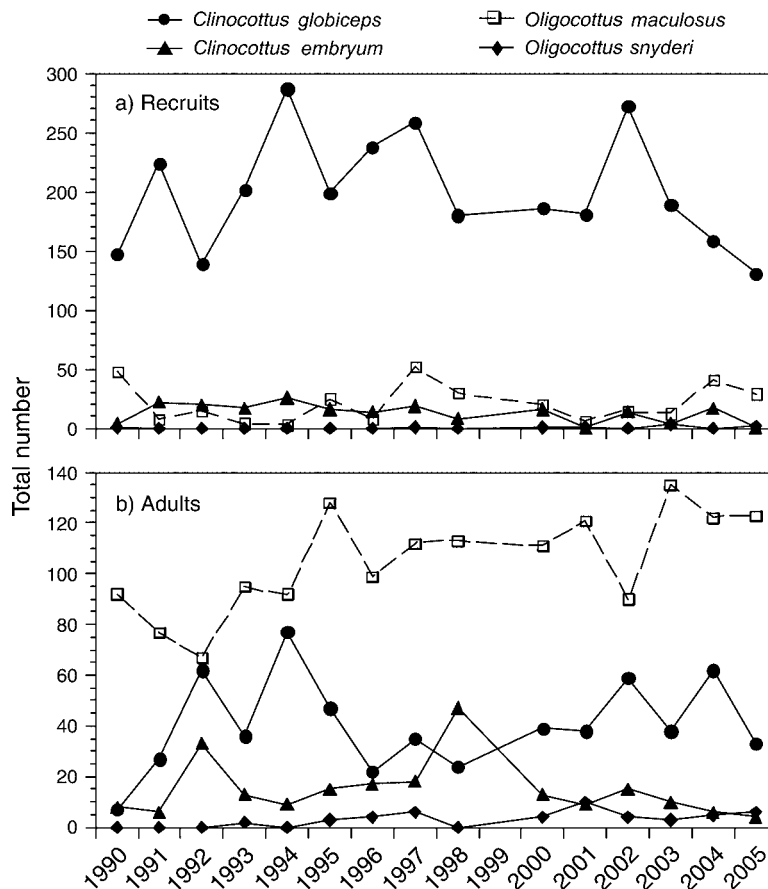


FIG. 1. The total number of sculpins classified as (a) recruits and (b) adults in 13 census tide pools at Tatoosh Island, Washington, USA.

comparison of recruits at time t and adults at time $t + 1$ were more restricted than that obtained from a permutation of all possible combinations of recruits at time t and adult densities at time $t + n$.

Indicators of post-recruitment processes

An alternative to recruitment processes driving abundance patterns of adults is that the composition of adults is shaped by biotic interactions within the guild. I investigated this possibility by looking at statistical relationships among con- and heterospecifics. I estimated regression coefficients that represented conspecific interactions (density dependence) and heterospecific interactions (competition or facilitation) with the following equation:

$$\ln\left(\frac{N_{t+1,i}}{N_{t,i}}\right) = r_i + aN_{t,i} + bN_{t,j} + cN_{t,k}$$

where N_t is the abundance of species i , j , or k at annual time t , a represents density dependence, and b and c are coefficients for heterospecific interactions. A constant, r_i , represents a term for recruitment. Thus, I asked whether yearly changes in the abundance of a species were sensitive to the abundance of itself vs. other dominant

species. I did these analyses only for adults where individuals were present for multiple years, and I hypothesized that density-dependent interactions would be important. I used this dynamic regression approach because I have found it to be a better indicator of species interactions demonstrated experimentally compared with regressions based only on single or static censuses (Pfister 1995). Confidence intervals on regression coefficients were again based on resampling the data 1000 times because of the potential violation of independence caused by using time series data.

RESULTS

Over the course of the study, the most obvious distinction between the composition of new recruits to intertidal pools and the composition of adults was the dominance by *C. globiceps* among recruits, while *O. maculosus* always dominated among adults (Fig. 1). Although the abundance of *C. embryum* as a recruit was comparable to *O. maculosus*, it consistently ranked third in abundance as an adult. *O. snyderi* was rare at Tatoosh Island throughout the study period, although it can be abundant at other sites several kilometers distant (Pfister 1996). Thus, for the three dominant species in this

TABLE 1. The correlation coefficients between fish recruitment and metrics of ocean conditions, including sea surface temperature (SST), an upwelling index, and the oyster condition index (OCI).

Species	SST	Upwelling index	OCI
<i>C. embryum</i>	0.172	-0.045	-0.301
<i>C. globiceps</i>	0.165	-0.257	0.038
<i>O. maculosus</i>	0.128	0.092	-0.136
All recruits	0.225	-0.224	-0.060

Notes: No estimates were statistically significant. For all analyses, $n = 15$ years.

assemblage, recruit composition was very distinct from that of adults.

The relative constancy of recruitment composition occurred, despite two El Niño events during the study (1993, 1997), suggesting that recruitment success is not tightly coupled to oceanic events. There were few correlations between the metrics of ocean conditions and fish recruitment patterns for any species (Table 1). The abundance of the total number of recruits or the abundance of each species separately was uncorrelated with either the average sea surface temperature or the upwelling index during the months when larvae would be expected to be in the water column (April–June). Similarly, an independent metric of ocean condition, the oyster condition index, from Willapa Bay, Washington, USA, also showed no significant relationship to recruitment patterns for any species.

Several habitat associations were significant for recruits of different species (Table 2). There was a negative association of *C. globiceps* with gravel and articulated corallines. *O. maculosus* and *C. embryum*

recruits were negatively associated with pool volume and positively associated with mussels. For adults, *C. embryum* densities were positively associated with gravel and crustose coralline algae and negatively associated with tide pool volume. *C. globiceps* showed a positive association with mussels, while there were no significant ($P < 0.05$) habitat associations for adult *O. maculosus*. In most cases, a model with some habitat variables (“best model”) had a significantly reduced AIC estimate compared with a “null model” that contained no habitat variables (based on a Likelihood Ratio Test). The exception to this trend was *O. maculosus* adults, where no habitat variables were significantly explanatory. The autocorrelation estimate within tide pools did not differ from zero for recruits of any species, but was significantly positive for adults of *C. embryum* and *O. maculosus* only. For both of those species, the model for adult density was improved (lower AIC) by the inclusion of the autocorrelation. Thus, there were several significant explanatory habitat variables among species and life stages, but they were rarely similar among species or among life stages.

The relative constancy of composition suggested in Fig. 1 was further supported by a lack of strong evidence for directional change in several analyses. First, estimates of disparity among census dates, using the Euclidean distance (ED), were unrelated with lag time in years for recruits ($P = 0.395$, based on Monte Carlo simulation of regression results; Fig. 2a). Although there was a slight, but significant, positive relationship for adults ($P = 0.002$; Fig. 2b), only 6.6% of the variation was explained by lag time for adult composition, suggesting that directional change may have occurred

TABLE 2. Habitat associations of the three dominant tide pool sculpin species determined with linear mixed-effects models for each species and life stage separately.

Species and life stage	Habitat variables	Coefficient sign	AIC			Autocorrelation
			Null model	Full model	Best model	
<i>Clinocottus embryum</i>						
Adults	tide pool volume*	–	214	200	195***	0.432***
	gravel***	+				
	crustose corallines†	+				
Recruits	tide pool volume*	–	245	250	240*	0.041
	mussels†	+				
<i>Clinocottus globiceps</i>						
Adults	mussels*	+	267	271	264*	0.129
Recruits	gravel†	–	287	293	283*	-0.121
	articulated corallines*	–				
<i>Oligocottus maculosus</i>						
Adults	none significant		246	259	246	0.383***
Recruits	tide pool volume*	–	281	274	269***	0.136
	mussels†	+				

Notes: Significant habitat variables and the sign of their coefficients are listed and were determined with AIC stepwise procedure to identify a “best model” from a “full model” of all possible habitat variables. A “+” indicates a variable that was positively related to species abundance, while a “–” indicates a negative relationship. The “null model” AIC is one in which no habitat variables were included. Significant autocorrelation contributions to the AIC are also indicated. Significance for the best model AIC is based on comparison (with a likelihood ratio test [LRT]) to the null model using maximum likelihood estimation (MLE).

* $P < 0.05$; *** $P < 0.001$; † $0.10 > P > 0.05$.

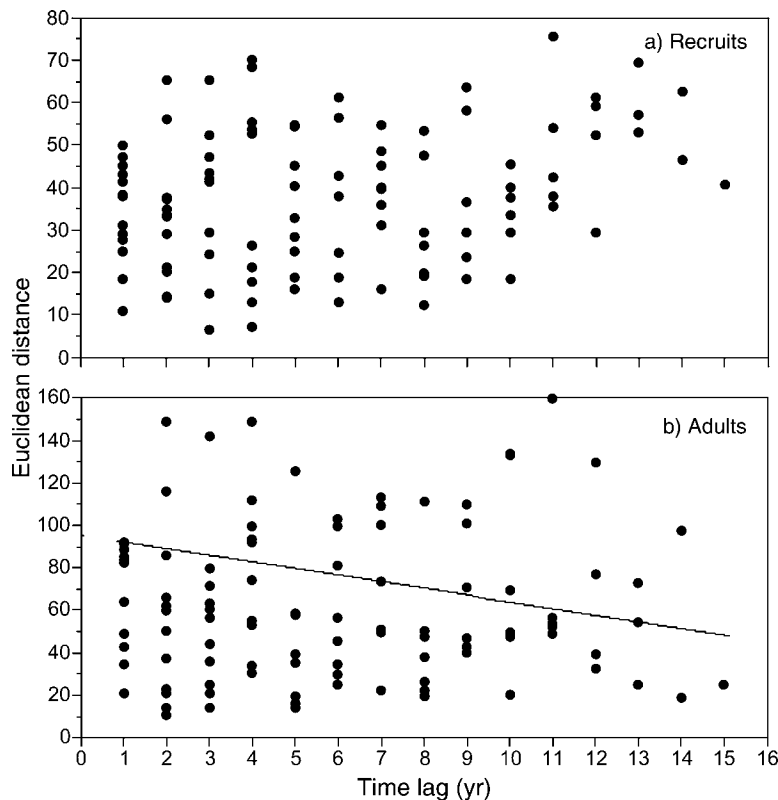


FIG. 2. The Euclidean distance (ED) among census periods as a function of the time lag among census dates for (a) recruits and (b) adults. Regression indicated a slope of 0.221 for recruits and 1.181 for adults with intercepts of 61.912 and 30.964, respectively. Bootstrapped P values were 0.395 for recruits and 0.002 for adults. The best-fit line for the adult data is shown.

at a very slow rate. A second analysis, using ordination of the adult composition data with PCA, showed mixed evidence of compositional changes through time (Fig. 3). Two components had eigenvalues >1 , explaining 75% of the variance in adult abundance patterns. The first principal component was associated negatively with *O. maculosus* and positively with *C. embryum* abundance, while the second was positively associated with *C. globiceps* abundance. Two compositional patterns were suggested, including a clustering of five of the last six years, perhaps indicating an emerging trend in species composition through time. Also, the years following ENSO events tended to be different with respect to the second principal component, perhaps reflecting the relatively high abundance of *C. globiceps* in 1994 and low abundance in 1998.

Constancy through time in the rank abundances of adult populations implies some repeatable pattern in how recruit composition is translated to the adult assemblage. When I tested whether a dissimilarity matrix for recruits was correlated with the vectors of change from recruits at time t to adults at time $t + 1$, I found evidence of a strong positive relationship ($r = 0.670$, $n = 83$), initially suggesting that similar recruitment composition among years yields similar vectors of change to the adult assemblage in the next year.

However, resampling the data suggest that this correlation, though high, is not significant, because most combinations of recruitment in year t with adults in year $t + n$ yield a high correlation. The CBD estimates for the observed differences between recruits at year t vs. adults at year $t + 1$ also yielded an estimate (255.5) that fell near the mean of all possible combinations of recruits at year t and adults at year $t + n$. Thus, although the CBD metric of Eq. 1 might be used to suggest predictability in the translation of recruits to adults among years, the range of adult densities seems to constrain distance metrics such as CBDs to be within a relatively small range.

Competition is one mechanism by which the pattern of translation from recruits to adults can be directional and repeatable and the presence of competition is suggested by the data. When I estimated the relative contribution of intra- vs. interspecific competition for each species using Eq. 2, I found that all three of the common species had negative coefficients for intra-specific competition (the a in Eq. 2; Table 3), although only *O. maculosus* was marginally significant ($0.10 > P > 0.05$). When I estimated interspecific interactions (b in Eq. 2), the change in *C. globiceps* numbers was negatively related to both *O. maculosus* and *C. embryum* numbers, though only the interaction with *C. embryum*

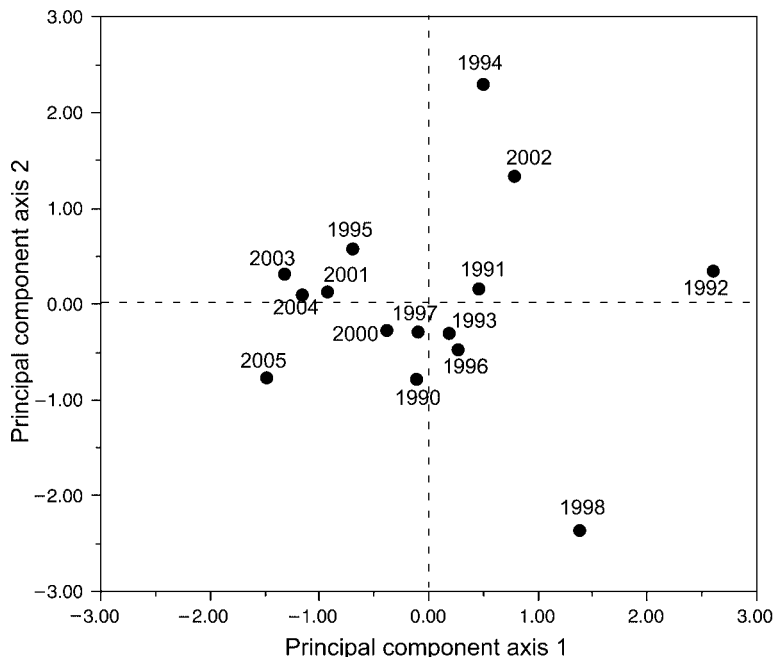


FIG. 3. An ordination of the abundance of adult sculpins using principal-components analysis (PCA). The first eigenvalue was 1.192 and explained 39.75% of the total variance, while the second was 1.067 and explained an additional 35.57%. Principal-component axis 1 was negatively associated with *Oligocottus maculosus* abundance and positively associated with *Clinocottus embryum* abundance, while axis 2 was positively associated with *C. globiceps*.

was marginally significant. In contrast, there was a trend for the change in *O. maculosus* densities through time to be positively related to *C. globiceps* numbers ($0.10 > P > 0.05$), while the change in *C. embryum* numbers were insensitive to other species. In summary, the *C. globiceps* population showed evidence for the greatest negative effects from the other two dominant species.

DISCUSSION

Over 15 years, *C. globiceps* numerically dominated the assemblage of recruits in tide pools, while *O. maculosus* was numerically dominant in the adult assemblage. This reversal of fortune for *C. globiceps* probably has several causes. First, *C. globiceps* was shown to be competitively inferior to *O. maculosus* in manipulative experiments at nearby Makah Bay (Pfister 1995). The removal of *O. maculosus* resulted in increased growth rates by *C. globiceps*, while the removal of *C. globiceps* had no effect on *O. maculosus*. This asymmetric competitive effect was also reflected in dynamic regression models where the census interval was only two weeks. Here, when I used dynamic regression with an interval of one year, I again detect asymmetric competition, where *O. maculosus* has a negative effect on *C. globiceps* but not the reverse. In addition to increased sensitivity to interspecific competition, *C. globiceps* also showed the strongest response to conspecific density, suggesting its numbers might be further limited by density dependence. Although there was only weak evidence for density dependence in *O. maculosus* and *C. embryum*, previous analyses of these

fishes at Tatoosh Island showed strong evidence for density dependence on shorter time scales (1 to 1.5-month intervals for three years; Pfister 1996). These shorter time scale analyses also demonstrated both higher growth and mortality rates for *C. globiceps* in comparison with *O. maculosus*. The timing of recruitment also differs for the two species, with *C. globiceps* recruiting earlier during the spring than the other two species (Pfister 1997). Thus, based on the shorter term censuses and experiments done previously, one would

TABLE 3. The intra- and interspecific interactions estimated from coefficients from multiple regressions using Eq. 2 (see *Methods: Indicators of post-recruitment processes*).

Parameter	Change in abundance†		
	<i>C. embryum</i>	<i>C. globiceps</i>	<i>O. maculosus</i>
Independent variable			
<i>C. embryum</i>	-0.048	-0.034‡	0.006
<i>C. globiceps</i>	-0.005	-0.027	0.007‡
<i>O. maculosus</i>	-0.009	-0.011	-0.005‡
Constant (r_i)	1.812	2.797	0.171
Parametric regression results			
r^2	0.233	0.816	0.669
$F_{3,9}$	0.910	13.270	6.060
P	0.473	0.001	0.015

Notes: The F and r^2 estimates are based on parametric regressions, while the significance of the coefficients is based on resampling analyses. See Table 1 for full species names.

† $N_{t+1,i} - N_{t,i}$.

‡ Indicates a coefficient where $0.10 > P > 0.05$.

have predicted that *C. globiceps* could only persist in the system through repeatedly high rates of recruitment; a pattern borne out by the longer term censuses shown here.

Although there is much focus in marine systems on the potential for events during the larval stage to affect community structure (Underwood and Denley 1982, Sale 1978, Warner and Chesson 1985, Menge and Sutherland 1987, Connolly and Roughgarden 1999, Connolly et al. 2001), there are relatively few multi-species data sets that span a sufficient time interval to test how recruitment and adult assemblages are related. The data presented here span several generations of these fishes and indicate strongly that the abundance of recruits is a relatively poor predictor of adult abundance, especially for the two most abundant species (*O. maculosus* and *C. globiceps*). Instead, post-recruitment events appear to better explain the composition of the adult community. *O. maculosus*, though relatively less abundant as a recruit, has higher juvenile and adult survivorship (Pfister 1996, 1997). Not only are the relative abundances of recruits poor predictors of adult assemblage patterns, but recruitment per se does not appear to have an effect on population change equivalent to that of adult survivorship based on previous demographic analysis of these species at time scales of both months and years (Pfister 1996). Metrics relating how recruitment is translated into adult abundance were also very revealing. There was a positive relationship between how similar a vector of recruit abundances were with how those vectors were translated into adult abundance, but the correlation was not unexpected given any combination of recruit and adult abundances from different years. In other words, there seems to be enough constraint in how recruitment is translated in to adult abundance over all the years of the study that shuffling years around does not greatly change the metrics used to describe observed annual changes.

Tatoosh Island's placement in the northeast Pacific has been characterized as being a part of the California Current system that has relatively weak, but persistent upwelling (Roughgarden et al. 1988, Menge et al. 2004). Because weaker upwelling is thought to lead to greater retention of larvae inshore, the areas around Tatoosh Island might thus have an uninterrupted supply of larvae that sets the stage for the dominance of post-recruitment events. Only studies from a greater geographic area will address this, but it is notable that there are other locales to the south where recruitment is greatly affected by El Niño events and recruitment failure by related species has been demonstrated (Davis 2000). It may also be that there are sufficient "relaxation" events during seasonal upwelling that tide pool sculpin larvae are retained near their natal areas (e.g., Shanks and Eckert 2005). Although the planktonic duration of tide pool sculpin larvae is reported to be 30–60 days (Washington et al. 1984), allowing much

opportunity for transport, Marliave (1986) has observed sculpin larvae schooling close to the benthos and avoiding transport. Because Tatoosh Island is an area with relatively high wave energy and tidal currents, it is difficult to imagine how the larvae of these fishes avoid transport and advection, and it is surprising to see such relative constancy in the numbers of larvae over the 16-year period. In the absence of detailed information about the transport of larvae and their duration in the water column, the hypotheses about how they should respond to water column events remain speculative. Regardless, I have shown that a simple focus on events and correlates of recruitment would be insufficient to make inferences about the structure of the adult assemblage. Post-recruitment processes appear to persistently modify the recruitment assemblage into a relatively constant adult composition.

The lack of a distinct and lasting signature of past recruitment events and the lack of fluctuations in recruitment among the tide pool species I studied negate a storage-effect mechanism of coexistence (Warner and Chesson 1985, Chesson 2003). In fact, there was little evidence that fluctuation in environmental variables might have differential effects on species. Instead, a striking feature of these data is the relative insensitivity of all species in this assemblage to annual ocean condition variation, particularly El Niño events. On a temporal scale of months, however, significant correlations between recruitment and sea surface temperature and indices of upwelling do occur (Pfister 1997), suggesting that, although the magnitude of an annual recruitment pulse is not tightly coupled to oceanic events, the timing of that pulse may be related to such events. The timing of the recruitment pulse was, however, ranked consistently among species in the three years that recruitment was studied on a monthly time scale (Pfister 1996, 1997). The competitively inferior *C. globiceps* always recruited earlier than *O. maculosus*. Thus, there seems to be little evidence to date for covariance between competition and environmental variables required for coexistence via the storage effect.

Another mechanism of coexistence in this competitive system could include niche partitioning via habitat preferences. However, the evidence for strong habitat associations in these species is relatively weak and inconsistent among recruits and adults. In fact, the competitive dominant *O. maculosus* has no strong habitat affinities as adults, suggesting that it can be present in almost all pools, a pattern borne out by the censuses. Although linear mixed-effects models suggested there were some positive and negative habitat associations, it is unclear whether the associations are distinct enough among species to drive habitat-specific patterns of abundance. Thus, it seems parsimonious to exclude niche partitioning of habitat as a mechanism that strongly promotes coexistence of these species. An alternative mechanism of competitive coexistence is a competitive lottery (e.g., Munday 2004). However, the

documented post-recruitment competitive hierarchy clearly negates this hypothesis.

Predation events can also drive the post-recruitment demographic patterns and coexistence. In other fish assemblages, predation has been demonstrated to be an important process regulating the abundance of smaller-bodied prey species (e.g., Hixon and Carr 1997) and mediating the role of density dependence (Johnson 2006). Although I have little direct evidence for predation on these fishes, piscivorous fishes are present in the area and include cabezon, red irish lord, and lingcod (*personal observation*), and birds such as pigeon guillemots and cormorants (Palmer 1962, Drent 1965, Ainley et al. 1990). Predation might be differentially important if species differed greatly in their movement rates. Rates of colonization are nearly identical for adult *C. globiceps* and *O. maculosus* (e.g., Pfister 1998), suggesting that mortality events do not change the rate at which the two dominant species occupy tide pools. Predation would contribute to coexistence in this system if *O. maculosus*, the competitive dominant, suffered higher mortality from predation. However, mortality rates are the lowest for *O. maculosus*.

The existence of a competition–colonization trade-off seems to be a strong feature of this assemblage of fishes: *C. globiceps*, the competitively inferior species has the greatest representation as a recruit. Whether this trade-off contributes to coexistence is less clear, and the role that competition–colonization trade-offs play in theoretical models of coexistence is varied (Amarasekare 2003). While there is much evidence that the trade-off exists, theory suggests that the trade-off will only be important to coexistence if competition is strongly asymmetric and environmental heterogeneity provides a refuge to the inferior competitor (Levine and Rees 2002). Although there are a number of examples where competition–colonization trade-offs are associated with coexistence using patch occupancy models (Levins and Culver 1971, Horn and MacArthur 1972, Levin 1974), more recent modeling has illuminated some of the features that promote coexistence, including environmental heterogeneity (Chesson and Warner 1981), patch density (Yu and Wilson 2001), demographic stochasticity (Kisdi and Geritz 2003), and the process of displacement competition (where a colonist can competitively displace a resident) rather than replacement (where a colonist is dependent upon the death of the resident and provision of vacant space) (Yu and Wilson 2001, Kisdi and Geritz 2003). To date, I do not know enough about the precise mechanism by which competitive interactions affect mortality and displacement or replacement rates in the fishes studied here. Tide pool sculpins are not overtly aggressive, nor do they defend territories. In short-term manipulative experiments, the competitive effects were manifested through decreased growth rates of the competitively inferior *C. globiceps*: an effect that should lead to reduced size, reduced overwinter survivorship, and reduced fecundity, but will

not immediately make habitat available. The dynamic regressions suggest that there is density dependence and carrying capacities are being attained, but the strong tendency for these fishes to home to the area or pool where they recruited, even just days after recruitment, make it difficult to do augmentation experiments that reveal how space is partitioned among species at recruitment. However, the existence of spatial heterogeneity in habitat variables and the different rates of adult mortality among the species, suggest that coexistence via the competition–colonization trade-off is feasible.

ACKNOWLEDGMENTS

I thank the Makah Indian Nation for continued access to the study site and the National Science Foundation (OCE 9711802, OCE 0117801), the Andrew Mellon Foundation, and an EPA-STAR Cooperative Agreement number R-82940201-0 to the University of Chicago for funding. My gratitude to the many people who helped fish, bail, and refill over the years including: J. Sheridan, R. Raynor, B. Scott, A. Miller, F. Stevens, J. Salmunovitch, L. Weis, K. Rose, R. Kordas, K. Edwards, J. Duke, M. Novak, E. Barnes, J. Orcutt, C. Neufeld, L. Weintraub, A. Kandur, P. Dospoy, and J. T. Wootton. K. Edwards helped with data analysis, and J. T. Wootton and Z. Zheng with code, and J. Forester guided me through linear mixed-effect models. R. T. Paine and J. T. Wootton were always ready discussants. Two anonymous reviewers improved the manuscript.

LITERATURE CITED

- Ainley, D. G., C. S. Strong, T. M. Penniman, and R. J. Boekelheide. 1990. The feeding ecology of Farallon seabirds. Pages 51–127 in D. G. Ainley and R. J. Boekelheide, editors. Seabirds of the Farallon Islands. Stanford University Press, Stanford, California, USA.
- Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* **6**: 1109–1122.
- Caffey, H. M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* **55**:313–332.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* **27**:477–500.
- Chesson, P. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. *Theoretical Population Biology* **64**:345–357.
- Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* **117**:923–943.
- Collins, S. L., F. Micheli, and L. Hartt. 2000. A method to determine rate and pattern of variability in ecological communities. *Oikos* **91**:285–293.
- Connolly, S. R., B. A. Menge, and J. Roughgarden. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* **82**:1799–1813.
- Connolly, S. R., and J. Roughgarden. 1999. Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. *Ecological Monographs* **69**: 277–296.
- Davis, J. L. D. 2000. Changes in a tidepool fish assemblage on two scales of environmental variation: Seasonal and El Niño Southern Oscillation. *Limnology and Oceanography* **45**: 1368–1379.
- Davis, J. L. D., and L. A. Levin. 2002. Importance of pre-recruitment life-history stages to population dynamics of the

- woolly sculpin *Clinocottus analis*. Marine Ecology Progress Series **234**:229–246.
- Doherty, P. J., and T. Fowler. 1994. An empirical test of recruitment limitation in a coral reef fish. *Science* **263**:935–939.
- Drent, R. H. 1965. Breeding biology of the pigeon guillemot, *Cephus columba*. *Ardea* **53**:99–160.
- Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**:57–68.
- Frogner, K. J. 1980. Variable developmental period: intraspecific competition models with conditional age-specific maturity and mortality schedules. *Ecology* **61**:1099–1106.
- Fulton, M. R., and P. A. Harcombe. 2002. Fine-scale predictability of forest community dynamics. *Ecology* **83**:1204–1208.
- Gaines, S. D., and M. D. Bertness. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* **360**:579–580.
- Hart, J. L. 1973. Pacific fishes of Canada. Fisheries Research Board of Canada, Bulletin number 180. Ottawa, Canada.
- Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* **277**:946–949.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. *Rapports et Proces-Verbaux des Reunions, Conseil International pour l'Exploration de la Mer* **20**:1–228.
- Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. *Ecology* **53**:749–752.
- Johnson, D. W. 2006. Density dependence in marine fish populations revealed at small and large spatial scales. *Ecology* **87**:319–325.
- Kisdi, E., and S. A. H. Geritz. 2003. On the coexistence of perennial plants by the competition–colonization trade-off. *American Naturalist* **161**:350–354.
- Levin, S. A. 1974. Dispersion and population interactions. *American Naturalist* **108**:207–228.
- Levine, J. M., and M. Rees. 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *American Naturalist* **160**:452–467.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences (USA)* **68**:1246–1248.
- Marliave, J. B. 1986. Lack of planktonic dispersal of rocky intertidal fish larvae. *Transactions of the American Fisheries Society* **115**:149–154.
- Menge, B. A., C. Blanchette, P. Raimondi, T. Freidenburg, S. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: testing model predictions along an upwelling gradient. *Ecological Monographs* **74**:663–684.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predations in relation to environmental stress and recruitment. *American Naturalist* **130**:730–757.
- Munday, P. L. 2004. Competitive coexistence of coral-dwelling fishes: the lottery hypothesis revisited. *Ecology* **85**:623–628.
- Paine, R. T. 2002. Advances in ecological understanding: by Kuhnian revolution or conceptual evolution? *Ecology* **83**:1553–1559.
- Palmer, R. S. 1962. Handbook of North American birds. Volume I. Yale University Press, New Haven, Connecticut, USA.
- Pfister, C. A. 1995. Estimating competition coefficients from census data: a test with field manipulations of tidepool fishes. *American Naturalist* **146**:271–291.
- Pfister, C. A. 1996. Consequences of recruitment variation in an assemblage of tide pool fishes. *Ecology* **77**:1928–1941.
- Pfister, C. A. 1997. Demographic consequences of within-year variation in recruitment. *Marine Ecology Progress Series* **153**:229–238.
- Pfister, C. A. 1998. Extinction, colonization, and species occupancy in tidepool fishes. *Oecologia* **114**:118–126.
- Pfister, C. A. 1999. Recruitment. Pages 181–196 in M. H. Horn, K. L. M. Martin, and M. A. Chotkowski, editors. *Intertidal fish ecology, behavior, and physiology*. Academic Press, San Diego, California, USA.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-effects models in S and S-PLUS*. Springer-Verlag, New York, New York, USA.
- R Development Core Team. 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* **241**:1460–1466.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* **111**:337–359.
- Sale, P. F. 1978. Coexistence of coral reef fishes: a lottery for living space. *Environmental Biology of Fishes* **3**:85–102.
- SAS Institute. 2003. JMP Statistical Software. SAS Institute, Cary, North Carolina, USA.
- Schoener, A., and D. F. Tufts. 1987. Changes in oyster condition index with El Niño–Southern Oscillation events at 46 degree N in an eastern Pacific bay. *Journal of Geophysical Research* **92**:14429–14435.
- Shanks, A. L., and G. L. Eckert. 2005. Population persistence of California Current fishes and benthic crustaceans: a marine drift paradox. *Ecological Monographs* **75**:505–524.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2–16.
- Underwood, A. J., and E. J. Denley. 1982. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151–180 in D. Strong, D. Simberloff, and L. Abele, editors. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *American Naturalist* **125**:769–787.
- Washington, B. B., H. G. Moser, W. A. Laroche, and W. J. Richards. 1984. Scorpaeniformes: development. Ontogeny and systematics of fishes. Special Publication 1. American Society of Ichthyologists and Herpetologists. Allen Press, Lawrence, Kansas, USA.
- Yoshiyama, R. M., K. B. Gaylord, M. T. Philippart, T. R. Moore, J. R. Jordan, C. C. Coon, L. L. Schalk, C. J. Valpey, and I. Tosques. 1992. Homing behavior and site fidelity in intertidal sculpins (Pisces: Cottidae). *Journal Experimental Marine Biology and Ecology* **160**:115–130.
- Yu, D. W., and H. B. Wilson. 2001. The competition–colonization trade-off is dead; long live the competition–colonization trade-off. *American Naturalist* **158**:49–63.