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HABITAT USE AND COMMUNITY STRUCTURE IN AN ASSEMBLAGE OF COTTID FISHES

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Abstract. I applied an observational approach, using strip transects, to document the abundance and the spatial distributions of members of an assemblage of subtidal fishes (Scorpaeniformes: Cottidae) in the San Juan Islands, Washington, USA. I then assessed the extent to which species-specific distributions were correlated with habitat availability and the potential for interspecific competition to modify patterns of abundance and resource use. The six common cottid species were Arctedius fenestralis, A. harringtoni, Asemichthys taylori, Chitonotus pugetensis, Icelinus borealis, and Jordania zonope. A comparison of their observed distributions with the distributions of microhabitats along the transects revealed that all species demonstrated significant affinities for or avoidance of many of the predominant substrates: clean rock, silt rock, shell sand, gravel, mud, and algae. Using a stepwise regression technique, I found that the densities of individual cottid species were significantly correlated with the percentage cover of these substrate types along the transects and with transect depth.

Several lines of evidence suggest that interspecific competition does not play a strong role in this assemblage. Species pairs that co-occurred on at least some transects did not show disjunct distributions. Microhabitat overlap of these species pairs was higher in sympathy (comparison of transects with both species present) than in allopatry (comparisons of transects with only one species present), counter to the expectation of niche divergence. Correlations of species densities after correcting for habitat heterogeneity with the Schoener-Crowell-Pimm technique revealed only one significant negative density correlation out of thirty potential correlations. Cottid diversity was not correlated with structural diversity along transects in spite of strong associations of each species with habitat structure. This suggests that the transect areas were undersaturated in the number of individuals and/or species of cottid fishes. The apparent lack of competition among subtidal cottids contrasts with studies on intertidal fish communities dominated by cottids for which there is observational evidence of interspecific competition.

Key words: community structure; Cottidae; habitat selection; interspecific competition; microhabitat overlap; observational approach; resource partitioning; species density; temperate fish communities; unsaturated habitats.

INTRODUCTION

A central goal of ecology is the identification of the roles that abiotic and biotic factors play in determining the distribution and abundance of species. In particular, attention has been directed to the roles of these factors in determining patterns of resource use among closely related species. This interest stems from one of the central paradigms of ecology, the principle of competitive exclusion (Gause 1934). A major focus of ecological research has been to identify those conditions that allow coexistence of species using similar resources, e.g., predation (Paine 1974), non-equilibrial physical processes (Sale 1977, Wiens 1977, Sousa 1979) and non-linear competitive hierarchies (Buss and Jackson 1979) or that reduce overlap in resource use, e.g., niche partitioning (Werner 1977, Hixon 1980, Pacala and Roughgarden 1982), character displacement (Grant and Schluter 1984), and disjunct distributions (Hairston 1980, Case 1983).

The term “resource partitioning” has been used in a general sense to describe any differences in resource use that exist between species and in a strict sense to describe only those changes in resource use due to competitors (Ebeling and Laur 1986). That species differ in resource use is a common ecological observation (see reviews in Schoener 1974a, Toft 1985, Ross 1986). More pertinent to the understanding of community dynamics is assessing to what extent these differences in resource use reflect inherent interspecific inequalities in the abilities to use and/or the preferences for using resources (autecological interactions) and to what extent biotic processes, including predation and competition (synecological interactions) modify autecological differences (Strong 1983).

Both experimental and observational approaches have been used to investigate the factors influencing the distribution and abundance of guild members. The experimental approach, manipulation of a single factor

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while holding others constant, is the stronger method, but is not without drawbacks (Cody 1974, Schoener 1974a, Connell 1975, Underwood and Denley 1984, Diamond 1986). In the observational approach, correlations are made between the density or distribution of a species and the abundance or intensity of a biotic or abiotic factor as both vary spatially or temporally. The weakness of the observational approach is the leap from correlation to causation. Several studies have provided examples in which experiments have refuted the importance of processes inferred by observed patterns or found that the effects were even reversed (see McGuinness 1988). Yet, in multispecies guilds, observational studies can be valuable in generating hypotheses, especially in identifying subsets of factors or species that then may be subjected to experimental analysis (e.g., Brown et al. 1986).

This study uses an observational approach (multiple strip transects at several subtidal sites) to document habitat use and to identify possible mechanisms underlying habitat partitioning among members of a guild of subtidal fishes in the family Cottidae. Ninety cottid species can be found between Baja California and the Aleutian Islands (Howe and Richardson 1978). Within this geographic range cottids are often the dominant fishes in tidepool and nearshore subtidal habitats (Simenstad et al. 1977, Yoshiyama et al. 1986). Many studies have documented the importance of physical and biological factors, including competition, in determining the distribution of intertidal species (Morris 1960, 1961, Graham 1970, Green 1971, Nakamura 1976a, b, Cross 1981, Richkus 1981, Yoshiyama 1981, Grossman 1982, 1986b, Wells 1986). Subtidal cottids are also quite abundant, but the factors determining the distributions and abundances of these species are poorly known. In part, this reflects the small size, sedentary behavior, and cryptic coloration of many species, which make them much less visible during underwater investigations (e.g., Burge and Schultz 1973, Ebeling et al. 1980, Larson and DeMartini 1984).

The goal of this study was to document patterns of abundance and habitat use among members of the assemblage of subtidal cottids, to correlate species-spe-

Table 1. Distribution of transects and average cottid density on each transect by site. Habitat abbreviations: CR = clean rock, SR = silt rock, G = gravel, SS = shell sand, M = mud, A = algae. Species abbreviations: Ahar = *Artedius harringtoni*.
cific patterns of habitat use with patterns of habitat availability, and to assess the degree to which interspecific competition appears to modify patterns of species abundance and resource use. I examined three patterns that would be expected if intraguild competition is a strong force influencing the distribution and abundance of cottid species: disjunct distributions, niche divergence, and inverse density relationships. Although other mechanisms besides competition may also be consistent with these patterns, invalidating these patterns would decrease the likelihood that intraguild competition was a strong mechanism influencing the distributions and abundances of these species.

**Materials and Methods**

**Study area**

I conducted this study in the waters around the San Juan Islands of Washington state, USA. The San Juan Islands lie at the junction of Puget Sound, the Strait of Juan de Fuca, and Barkely Sound (Fig. 1). The complex topography of these islands (Mayers and Bennett 1973) and the mixed semidiurnal tides (Herlinveaux 1954) interact to create a variety of physical habitats (e.g., deep mud-bottomed fjords, current-swept rock reefs, sand flats) within a small area. These highly productive waters are well known for their rich marine life (MacPhee and Clemens 1962, Ellis 1971, Kozloff 1973, Foreman and Root 1975). Cottids are no exception; I have found in the San Juan Islands 31 of the 90 species described from the northeast Pacific (S. F. Norton, personal observation).

**Fish and habitat sampling**

Fish transects were conducted at six primary sites (4–12 transects/site) and two secondary study sites (one transect/site) (Fig. 1) in the summer of 1985. These sites are mosaics of several common habitat types in the nearshore subtidal in the San Juan Islands (Table 1). Most of the 45 transects were 30 m long, but several of the deeper transects were shorter due to time constraints imposed by scuba-diving at these depths. Each transect was placed parallel to shore within a narrow depth range, and an effort was made to maximize the diversity of substrates sampled by each transect. The influence of depth on cottid abundances was evaluated by running transects at several depths (between 7 and 30 m) at each primary site.

The initial pass along each transect sampled habitat use and density of cottids; a second sampled the availability of different substrates along the transect. During the first pass I recorded the species and the substrate on which it was lying for each cottid individual encountered within 0.5 m of the right side of the transect line. I carried a 0.5-m rod as a reference width for the transect. To accurately sample these cryptic sedentary fishes I swam slowly along the bottom at ~1.5 m/min. These data were recorded in 5-m blocks. During the second pass I sampled the availability of different substrates (microhabitats) by recording the substrate under the transect line every 10 cm. Observations from preliminary dives were used to identify six dominant substrates: (1) clean rock (CR), characteristic of high-current sites; (2) silt rock (SR), rock covered with a fine layer of silt, characteristic of low-current sites; (3) shell sand (SS), a complex of shell fragments and sand that collect below rockwalls; (4) gravel (Gr); (5) mud (M); and (6) foliose algae (A).

**Data analysis**

I examined the influence of biotic and abiotic factors on the distribution and abundance of cottids in two ways. The microhabitat analysis compared the distribution of individuals of each cottid species to the distribution of substrates available along the transects. This analysis also examined the distributional patterns of species pairs for disjunct distributions and niche shifts. I defined a microhabitat as a physically uniform area of substrate (e.g., shell sand, mud, etc.) within which a cottid might spend part of the day. In the macrohabitat analysis I applied the regression technique of Schoener (1974b) and Crowell and Pimm (1976) to examine the role that substrate abundance and the densities of other cottid species have on the density of each species along the transects. Each transect was viewed as a macrohabitat containing a unique distribution of microhabitats.

<table>
<thead>
<tr>
<th></th>
<th>Ahar</th>
<th>Afen</th>
<th>Asem</th>
<th>Chit</th>
<th>Ice</th>
<th>Jord</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cottid density</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Inds·m⁻²·transsect⁻¹, X ± 1 SD)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ahar</td>
<td>0.81 ± 0.17</td>
<td>0.07 ± 0.13</td>
<td>0.13</td>
<td>0.29 ± 0.26</td>
<td>0.38 ± 0.39</td>
<td>0.51 ± 0.26</td>
</tr>
<tr>
<td>Afen</td>
<td>0.68 ± 0.29</td>
<td>0.63 ± 0.52</td>
<td>0.13</td>
<td>0.72 ± 0.45</td>
<td>0.08 ± 0.11</td>
<td>0.80 ± 0.39</td>
</tr>
<tr>
<td>Asem</td>
<td>0.24 ± 0.23</td>
<td>0.13 ± 0.18</td>
<td>0.29</td>
<td>0.72 ± 0.45</td>
<td>0.08 ± 0.11</td>
<td>0.80 ± 0.39</td>
</tr>
<tr>
<td>Chit</td>
<td>1.35 ± 0.98</td>
<td>0.96 ± 0.47</td>
<td>0.72</td>
<td>0.72 ± 0.45</td>
<td>0.08 ± 0.11</td>
<td>0.80 ± 0.39</td>
</tr>
<tr>
<td>Ice</td>
<td>0.31 ± 0.42</td>
<td>0.09 ± 0.11</td>
<td>0.29</td>
<td>1.63 ± 1.34</td>
<td>0.75 ± 0.57</td>
<td>0.75 ± 0.57</td>
</tr>
<tr>
<td>Jord</td>
<td>0.37 ± 0.42</td>
<td>0.40 ± 0.20</td>
<td>0.47</td>
<td>0.47 ± 0.29</td>
<td>0.42 ± 0.67</td>
<td>0.39 ± 0.39</td>
</tr>
<tr>
<td>2.60</td>
<td>0.13</td>
<td>0.40</td>
<td>0.47</td>
<td>0.47 ± 0.29</td>
<td>0.42 ± 0.67</td>
<td>0.39 ± 0.39</td>
</tr>
<tr>
<td>0.41 ± 0.53</td>
<td>0.20 ± 0.52</td>
<td>0.31 ± 0.42</td>
<td>0.42 ± 0.67</td>
<td>0.39 ± 0.39</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Microhabitat analysis

Intersite consistency in the microhabitat distribution of a species was measured using Kendall's coefficient of concordance and was tested for significance by Friedman's rank test (Kendall 1962). Because no cottid species was found at all sites, the rank tests for each species only included those sites where the species was observed. For both *Artedius fenestralis* and *Chitonotus pugetensis*, encountered only at the two East Sound sites, the coefficient of rank concordance and Friedman's test were evaluated among transects.

A view of the overall distribution of each species among subtidal microhabitats in the San Juan Islands was constructed by combining the data on the microhabitat association of individuals over all transects. The hypothesis that individual species were distributed among microhabitats in proportion to the availabilities of these microhabitats was evaluated with G tests. Because all species demonstrated non-random habitat use, additional tests were conducted to determine which microhabitats were significantly "preferred" or "avoided" by each species (i.e., over- and under-represented). In these tests, the observed microhabitat distributions on a single substrate and on the sum of the other substrates were compared to expected distribution of individuals on these two substrate classes if cottid distributions were based on microhabitat availability. Each microhabitat was singled out in turn (e.g., comparison of the observed distribution of *Artedius harringtoni* on shell sand and all other substrates with the distribution expected if *A. harringtoni* used shell sand and the other substrates in the frequencies sampled on the transects). The critical G values were adjusted to reflect the a posteriori nature of these comparisons (Sokal and Rohlf 1981).

If competition among cottid species is influencing the microhabitat distribution, one might predict that species pairs would show checkerboard or disjunct distributions, where one species excludes another from an area. This hypothesis was evaluated by totaling the number of 5-m transect sections (2.5 m²) where (1) both species of a pair were present, (2) both species were absent, and (3) only one species was present. Only transects where at least one member of a species pair was present were included, reducing the interdependence of the comparisons (Toft et al. 1982). Independence in the distribution of species pairs among 5-m transect sections was evaluated using G tests.

Even if species pairs do not show checkerboard distributions, competition by one member of a species pair may influence the microhabitat distribution of the other. If this occurs, one would expect the species pairs to show higher overlap in microhabitat use when in allopatry than when in sympathy (i.e., niche divergence). The potential of one species to alter the distribution of another was evaluated using G tests that compared the microhabitat distribution of one species in those 5-m transect sections that also contained the potential competitor (sympathy, i.e., transects containing both members of a species pair) with the microhabitat distribution in 5-m transect sections that lacked the potential competitor (allopatry, i.e., transects containing only one member of a species pair). An overlap index (Schoener 1970) was used to calculate microhabitat overlap between members of species pairs in sympathy and in allopatry.

Under different scenarios of competition, resource overlap may vary directly or inversely with the intensity of competition (Lawlor 1980). One difficulty with traditional overlap measures as approximate measures of competition is that overlap measures based on proportional utilization confound the selectivity of the consumer with the availability of resources in the environment (Lawlor 1980). Lawlor proposed that similarity of electivities between two species may be a better measure of potential competition. I used the asymmetric MacArthur-Levins equation to calculate both interspecific microhabitat overlap, based on proportional utilization, and microhabitat similarity, based on electivities determined using Manly's (1974) formula. The former measure is an estimate of overlap of the realized niches of the species pairs, while the latter should be a better indicator of overlap of the fundamental niche of these species.

Macrohabitat analysis

The method of Schoener (1974b) and Crowell and Pimm (1976), as modified by Rosenzweig et al. (1984), was used to examine the influence of substrate abundance and the density of potential competitors on cottid densities. In the Schoener-Crowell-Pimm (SCP) method, an initial multiple regression uses the density of a single species measured at several sites as the dependent variable and several habitat variables (e.g., rainfall, percentage cover of different substrates, temperature, etc.) as the independent variables. The regression coefficients provide estimates of the influence of the habitat variables on species abundance. The residuals of this regression should be estimates of species densities at each site that are largely free of habitat heterogeneity. A second set of multiple regressions uses the matrix of these residuals for all the species in the guild to assess the strength of interspecific interactions. Each species serves as the dependent variable and is regressed against the residuals of the other species. Negative interspecific regression coefficients derived from the SCP technique have been invoked as evidence for competition (e.g., Crowell and Pimm 1976, Hallett and Pimm 1979, Dueser and Hallett 1980, Rosenzweig et al. 1984, Dueser and Porter 1986, but see Rosenzweig et al. 1985 and Abramsky et al. 1986). Simulation studies indicate that competition coefficients calculated by the SCP technique are robust to deviations of populations away from equilibrium (Hallett and Pimm...
### TABLE 2. Rank correlation of microhabitats. Friedman's test, a non-parametric multisample rank-correlation statistic, was used to test for consistency of habitat use among sites or among transects (species designated with *). Kendall's $W$ is indicative of the sample correlation coefficient.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of sites</th>
<th>No. of substrates</th>
<th>$W$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artedius harringtoni</td>
<td>5</td>
<td>6</td>
<td>0.57</td>
<td>&lt;.025</td>
</tr>
<tr>
<td>Asemichthys taylori</td>
<td>6</td>
<td>6</td>
<td>0.60</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>Icelinus borealis</td>
<td>4</td>
<td>6</td>
<td>0.43</td>
<td>&lt;.25</td>
</tr>
<tr>
<td>Jordania zonope</td>
<td>6</td>
<td>6</td>
<td>0.51</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>Artedius fenestralis*</td>
<td>12</td>
<td>5</td>
<td>0.33</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>Chitonotus pugetensis*</td>
<td>12</td>
<td>5</td>
<td>0.48</td>
<td>&lt;.001</td>
</tr>
</tbody>
</table>

1979) and for problems with the independence of the variables (Carnes and Slade 1988).

In this study the seven independent variables for the habitat–species regressions were the percentage cover estimates for the six substrate types on each transect and the depth of each transect. In the species–species regressions the residual densities of a single species from the habitat regressions served as the dependent variable and the residual densities of the other species were the independent variables. The distribution of percentage cover data was not significantly different from normal after arcsine square-root transformation. Similarly, the distribution of the density data was normally distributed after square-root transformation.

In both stepwise regressions (habitat–species and species–species) a minimum significance level of 0.15 was required at each step before entry of any variable into the overall model. Other regression approaches (full regression models or models using the original cottid densities as independent variables in the species–species regressions) were explored as suggested by Rosenzweig et al. (1984), but were poorer descriptors than the stepwise method; i.e., they accounted for less of the variation in cottid density. There were strong qualitative similarities in the results regardless of the type of regression model. Examination of plots of the residuals vs. the independent variables of the habitat–species and species–species regressions revealed no obvious curvilinear relationships (i.e., no evidence for concave zero-isoclines; Schoener 1974b).

### RESULTS

Cottids are abundant in the nearshore subtidal of the San Juan Islands; eight species totaling 1172 individuals were encountered during 45 transects. Cottid density was 1.8 ± 0.16 individuals per square metre per transect (mean ± 1 se). The six common cottids were *Arteđius fenestralis*, *A. harringtoni*, *Asemichthys taylori*, *Chitonotus pugetensis*, *Icelinus borealis*, and *Jordania zonope* (Table 1). Two other cottid species, *Hemilepidotus hemilepidotus* ($N = 1$) and *Rhamphocottus richardsoni* ($N = 8$) were rare and are excluded in the analyses. Fishes sampled on the transects included both newly settled juveniles and adults of all species. Other fishes encountered occasionally during the transects included *Pholis clemensi*, *Ronquilus jordani*, the rockfishes *Sebastes auriculatus*, *S. caurinus*, *S. empheaus*, and *S. flavidus*, and the hexagrammids *Ophiodon elongatus* and *Hexagrammos decagrammus*.

### Selection of microhabitats by cottid fishes

The microhabitat distributions of cottid species were generally consistent among sites or transects (Table 2). None of the cottid species were found to use microhabitats in proportion to their availability along the transects (Fig. 2; $G$ tests, $P < .001$); each species showed significant microhabitat preferences and avoidances. Both *J. zonope* and *Arteđius harringtoni* were found predominately on clean rock surfaces and avoided nonsolid substrates. *C. pugetensis* and *Asemichthys taylori* were found almost exclusively on shell sand and avoided clean rock. Encounters with *Arteđius fenestralis* were divided between shell sand and silt-covered rock. *I. borealis* was common on gravel substrates and rare on silt rock and shell sand.

Interspecific microhabitat overlap (based on realized overlap of resource use) and interspecific microhabitat similarity (based on overlap of resource electivities) varied greatly among the species pairs (Table 3; overlap: mean ± 1 sd = 0.46 ± 0.42; similarity: mean ± 1 sd = 0.40 ± 0.25). These measures of the overlap of actual and potential resource use were highly correlated ($r^2 = 0.58$, $F = 38.7$, $P < .001$). Nine of 30 overlap coefficients and 4 of 30 similarity coefficients were in the “biologically significant” range, >0.60 (see references in Grossman 1986a). High overlap values were found for *J. zonope* and *A. harringtoni*, *Asemichthys taylori* and *C. pugetensis*, *Arteđius fenestralis* and *C. pugetensis* (all reciprocal), and for *J. zonope* and *A. harringtoni*.

### TABLE 3. Two measures of interspecific overlap in the spatial distributions of six common cottid species in the San Juan Islands. The table shows the overlap or similarity of the column species vs. the row species. Species abbreviations as in Table 1.

<table>
<thead>
<tr>
<th></th>
<th>Ahar</th>
<th>Afen</th>
<th>Asem</th>
<th>Chit</th>
<th>Ice</th>
<th>Jord</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Asymmetrical interspecific microhabitat overlap (MacArthur-Levins index).</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ahar</td>
<td>0.091</td>
<td>0.123</td>
<td>0.081</td>
<td>0.557</td>
<td>1.076</td>
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<tr>
<td>Afen</td>
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<td>0.943</td>
<td>0.290</td>
<td>0.116</td>
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<tr>
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<td>0.518</td>
<td>0.843</td>
<td>0.219</td>
<td>0.058</td>
<td></td>
</tr>
<tr>
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<td>0.609</td>
<td>1.122</td>
<td>0.236</td>
<td>0.043</td>
<td></td>
</tr>
<tr>
<td>Ice</td>
<td>1.238</td>
<td>0.376</td>
<td>0.585</td>
<td>0.475</td>
<td>1.296</td>
<td></td>
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<tr>
<td>Jord</td>
<td>0.925</td>
<td>0.058</td>
<td>0.060</td>
<td>0.034</td>
<td>0.501</td>
<td></td>
</tr>
<tr>
<td>B. Asymmetrical interspecific electivity similarity (MacArthur-Levins index).</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td>0.336</td>
<td>0.404</td>
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<td>0.696</td>
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<td>0.081</td>
<td></td>
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<tr>
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<td>0.965</td>
<td>0.349</td>
<td>0.115</td>
<td></td>
</tr>
<tr>
<td>Ice</td>
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<td>0.507</td>
<td>0.450</td>
<td>0.452</td>
<td></td>
</tr>
<tr>
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<td>0.329</td>
<td>0.101</td>
<td>0.103</td>
<td>0.315</td>
<td></td>
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</table>
harringtoni on I. borealis, and Asemichthys taylori on Artedius fenestralis. High microhabitat similarities were found for J. zonope and A. harringtoni, and for Asemichthys taylori and C. pugetensis (each reciprocal). Both indices indicate that if substrate availabilities were limited, competition was likely to occur among these cottid species pairs.

In contrast to the expectation of negative co-occurrence patterns under the competition paradigm, six cottid species pairs showed neutral co-occurrence patterns and three had positive co-occurrence patterns; none were negative (Fig. 3). Another possibility consistent with competition is that a species may alter its microhabitat use in the presence of a competitor (niche divergence). Although several species pairs did show significant differences in patterns of microhabitat use in the presence of potential competitors, interspecific overlap in microhabitat use was higher in sympatry than in allopatry, opposite to predictions of niche divergence under competition (Fig. 4).
Species Co-occurrence

![Species Co-occurrence Diagram]

**Fig. 3.** Co-occurrence of species pairs in 5-m transect sections. Species pairs connected by arrows demonstrated significant positive co-occurrence patterns. Species pairs connected by dotted lines demonstrated independent patterns of occurrence.

Influence of habitat structure and heterospecifics on cottid densities

Densities of each species were significantly influenced by the relative abundances of particular habitat types in an area (Table 4). Stepwise regressions using the macrohabitat variables account for between 40 and 60% of the variance in species density (Table 4: $R^2$ Habitat). As with microhabitat associations, the density of each species demonstrated significant positive and negative correlations with areas dominated by particular habitat types. Densities of *Artedius fenestralis* and *Asemichthys taylori* were higher on transects with a high percentage cover of silt rock and shell sand. The density of *Artedius harringtoni* decreased with increasing depth and increased in areas dominated by clean rock surfaces. Abundance of *C. pugetensis* showed negative relationships with clean rock, gravel, and algal abundances. The density of *J. zonope* was positively correlated with the percentage cover of clean rock and algae. Abundance of *I. borealis* increased with increasing depth and in areas dominated by gravel and algae, but this species avoided silt rock and shell sand.

![Allopatric - Sympatric Overlap Diagram]

**Fig. 4.** Changes in microhabitat use between sympatry and allopatry and microhabitat overlap in allopatry (left value) and sympatry (right value) for cottid species pairs. Overlap measures were calculated using the index described in Schoener (1970). An arrow connecting two species indicates that the species at the head of the arrow demonstrates significant differences in its distribution among substrates when in sympatry vs. in allopatry on 5-m transect sections with the species at the tail of the arrow.
Table 4. Stepwise regression coefficients of cottid densities vs. habitat variables and of species vs. species residuals after removal of habitat effects. Species and habitat abbreviations as in Table 1.

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Ahar</th>
<th>Afen</th>
<th>Asem</th>
<th>Chit</th>
<th>Ice</th>
<th>Jord</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR</td>
<td>9.133**</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SR</td>
<td>12.43**</td>
<td>3.84†</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G</td>
<td></td>
<td>-4.28*</td>
<td>11.00**</td>
<td></td>
<td>-6.98*</td>
<td>6.60†</td>
</tr>
<tr>
<td>SS</td>
<td></td>
<td>4.72*</td>
<td></td>
<td></td>
<td></td>
<td>-4.43†</td>
</tr>
<tr>
<td>M</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-14.16**</td>
</tr>
<tr>
<td>Depth</td>
<td>-0.07†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ahar</td>
<td></td>
<td>-0.40*</td>
<td></td>
<td></td>
<td>-0.29†</td>
<td>0.32*</td>
</tr>
<tr>
<td>Afen</td>
<td></td>
<td>0.05**</td>
<td></td>
<td></td>
<td></td>
<td>0.24‡</td>
</tr>
<tr>
<td>Asem</td>
<td></td>
<td>0.38*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chit</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.02**</td>
</tr>
<tr>
<td>Ice</td>
<td></td>
<td>-0.21‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jord</td>
<td></td>
<td>0.30‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

R² Habitat: 0.400, 0.440, 0.448, 0.608, 0.450, 0.407
R² Density: 0.214, 0.258, 0.072, 0.180, 0.031, 0.150
R² Total: 0.614, 0.698, 0.520, 0.788, 0.481, 0.557

† Significant at P < .15; ‡ significant at P < .10; * significant at P < .05; ** significant at P < .01.

From the results of the second series of regressions, the subtidal cottid community in the San Juan Islands shows little evidence of being structured by competition for space. Of 30 possible interspecific coefficients, only 10 passed the initial significance cutoff (P < .15) in the stepwise regression models; 6 of these are significant at the .05 level or better (Table 4). Only one of these six coefficients is negative (A. fenestralis on A. harringtoni). The interspecific regression models account for between 3 and 26% of the total variation in cottid densities (Table 4: R² Density). Together the habitat and interaction regressions account for between 48 and 79% of the variation in the initial densities of the cottid species (Table 4: R² Total).

Diffuse competition (the aggregate influence on one species by the other members of a guild, MacArthur 1972) does not appear to be important in this guild. I conducted a regression analysis for each species in which the dependent variable was the residual density of the single species and the independent variable was the sum of the residual densities of all the other species after habitat effects had been removed. None of the regressions indicated a negative relationship as predicted under a diffuse competition model (Table 5). On the contrary, abundances of both Asemichthys taylori and J. zonope were significantly higher in areas with high densities of other cottids.

**DISCUSSION**

The results from this study indicate that subtidal cottids in the San Juan Islands are distributed differentially among six common structural habitats. The patterns of distributions and the abundances of these species are more consistent with mechanisms based on autecological responses of species to spatial heterogeneity in the distribution of habitats (the individualistic concept, Gleason 1926) than they are with syncenologica
tical mechanisms. Under the individualistic concept, differences in resource use among guild members (resource partitioning sensu lato, e.g., Schoener 1974a, Ross 1986) reflect the unique adaptations and evolutionary histories of each species, and not coevolutionary interactions among guild member (resource partitioning sensu stricto, Roughgarden 1976). The individualistic concept has been invoked to explain niche differences in a variety of systems (Strong 1983), e.g., terrestrial plant communities (Gleason 1926), aquatic snails (Aho et al. 1981), shrub-steppe birds (Wiens and Rotenberry 1981), and temperate fishes (Grossman et al. 1982, Ebeling and Laur 1986).

**Influence of habitat factors**

The influence of habitat on species distributions may change when examined over different spatial scales (e.g., Wiens and Rotenberry 1981, Morris 1987, Snyder and Best 1988). Within the San Juan Islands, most cottid species demonstrated significant rank consistency in the use of substrates at different sites or among transects. On a broader scale, the habitat distributions of subtidal cottids in the San Juan Islands are similar to qualitative observations of their distributions in other

Table 5. Diffuse competition: influence of the aggregate density of other cottid species on the density of single species after correction for habitat effects.

<table>
<thead>
<tr>
<th>Species</th>
<th>Regression coefficient</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctedius harringtoni</td>
<td>0.025</td>
<td>0.14</td>
<td>&gt;.70</td>
</tr>
<tr>
<td>Arctedius fenestralis</td>
<td>-0.061</td>
<td>1.31</td>
<td>&gt;.25</td>
</tr>
<tr>
<td>Asemichthys taylori</td>
<td>0.245</td>
<td>19.73</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Chitonotus pugetensis</td>
<td>0.004</td>
<td>0.02</td>
<td>&gt;.90</td>
</tr>
<tr>
<td>Icelinus borealis</td>
<td>-0.069</td>
<td>1.34</td>
<td>&gt;.25</td>
</tr>
<tr>
<td>Jordania zonope</td>
<td>0.118</td>
<td>7.13</td>
<td>&lt;.05</td>
</tr>
</tbody>
</table>

In this study, habitat structure had similar effects in the micro- and macrohabitat distributions of cottids. The densities of a cottid species were enhanced in those habitats dominated by substrates for which it had high microhabitat electivities. Of the 21 significant microhabitat associations and 10 significant macrohabitat correlations (i.e., \( P \leq .05 \)), seven pairs of habitat effects were shared across the two scales of analysis, e.g., positive microhabitat association and positive macrohabitat correlation of *Artedius harringtoni* and clean rock. Conflicts existed for only one species: on a microhabitat scale *Asemichthys taylori* was rarely observed on silt rock, but on a macrohabitat scale its overall density was enhanced on transects with a high percentage cover of this substrate. This likely reflects the positive association of these substrates in East Sound transects.

At this low-current site, the source of shell fragments was from barnacle tests from the silt-covered rockwalls.

Studies of intertidal cottid communities have documented a similar strong role of habitat structure on their distributions. Important environmental features correlating with distributional patterns of intertidal cottids include the predominant substrates in the tide pool and the degree of wave exposure, tidal height, and pool size (Green 1971, Nakamura 1976a, b, Cross 1981, Yoshiyama 1981, Yoshiyama et al. 1986). As with subtidal cottids, the associations of intertidal cottids with particular substrates are relatively consistent throughout their geographic ranges (up to 1000 km) in spite of changes in the composition of the intertidal fish community (e.g., Yoshiyama et al. 1986).

Tests of microhabitat choice have shown that the associations of several intertidal species with particular environmental features in the field can be replicated in the laboratory and do not change in the absence of potential competitors (Nakamura 1976a, Richkus 1981). Marlavié (1977) demonstrated that the substrate preferences of several intertidal fishes, including two cottids, appear to be set at the time of larval settlement.

**Influence of intergeneric competition**

Three lines of evidence indicate that interspecific competition does not influence the distribution of subtidal cottids. First, there is no evidence that some species excluded others from an area (disjunct distributions). Second, although the presence of other species was associated with changes in the microhabitat associations of several species, the microhabitat overlap between all species pairs was higher in sympathy (transects containing both species) than in allopatry (transects with one species absent), opposite to the expectation under typical competitive models. This reflects some convergence of species onto the predominant substrate type in sympatric areas. Finally, using the Schoener-Crowell-Pimm (SCP) method, only 1 of 30 interspecific interaction coefficients was negative, indicating a lack of strong negative correlation of species' densities.

Recently, the SCP method has come under intense scrutiny regarding the mechanics of the technique and the experimental corroboration of its results (Rosenzweig et al. 1984, Pimm 1985, Schoener 1985, Abramsky et al. 1986, Carnes and Slade 1988). The SCP method has been applied repeatedly to examine the influence of competition in small mammal communities (Crowell and Pimm 1976, Dueser and Hallett 1980, Hallett 1982, Porter and Dueser 1982, Rosenzweig et al. 1984); a consistent result of these studies has been that an overwhelming predominance of significant and negative interspecific interactions remain after removal of habitat effects. This pattern has been interpreted to be the result of strong competition among members of these communities, but experimental verification of these putative competitive interactions has yet to appear.

In the one experimental test of the SCP method, it failed to detect consistently competition between two bee species that were shown experimentally to be strong competitors (Abramsky et al. 1986). The predictions of the SCP method were upheld when the experimental manipulations of bee populations were conducted over a range of densities similar to those used in the regressions, but failed when the experiments were conducted at densities far beyond the range used in the regression analysis. Pimm (1985) has argued that the “failure” of this second test may less reflect inadequacies of the SCP method than inherent difficulties with linear extrapolations beyond the range of observed values, especially if competitive effects are non-linear as predicted in several theoretical treatments (Rosenzweig 1981, Schoener 1985).

The SCP method for calculating interspecific interaction coefficients may be viewed as a conservative test of competition. It assumes that habitat effects on species distributions have priority over interspecific effects. As originally formulated, this arrangement was necessary to adjust species densities at multiple sites that differed in the equilibrium densities of potential competitors due to differences in the distribution of habitats (one of the major drawbacks of the observational approach) before comparing species densities (Schoener 1974b). One result of this arrangement is that some of the variation in cottid densities attributed to habitat in the initial habitat–species stepwise regression may actually be niche partitioning caused by competitive interactions among species. This would reduce the ability of the SCP technique to detect significant negative species interactions.

On the other hand, some of the variation in cottid densities attributed to species interactions in the species–species regressions may be due to covariance between environmental factors not included in the initial
habitait regressions (e.g., food supply, substrate relief, etc.) and species densities. The effects of these “hidden” habitat factors on species densities would not be “corrected” when calculating the residual densities of some species. The positive associations between several pairs of cottids (Table 4) are probably due to such covariance and not to mutualistic interactions between species.

Although mindful of the drawbacks of the SCP approach, it has fulfilled one of the advantages accrued when using an observational approach to examine resource partitioning within complex assemblages, i.e., identification of specific physical factors that are most likely to influence the distribution and abundance of a cottid species and identification of the species pairs that show inverse density relationships consistent with interspecific competition. These results predict that experimental manipulations of most cottid species are not likely to reveal strong competitive interactions. The one negative interaction coefficient, Artedius fenestratus on A. harringtoni, may be an artifact due to covariance with an environmental variable not included in the original analysis (e.g., current speed), or may be due to strong competitive interactions between closely related species that have similar diets (Norton 1989). Experimental manipulations of these two species are necessary to distinguish between these possibilities.

Another line of evidence consistent with a general lack of interspecific competition among subtidal cottids is the lack of a correlation between cottid diversity and habitat diversity (Shannon-Weiner index, $H'$) along the subtidal transects, despite strong association of individual cottid species with habitat variables ($r^2 = 0.047, F = 3.784, P > .05$). Other studies have documented a positive relationship between complexity of the physical environment and species diversity (see references in Gorman and Karr 1978, Boecklen 1986). This observation implies that the subtidal cottid community may be undersaturated; some transects lack either the full complement of species and/or individuals that one would expect given the available habitats. Undersaturation may be due to mortality caused by predators (e.g., Paine 1974) or by physical processes (Souza 1979, Grossman et al. 1982), or to recruitment limitations (Shulman 1985, Victor 1986).

**Comparison of intertidal and subtidal cottid communities**

Several authors have concluded that the distributions of rocky intertidal fishes are strongly structured by competition for space (Yoshiyama 1981, Cross 1981, Yoshiyama et al. 1986). These conclusions rest on observations of apparent resource partitioning via niche complementarity (Cross 1981, Yoshiyama 1981), of reciprocal patterns of abundance (Cross 1981), of increased microhabitat breadth in areas of decreased species richness (Cross 1981), and of high microhabitat overlap (Yoshiyama 1981). Results from experiments that manipulated the densities of putative competitors (Yoshiyama 1981) or the abundance of spatial resources (Cross 1981) have been inconclusive. However, Grossman (1986a) has argued that strong competition does exist among intertidal fishes, but that the limiting resource is food, not space.

In light of the apparent importance of competition among members of the intertidal assemblage, it is surprising that the subtidal cottid community of the San Juan Islands shows little evidence of competitive regulation, especially in the absence of other structuring forces (e.g., predation or physical disturbance). Examination of the diets of other potential predators and competitors (e.g., rockfishes and hexagrammids) indicates that these fishes rely primarily on prey sizes and types that are not utilized by cottid fishes, and cottids are not normally encountered in the diets of these species (Moulton 1977; F. S. McEuen, personal communication, S. F. Norton, personal observation). Also, physical disturbance is much less pronounced in the subtidal than in the intertidal (Cross 1981, Levings et al. 1983).

The densities of subtidal cottids may be kept below levels necessary to saturate the available resources by recruitment processes, especially when compared to the densities of intertidal species. The transport mechanisms (the strong currents in the San Juan Islands and a larval period of several weeks or months for cottids) seem sufficient to ensure access of potential recruits to all intertidal and subtidal habitats. However, the supply of recruits of subtidal species may be limited by heavy predation on benthic eggs in the subtidal by invertebrates and by other fishes (DeMartini 1978).

In conclusion, habitat partitioning by subtidal cottid species is more likely the result of inherent micro- and macrohabitat preferences of individual species for particular substrates rather than responses to the presence of heterospecifics. The lack of any relationship between species diversity and habitat structural diversity despite strong habitat preferences implies that subtidal cottid populations are below environmental carrying capacity. In the absence of great physical disturbance and predation pressure, population regulation may be due to recruitment limitation, especially through egg predation.

**Acknowledgments**

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