

Resource matching across habitats is limited by competition at patch scales in an estuarine-opportunist fish

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Abstract: I used field observations, assays, and experiments with the euryhaline cottid *Cottus aleuticus* to evaluate the extent to which average resource availability drives the large-scale distribution of these fish among upstream and estuarine habitats and how interspecific competition from a congener affects its performance in the estuary. Population densities of *C. aleuticus* were only consistent with resource densities across years during two of five study years, indicating a lack of resource matching at large temporal scales. On shorter temporal scales, fish growth rates that were two to three times higher in the estuary compared with the stream were inconsistent with the predictions of resource matching theory. A manipulation of *C. aleuticus* density showed that the estuary could support at least twice the number of individuals that occurred there; thus, the profitable estuary is underutilized. Interspecific competition with *Cottus asper* was partially responsible for this underutilization as indicated by a substantial reduction in growth and condition among *C. aleuticus* individuals in experimental manipulations that compared intra- and inter-specific effects. Observed spatial overlap between these two cottids combined with the results of the competition experiment suggests that *C. aleuticus* is more strongly limited in its ability to use estuarine habitats opportunistically by interspecific competition than by intraspecific competition.

Résumé : Des observations de terrain, des tests et des expériences avec le cottidé euryhalin *Cottus aleuticus* ont permis d'évaluer en quelle mesure la disponibilité moyenne des ressources explique la répartition à grande échelle de ce poisson dans les habitats fluviaux d'amont et dans l'estuaire et comment la compétition interspécifique par un congénère affecte sa performance dans l'estuaire. Les densités de population de *C. aleuticus* ne correspondent aux densités des ressources que durant deux des cinq années de l'étude, ce qui indique une absence d'appariement des ressources aux grandes échelles temporelles. Aux échelles temporelles plus courtes, les taux de croissance des poissons, qui sont deux-trois fois plus élevés dans l'estuaire que dans les cours d'eau, ne s'accordent pas avec les prédictions de la théorie de l'appariement des ressources. Une manipulation de la densité de *C. aleuticus* montre que l'estuaire pourrait contenir au moins deux fois plus d'individus qu'il n'y en a actuellement; ainsi l'estuaire, un habitat plus avantageux, est sous-utilisé. La compétition interspécifique avec *C. asper* est en partie responsable de cette sous-utilisation; en effet, des manipulations expérimentales qui comparent les effets intraspécifiques et interspécifiques montrent une réduction substantielle de la croissance et de la condition chez *C. aleuticus*. Le chevauchement spatial observé entre ces deux cottidés en plus des résultats des expériences sur la compétition laissent croire que *C. aleuticus* est plus limité dans sa capacité à utiliser de façon opportuniste les habitats de l'estuaire par la compétition interspécifique que par la compétition intraspécifique.

[Traduit par la Rédaction]

Introduction

Heterogeneous environments that differ in profitability among patch or habitat types offer the opportunity for organisms to persist within them through optimal habitat selection and fitness maximization depending on the ability of such organisms to respond to spatial and (or) temporal variation in resource abundance. Existing ecological theory can address the relative resource matching capabilities of organ-

isms that move among habitats and patches. Resource matching is predicted by the ideal free distribution (IFD) (Fretwell and Lucas 1970; Fretwell 1972) and theoretical advances of the IFD model address its relatively simplistic assumptions about the perceptual requirements of foragers (Spencer et al. 1996; Tyler and Hargrove 1997; Ranta et al. 1999), competitive differences among individuals in the population (Spencer et al. 1995; Hugie and Grand 1998; Tregenza and Thompson 1998), and the costs of movement

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that affect settlement patterns when habitats are occupied by individuals at low density (Greene and Stamps 2001) or emigration costs that may adjust the relative value of apparently better or poorer habitats (Morris 1987a).

An IFD-based equilibrium distribution occurs when the proportion of individuals in each habitat roughly matches the proportion of resources available in each and intake rates, individual growth, and survivorship become equal across habitats or patches. These manifestations are collectively referred to as numerical or performance resource tracking at the observed densities in each habitat (Folt et al. 1998). However, if numerical and performance responses do not indicate equilibrium between the two habitats as predicted by the IFD, then the population is likely constrained by other mechanisms that interact with the effects of density dependence.

Field populations typically fail to show numerical and performance responses consistent with the IFD (Kennedy and Gray 1993), and in many cases, perfect resource matching is not expected. Nevertheless, the IFD is an appropriate null model for testing habitat selection under varying habitat features (e.g., Giannico and Healey 1999). The study of fish distributions in estuarine tidal creeks and adjacent stream habitats might benefit from the use of IFD predictions in designing empirical tests in laboratory (e.g., Milinski 1979) or field (e.g., Fraser and Sise 1980; Power 1984; Nislow et al. 1998) settings that elucidate mechanisms that affect the ability of organisms to match the availability of their resources. In this manner, the IFD serves as a tool rather than a hypothesis to examine different consumer–resource systems (e.g., Oksanen et al. 1995) and the lack of an actual IFD motivates further investigation into the processes that negate matching.

Interspecific competition may constrain resource matching when a superior competitor excludes an inferior competitor from exploiting all patches in a habitat. The observed reduction in performance in the presence of a competitor should be as strong as or stronger than that observed in the presence of conspecifics. Under strong competition, stable coexistence depends on the presence of at least one axis of environmental heterogeneity along which species can partition resources (e.g., Connell 1961; MacArthur and Pianka 1966; Rosenzweig 1987). Complete partitioning of resources (e.g., Werner 1977; Werner and Gilliam 1984) or of different physical properties of the environment (e.g., Ross 1986; Matthews 1987; Denno et al. 1995) is predicted for fishes that experience competition on evolutionary time scales. However, overlap of species is frequently observed and might affect the short-term resource matching ability of one species in the zone of overlap (e.g., Weisburg 1986; Costello 1992; Garrison 2000). I will show that ecologically similar species in estuaries experience competitive effects that limit one species' estuarine distribution.

Estuaries are very productive habitats (e.g., Schelske and Odum 1962; Underwood and Kromkamp 1999), and their high productivity is exploited by both freshwater and marine organisms. Fishes that utilize estuarine habitats generally do so during early stages of their life histories and are typically euryhaline species that enter estuaries from marine habitats (e.g., Valesini et al. 1997; Gray et al. 1996) or streams and large rivers with oceanic interfaces (e.g., Blaber and Blaber

1980; Kneib 1984; Limburg et al. 1997). Some marine species, however, are known to enter estuaries as spawning adults (e.g., Yanez-Arancibia and Lara-Dominguez 1988). Most species are not permanent residents, and those that are primarily abundant as juveniles or present on short temporal scales are classified as either estuarine opportunists or stragglers (Lenanton and Potter 1987). Opportunists use estuaries as nursery areas, but it is difficult to determine whether estuarine resources contribute directly to an overall fitness advantage in individuals that use estuarine resources opportunistically. Some studies have considered the role of resource differences between estuaries and upstream habitats in observed distributions of some freshwater species in estuaries and have associated these patterns with experimental evidence that the enhanced foraging opportunities drive estuarine habitat selection (e.g., Frank and Leggett 1986; Sogard 1992; Kneib 1993).

Estuarine-opportunist fishes provide the opportunity to test the strength with which resources influence species distributions in the context of resource matching predictions at large and small spatial scales. In this study, I evaluate whether fish match average resource availability across habitat types (freshwater versus estuarine) and the role of intra- and inter-specific competition at the patch scale as mechanisms limiting their ability to do so. The freshwater cottid *Cottus aleuticus* uses both estuarine and upstream habitats, and if resources are the primary mechanism leading to density differences at the habitat scale, then this species should show numerical and performance resource tracking even when average fish density and resource availability are evaluated at the patch scale. I show that fish population and prey resource densities are higher, on average, in an estuary than in the stream above the mixohaline zone. Fish densities did not match resource availability because growth rates in the estuary under increasing intraspecific competition in *C. aleuticus* indicated that the habitat is not saturated as would be the case under the IFD's resource matching equilibrium prediction. Interspecific competition with *Cottus asper* at the patch scale in the estuary significantly reduces both growth and condition factor in *C. aleuticus* to a greater extent than I observed in fish presented with increased densities of conspecifics only and appears to be one mechanism operating to limit the use of estuaries by *C. aleuticus*.

Methods

Study system

Estuaries along the Pacific coast of North America contain juveniles of both marine and freshwater fishes, but assemblages tend to be dominated by marine species, particularly during summer recruitment (e.g., Horn and Allen 1976; Allen 1982; Yoklavich et al. 1991). The coastrange sculpin *C. aleuticus* is abundant in the lower to middle reaches of streams of the Pacific coast from Alaska to southern California (Moyle 1976; Lee et al. 1980). Populations may complete the entire life cycle in fresh water (McLarney 1968; Ikusemiju 1975), use estuaries as nursery areas for juveniles (Ringstad and Narver 1973), or show a "mixed/fluvial" life history pattern (i.e., spawn and raise juveniles in all areas of

the drainage or spawn in all areas but restrict juveniles to estuaries; Brown et al. 1995).

Cottus aleuticus and *C. asper* are the most abundant estuarine-opportunist freshwater fishes that occur in Big Beef Creek, a low-order stream draining into Hood Canal in the western Puget Sound region of Washington (USA). The stream is about 9 km in length, with the last 0.7 km in the intertidal zone. At high tide, the upstream portion of the mixohaline zone reaches salinity levels of 10–15 ppt, whereas the salinity closer to the mouth of the estuary is 20–25 ppt (K.M. Polivka, unpublished data). At low tide, the water in the active river channel is completely fresh (0–3 ppt). Current velocities in Big Beef Creek generally range from 10 to 108 cm·s⁻¹ throughout the active channel, although backwaters with negligible flow rates are present and rising tides alter the hydrodynamic environment in the estuary (Polivka 2002). Although temperature can be greater in the estuary by as much as 1–3 °C compared with upstream, *C. aleuticus* appears to occupy areas of each habitat with equal temperatures. For example, pooled measurements at several stations in estuarine and upstream habitats taken on separate days between 15 June and 25 July 1998 give mean ± SE values of 16.11 ± 0.62 °C upstream ($N = 9$ days), 17.52 ± 0.30 °C in the estuary at low tide ($N = 21$ days), and 19.17 ± 1.2 °C in the estuary at high tide ($N = 6$ days). However, low-tide temperature samples taken in 2001, restricted to areas of the estuary where *C. aleuticus* occurs, were nearly identical to those taken upstream (estuary mean = 16.7 ± 0.55 °C ($N = 5$), upstream mean = 16.0 ± 0.25 °C ($N = 10$); $t = 1.16$, $p = 0.27$, $df = 12$). Thus, temperatures in the two major habitats differ by either a small amount or zero and are not likely to confound measures of performance in *C. aleuticus*. Salinity differences during the tide cycle can be substantial, but at least one recent study has shown that euryhaline fishes achieve optimal growth rates in brackish water (Altinok and Grizzle 2001).

Long-term census of fish and prey abundance between habitat types

I made comparisons of mean patch density across habitats by using repeated censuses of abundance. During June–August 1998–2002, I estimated the densities of *Cottus* spp. by establishing 12 semipermanent stations along the length of Big Beef Creek from the mouth of the estuary to 1.2 km upstream of the mixohaline zone generally at intervals of 50–75 m. I established six additional stations in the upper intertidal when it became clear that *C. aleuticus* was primarily found in this area and that an estuary-wide estimate of average density was inappropriate to address the question of numerical resource matching between occupied patches in both habitats. I censused all fishes once or twice per month but generally made comparisons between years by using samples from mid- to late July because comparisons for the first study year were not made until July 1998 when a consistent methodology was established. At each station, roughly standardized to an area of 6.25 m², field crews made two passes using a seine (2 m × 1.2 m) with a 3-mm mesh such that few individuals could avoid capture, although it is assumed that a small fraction of the cottids escaped capture underneath the seine and that any larval or extremely small

juvenile individuals of all species could pass through the mesh. In general, the seining technique was identical between habitats, but the sampling frequency enabled me to determine that I was consistently seeing the same amount of variation among sites within each major habitat type as well as between habitat types. Although estuarine stations vary temporally (with the tide cycle) in depth, hydrodynamics, salinity, and temperature, censuses were always conducted at low tide in the active channel of the creek when the range of physical characteristics (including salinity) was similar for both habitats. For each species present, I recorded the standard length (SL) of each captured individual to the nearest millimetre. I compared the density of *C. aleuticus* between habitats and across years simultaneously with a two-factor analysis of variance (ANOVA). Seine censuses proved unreliable for capture of *C. asper* in upstream habitats where it appeared that they only occupied very deep pools that could not be efficiently sampled using this technique; therefore, I conducted qualitative censuses of *C. asper* abundance in upstream pools using unbaited minnow traps.

I determined the primary prey of *Cottus* in each habitat by sacrificing 10 individuals of both species with an overdose of tricaine methanesulfonate (MS 222) and identifying species found in gut samples. The primary prey items for *Cottus* in upstream habitats were stonefly larvae (*Hesperoperla* sp.) and small mayfly larvae (e.g., *Baetis* sp.), whereas primary prey items in the estuary were gammarid amphipods (*Eogammarus confervicolus* and *Corophium spinicorne*) and the marine isopod *Gnorimosphaeroma oregonense*.

I estimated the average biomass across estuarine and upstream patches of the major prey species combined by enclosing ceramic tiles (100 cm²) in plastic mesh structures (3-mm mesh size) to allow entry and settlement by invertebrates but to prevent access and predation by fish. Ten tiles were placed in each habitat type and I allowed 2–4 weeks for invertebrates to completely settle on the tiles, which is an appropriate temporal scale for sampling populations (e.g., Peckarsky and Cowan 1995). Tiles were placed in microhabitats near the fish census stations but not directly within fish census stations to prevent disturbance of the tiles during fish censuses. Owing to the long incubation period, only one census was taken during July–August 1998, whereas in other years, there were additional censuses using tiles or other methods (Polivka 2002). For consistency, I only compared prey density between habitats and years for the July–August censuses using the ceramic tiles to correspond to comparisons of fish density. At each census, I identified all individuals to species when possible (to genus or family otherwise), obtained the total dry mass of all prey present in each sample to the nearest 0.0001 g, and compared the biomass for each habitat and year with a two-factor ANOVA. Although the major prey types in each habitat differ taxonomically, their total biomass on enclosed tiles free of fish predation might be a reasonable estimate of productivity differences between the habitats.

In analyses of both fish and prey abundance, when I found significant year effects, I performed within-habitat analysis of among-year abundance (compared with post hoc tests in a one-way ANOVA) to identify the extent of temporal varia-

tion within each habitat independently of the other. This analysis was necessary to determine whether there was any correspondence between interannual variation in prey abundance and any interannual variation in fish abundance in either habitat.

Intraspecific competitive effects at the patch scale and resource matching at the habitat scale

If the observed densities in each major habitat type represent a resource matching equilibrium, I would expect to observe equal performance between habitats when fish are at ambient densities. Under such an equilibrium, the IFD predicts that no individual can gain fitness by moving to an alternative habitat or patch. Thus, experimental manipulation of densities and observation of performance-related response variables can identify the relative degree of saturation of major habitat types. I compared the growth of *C. aleuticus* at ambient fish densities for each habitat (calculated from census data) and at double the ambient density with in situ enclosures. If the density-dependent reduction in growth by increasing the number of estuarine fish reduces growth below that of fish at ambient density in the upstream habitat, then resources are more closely matched by fish. I also compared high-density upstream treatments and ambient density estuarine treatments, where fish density was approximately equal, thus showing the absolute difference in growth between habitats for small groups of *C. aleuticus*.

The rectangular enclosures were constructed with 3.25-mm-mesh galvanized hardware cloth and had dimensions of 61 cm × 61 cm × 31 cm. Twelve were placed in each major habitat type (estuary versus upstream) with approximately 3 cm of the respective substrate to allow incubation and colonization of prey items. Six replicates in each habitat were designated as controls (ambient density) and the other six were designated as experimental (double density) treatments. In each case, I used juvenile fish (29–35 mm initial SL) and, to simulate the densities observed in the census data obtained in each habitat, placed one or two individuals in each upstream control enclosure (ambient upstream density), two or three in estuarine controls (ambient estuarine density), two or three in upstream double-density enclosures, and four or five in estuarine double-density treatments. The range of individuals used in each treatment reflects the variation necessary to achieve a consistent total biomass per treatment that reflected ambient versus high-density conditions in each habitat. Some individuals had disappeared by the end of the experiment, and occasionally, their remains were found in the enclosures despite the rapid decomposition and consumption by scavengers (K.M. Polivka, personal observation). Whether or not remains were found, missing individuals were presumed dead and I calculated the per-enclosure survivorship for comparisons among treatments and habitats.

To identify fish for measurement of individual growth rates, I marked each fish with a small subcutaneous injection of water-based acrylic paint (Ceramcoat™) (Delta Technical Coatings, Whittier, California) at specific positions on the ventral surface of the fish and each fish received a unique color or mark position. Habitat and density effects on growth rates (in both SL and mass) were compared by a two-way ANOVA. I also estimated the Fulton condition index (CI) to test whether fish were differentially changing mass or length

in response to my experimental treatments (Anderson and Neumann 1996). The index was $\text{mass} \times \text{SL}^{-3.25}$ where I estimated the exponent with a regression of $\log(\text{mass})$ versus $\log(\text{SL})$. I used analysis of covariance to test for overall differences in mass among fish of a given length in each treatment type and to validate the CI. I tested for differences in the change in CI between habitats and density treatments with ANOVA.

Patch-scale competitive effects of *C. asper* on *C. aleuticus*

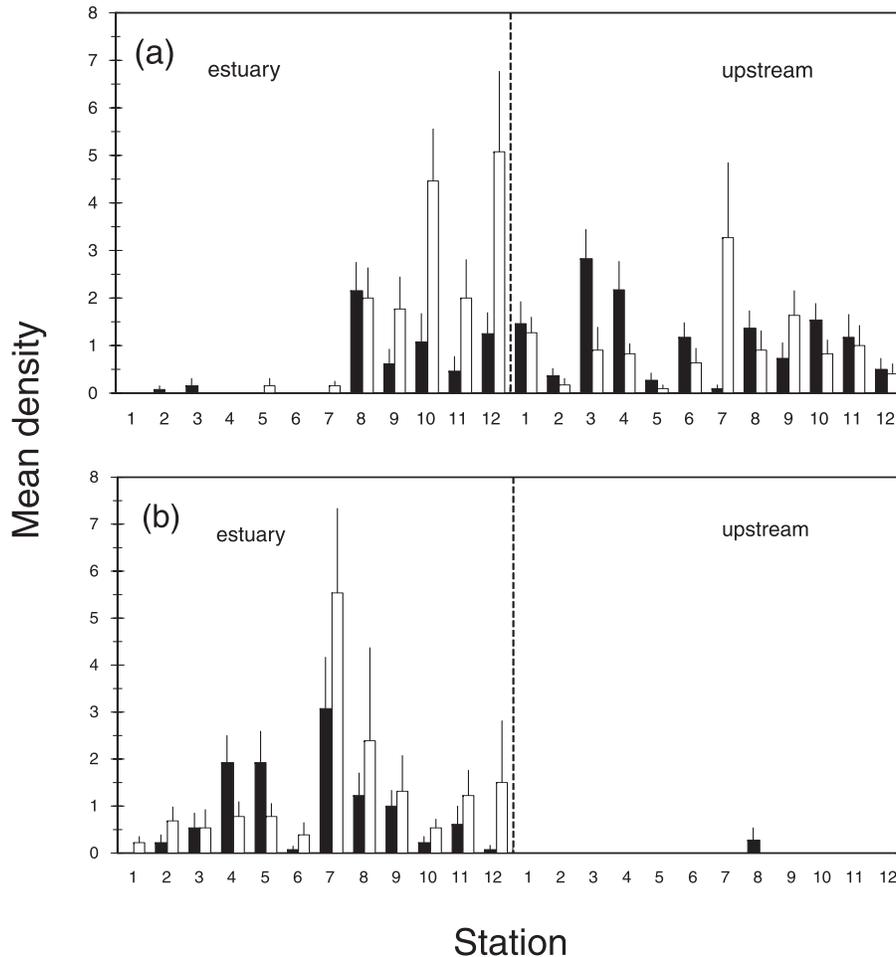
After determining the effects of conspecifics on the growth of *C. aleuticus*, I tested whether the presence of the congener *C. asper* limits the performance of *C. aleuticus* in estuarine habitats by examining the growth response among individuals at the patch scale. In 2000, I enclosed three juvenile *C. aleuticus* in 61 cm × 61 cm × 31 cm rectangular cages identical to those used previously. Although interannual differences in productivity could affect the outcome of competition, the slight, but nonsignificant, differences in estuarine fish density among years (see Results) led me to use a similar design for my experiments. In a second treatment, I again doubled the control density (six or seven *C. aleuticus*) and in a third treatment, I substituted three or four juvenile *C. asper* for the *C. aleuticus* added in the second treatment; thus, the total biomasses of fish in the second and third treatment were approximately equal. I marked each individual as before and measured the SL and mass of each fish for subsequent calculations of condition factor. Ten replicates of each treatment were placed directly in the active tidal creek channel in the estuary for 4 weeks. Enclosures were placed in a microhabitat of intermediate depth and current speed to avoid favoring one species or the other based on microhabitat associations reported in other studies (Ringstad and Narver 1973; White and Harvey 1999).

Results

Juvenile and adult *C. aleuticus* were found in both upstream habitats and the high intertidal census stations of the estuary, specifically in the upper 30% of the intertidal zone (Fig. 1a). Juveniles were three times more abundant than adults, numerically, in estuarine stations 8–12 (block ANOVA, $F = 13.76$, $p < 0.001$), but there was no numerical difference in adults and juveniles in upstream stations 1–12 ($F = 0.50$, $p = 0.481$). Only a few adult *C. asper* were found in a deeper pool upstream (census station 8) (Fig. 1b) and occasionally in minnow traps set in similar microhabitats not included in census stations. Overlap between *Cottus* spp. occurred primarily in estuarine census stations 8 and 9 but was fairly common throughout stations 8–12. In the estuary, *C. aleuticus* rarely overlapped with the primarily adult *C. asper* that occurred below station 7.

The density of *C. aleuticus* in upper estuarine stations was greater than the mean density upstream, varying from about 1.2 times greater during 1998 to nearly three times greater in 2001 (Fig. 2a). This pattern appears to be driven primarily by the density of juveniles in the estuary, given that adults appeared to be more frequently found upstream (Fig. 1a). Two way ANOVA indicated that major habitat type ($p < 0.001$) significantly explained variation in *C. aleuticus* density. Year of the study was a significant factor ($p = 0.010$)

Fig. 1. Mean abundance of young-of-the-year (open bars) and adult (solid bars) individuals of (a) *Cottus aleuticus* and (b) *Cottus asper* at 12 permanent census stations in both estuarine and upstream habitats in censuses taken from 1998 to 2002 ($N = 13$ (estuary) and 11 (upstream)). Increasing station numbers indicate stations moving in an upstream direction throughout the study site.



but the interaction of these two factors was not significant ($p = 0.771$) (Table 1a). Upstream fish were substantially more numerous in upstream censuses (Table 1b) in 1998 than in 2000–2002 (Tukey's honestly significant difference (HSD) test, $p < 0.05$), whereas estuarine populations did not differ statistically among the five years of the study ($p = 0.310$) (Table 1b); thus, the significant year effect (Table 1a) is likely due primarily to the 1998 mean fish abundance.

The difference in total prey biomass between the estuary and upstream habitats varied substantially from 1.5-fold (1998) to around 40-fold (2000 and 2002), and these differences are represented by a highly significant interaction between habitat and study year ($p = 0.001$) (Table 2a; Fig. 2b). The 1998 and 1999 differences in fish and prey abundances were of similar magnitude between habitats but differed vastly from 2000 to 2002; thus, numerical matching was not consistent. One-way ANOVA indicated that differences between years in upstream prey availability were only marginally significant ($p = 0.079$) (Table 2b) but that estuarine prey biomass was heterogeneous among years ($p = 0.004$) (Table 2b). In this habitat, according to censuses taken at patches upstream of estuarine station 8, prey biomass was significantly higher ($p < 0.05$) in 2000–2002 than in 1998–

1999, but within each of those groups of years, there were no significant differences (Tukey's HSD test).

Intraspecific competitive effects at the patch scale and resource matching at the habitat scale

Average individual growth rates of *C. aleuticus* stocked at ambient densities in the estuary and upstream did not indicate a resource matching equilibrium. Estuarine fish grew three times faster than those in upstream enclosures in the 1998 density manipulation experiment (Fig. 3), a result that differed slightly depending on whether the response variable examined was SL ($p = 0.053$) (Table 3a) or mass ($p = 0.003$) (Table 3b). Doubling the ambient density in each habitat reduced growth in mass within habitats ($p = 0.048$) but did not significantly reduce growth in SL ($p = 0.214$). Neither response variable revealed a significant interaction between habitat and density treatments, indicating that the density effect was similar in both habitats. Although growth did not show strong density dependence in the estuary, growth rates at double density are still as high as those attained at ambient density upstream. Thus, the estuary could support at least twice the observed number of individuals before growth would be equalized across both habitats in a manner

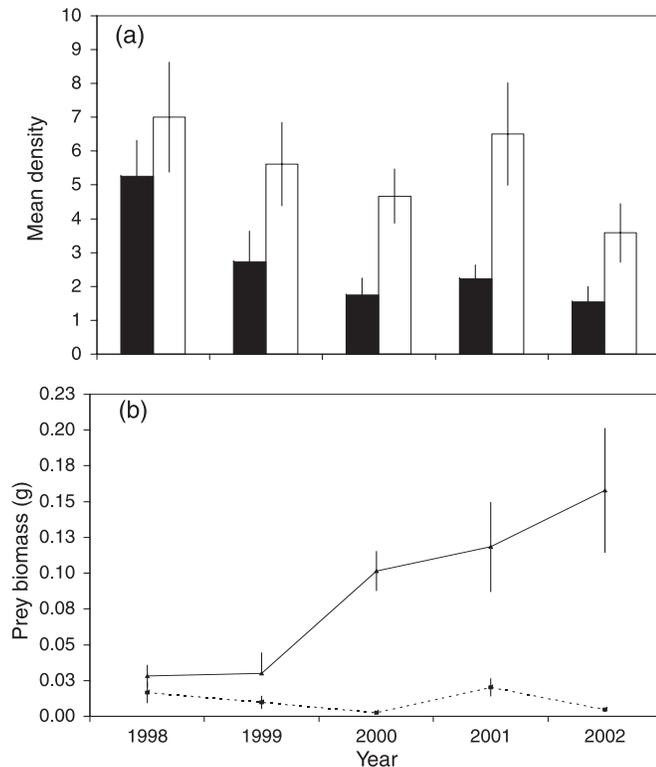
Table 1. (a) Two-way ANOVA of *Cottus aleuticus* density in upstream and estuarine habitats from 1998 to 2002 in each habitat and (b) one-way ANOVA to identify within-habitat heterogeneity in fish density among years.

Factor	df	SS	F	p
(a) Two-way ANOVA				
Year	4	172.01	3.47	0.010
Habitat	1	236.07	18.36	<0.001
Year × habitat	4	23.17	0.45	0.771
Error	113	1447.55		
Total	122	1878.80		
(b) One-way ANOVA				
Upstream				
Year	4	107.63	4.50	0.003
Error	54	323.22		
Total	58	430.85		
Estuary				
Year	4	93.4	1.23	0.310
Error	59	1124.3		
Total	63	1217.7		

Table 2. (a) Two-way ANOVA of prey biomass in upstream and estuarine habitats from combined census data from 1998 to 2002 in each habitat and (b) one-way ANOVA to identify within-habitat heterogeneity in prey biomass among years.

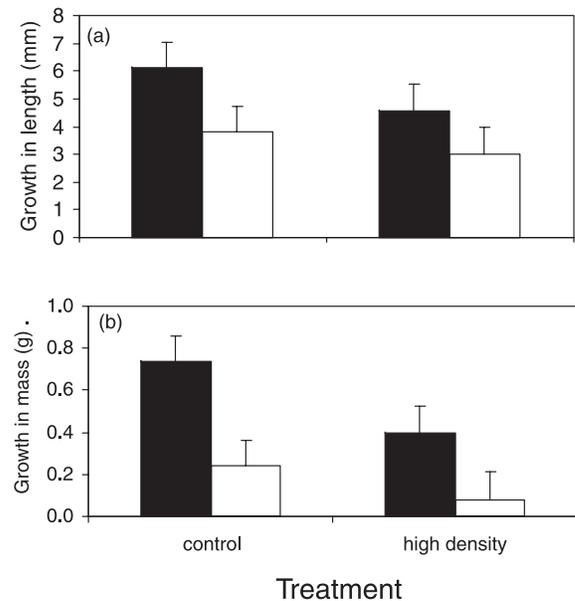
Factor	df	SS	F	p
(a) Two-way ANOVA				
Year	4	0.052394	4.50	0.003
Habitat	1	0.122993	45.69	<0.001
Year × habitat	4	0.055683	5.31	0.001
Error	74	0.193900		
Total	83	0.424970		
(b) One-way ANOVA				
Upstream				
Year	4	0.002056	2.27	0.079
Error	39	0.008823		
Total	43	0.010879		
Estuary				
Year	4	0.09676	4.57	0.004
Error	35	0.18508		
Total	39	0.28184		

Fig. 2. Mean annual abundance of (a) *Cottus aleuticus* and (b) mean annual prey biomass (mean ± SE) combined for all July–August sampling at fixed stations in estuarine versus upstream habitats for the midsummer censuses in all five years of the study (1998–2002). Solid bars, upstream fish abundance; open bars, estuary fish abundance; squares, upstream prey abundance; triangles, estuarine prey abundance.



consistent with the performance resource matching prediction of IFD-based habitat selection models. Strong productivity differences between the estuarine and upstream habitats are further indicated by the comparison between

Fig. 3. Growth measured as mean + SE change in both (a) standard length and (b) mass for replicate experimental enclosures of individual *Cottus aleuticus* maintained at ambient density (control) and twice the ambient density (high density) in both estuarine (solid bars) and upstream (open bars) habitats.



mean growth at double-density upstream and growth at ambient density in the estuary (roughly equal fish density per enclosure/patch) where growth in length was around 2.5 times greater (Fig. 3a) and growth in mass was around six times greater (Fig. 3b).

Although SL and mass both changed at different rates between habitats, the change in CI was not significantly different between habitats ($p = 0.116$), indicating that although fish grew slower upstream, they allocated growth similarly in length and mass in each habitat. The change in fish condition was 2.1 times greater at ambient densities, but this

Table 3. Two-way ANOVA on *Cottus aleuticus* growth rates indicated by change in (a) standard length, (b) mass, and (c) condition index for enclosed individuals maintained at ambient and twice the ambient density in both estuarine and upstream habitats.

Factor	df	SS	F	p
(a) Standard length				
Habitat	1	19.922	4.280	0.053
Density	1	7.710	1.656	0.214
Habitat × density	1	0.690	0.148	0.705
Error	18	83.792		
(b) Mass				
Habitat	1	0.907	11.726	0.003
Density	1	0.347	4.486	0.048
Habitat × density	1	0.045	0.578	0.457
Error	18	1.392		
(c) Condition index				
Habitat	1	0.09680	2.72	0.116
Density	1	0.12526	3.69	0.071
Habitat × density	1	0.00401	0.12	0.735
Error	18	0.61151		
Total	21	0.83759		

effect was not significant ($p = 0.071$), nor was there a significant interaction between habitat and density ($p = 0.735$). Thus, fish condition is reduced at high densities, but a two-fold increase in estuarine density did not produce a statistically distinct effect.

Mean \pm SE survivorship was similar between habitats when fish were at ambient density in each (upstream: 0.86 ± 0.09 , estuary: 0.75 ± 0.17 ; $t = 0.58$, $p = 0.58$, $df = 8$), indicating no differences in average per patch survivorship due to environmental factors in each habitat including resource availability but excluding interspecific competition and predation. At high densities, survivorship was reduced (upstream: 0.75 ± 0.17 , estuary: 0.59 ± 0.11 ; $t = 0.78$, $p = 0.46$, $df = 8$). Despite the downward trend in survivorship, ANOVA indicated no significant differences in survivorship between treatments ($F = 0.63$, $p = 0.605$, $df = 20$).

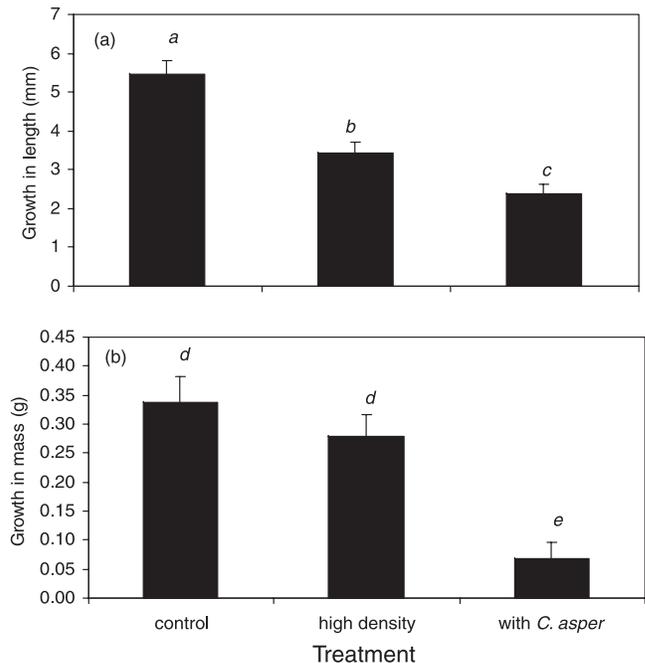
Patch-scale competitive effects of *C. asper* on *C. aleuticus*

In experimental enclosures, the presence of *C. asper* depressed the growth rate of *C. aleuticus* by a factor of more than 2, which was stronger than the intraspecific effect of doubling the density of *C. aleuticus* (Fig. 4; Table 4). Tukey's post hoc test indicated significant ($p < 0.05$) differences between all pairs of mean growth rates with the following exception: change in fish mass did not differ between the control and high-density treatments. A further consequence of interspecific competition for *C. aleuticus* is that fish condition (CI) changed by an average of -0.0817 ± 0.0217 in individuals placed with *C. asper* ($p = 0.010$) (Table 4c). Thus, *C. aleuticus* individuals faced with interspecific competition allocated proportionally more growth to SL than to mass, which reduced their CI from the start to the end of the experiment, whereas individuals in the ambient ($\Delta CI = -0.0021 \pm 0.0330$) and high-density ($\Delta CI = 0.0243 \pm 0.0175$) treatments added mass in equal or slightly higher proportion to SL relative to the competition treatment. Pairwise tests showed significant differences in CI between the

Table 4. Results of a one-way ANOVA on the effect of ambient densities, high densities, and the presence of *Cottus asper* on change in (a) standard length, (b) mass, and (c) condition index for *Cottus aleuticus* individuals.

Factor	df	SS	F	p
(a) Standard length				
Treatment	2	39.055	30.40	<0.001
Error	22	14.134		
Total	24	53.189		
(b) Mass				
Treatment	2	0.3541	16.93	<0.001
Error	22	0.2301		
Total	24	0.5842		
(c) Condition index				
Treatment	2	0.0552	5.77	0.010
Error	22	0.1051		
Total	24	0.1604		

Fig. 4. Change in (a) standard length and (b) mass of *Cottus aleuticus* in experimental enclosures in the estuary stocked at ambient estuarine density (control) and at twice the ambient density (high density) and in competition with *Cottus asper* (total fish biomass equal to that of the high-density treatment). Significant ($p < 0.05$) pairwise differences determined by Tukey's test are indicated by a–e.



competition treatment and both the ambient ($p = 0.029$) and high-density ($p = 0.004$) treatments but not between the ambient and high-density treatments ($p = 0.468$).

Discussion

This study considered a few of several possible mechanistic explanations for the patterns of distribution of stream fish that use estuaries opportunistically. Because estuaries are highly productive and because a limited number of species use estuaries opportunistically owing to physiological limita-

tions, I expected to observe a strong role for resources in the habitat selection patterns of fishes and that resources might not be a limiting factor that would result in competition between ecologically similar species. Resources made the estuary profitable for fish, but resource matching was limited strongly by interspecific competition, thus preventing an equilibrium where intraspecific competitive effects would equalize fitness. Although perfect resource matching is rare in most field situations (e.g., Kennedy and Gray 1993), I initially expected to observe greater resource and fish densities in the estuary and equal growth rates across experimental patches in each habitat when these responses were measured at ambient fish densities consistent with the predictions of the IFD (Fretwell and Lucas 1970; Fretwell 1972). Despite the possibility that IFD assumptions were violated in this study system, the numerical- and performance-tracking predictions initially served as a useful null model to examine the observed spatial and temporal patterns of fish and prey abundance (e.g., Giannico and Healey 1999) and the effects of interspecific competition on the relative gains in a highly productive estuary.

Cottus aleuticus was more abundant in the estuary than in the stream, but fish abundance failed to correspond to prey abundance after a significant increase in estuarine prey biomass in 2000 was not accompanied by a similar response in mean fish density, suggesting limits to resource matching. *Cottus aleuticus* can reduce prey density at small spatial scales (K.M. Polivka, unpublished data); thus, it is surprising that a population response was not seen. The lack of a response suggests one of several possible mechanisms that limit resource matching, not all of which are addressed by the experiments in this study. These include (i) mechanisms at the patch scale such as predation risk and interspecific competition, (ii) mechanisms at the population level such as bet-hedging strategies, (iii) violations of resource matching assumptions, or (iv) a lack of active habitat selection in this species.

Because resource abundance alone could not completely explain the abundance of *C. aleuticus* in the estuarine habitat, experimental exploration of biotic interactions such as interspecific competition and predation (K.M. Polivka, unpublished data) was justified. The perceived response of fish to resource differences between habitats rests on the assumption that energetic input from the environment can support a given biomass of invertebrate consumers and a measurement of their abundance in the absence of consumption by fish is a reasonable estimate of productivity in each major habitat type. Specific studies indicating differences in energetic value of *Hesperoperla* stoneflies and *Eogammarus* amphipods are lacking and other detailed metabolic data might be necessary to demonstrate unequivocally that the total prey biomass is substitutable between habitats. Nevertheless, there is a strong indication that fish have more available prey in the estuary and that populations are limited in their ability to respond numerically to high prey availability. Additional limitations such as movement costs between the major habitat types were not the focus of this study, but there has been some indication that there are survivorship costs to movement between the stream and the estuary (K.M. Polivka, unpublished data), presumably owing to the osmoregulatory changes required in a variably saline environment, but no

costs of moving from the upper intertidal zone to the lower intertidal zone (K.M. Polivka, unpublished data) where the salinity fluctuations are of greater magnitude.

Intraspecific competition had a similar effect on *C. aleuticus* in the estuarine and upstream portions of Big Beef Creek, but growth responses indicated that the estuary could support a density of *C. aleuticus* at least twice that observed in censuses before an IFD-based equilibrium would be reached. The difference in productivity between habitats might require upstream individuals to forage more widely and the artificial nature of the enclosures might limit the ability of fish to engage in normal foraging movements. However, enclosures tended to enhance the availability of upstream prey (K.M. Polivka, unpublished data), possibly owing to behavioral patterns of prey species, but not that of estuarine prey. Thus, the growth rate of upstream individuals may actually have been overestimated relative to growth rates experienced by free-ranging fish. I added a greater total number of individuals to the estuarine enclosures to double the density; thus, upstream enclosures showed the same reduction in growth with fewer additional individuals. An additional treatment where the same number of individuals were added in each habitat would be useful to examine the effects of density on growth. Density-dependent feedback mechanisms can have variable effects on a population in different habitat or patch types depending on the shape of the relationship between density and suitability (fitness) in each (Morris 1987b). Where density–fitness relationships can be determined directly or estimated from response variables with high correlation to fitness, isodars enable comparisons of habitat distributions when population size varies through time (Morris 1987b). Although population size was relatively steady in the estuary, isodars might also be useful for determining the effects of density dependence across habitats (e.g., Morris 2003) if the relationship between individual growth, survivorship, and fitness can be determined.

Interspecific competition reduced the condition of *C. aleuticus* to a greater extent than intraspecific competition. Thus, I concluded that at the microhabitat scale, *C. asper* was a superior competitor and that intraspecific competition did not limit resource matching as strongly as interspecific competition. The apparent change in growth allocation in *C. aleuticus* warrants further investigation; if *C. aleuticus* always sacrifices increases in body mass for increases in length as a result of interference competition, then there can be consequences for reproductive output via reduced gamete production (e.g., Caceres et al. 1994; Resetarits 1997) and ultimately fitness (but see Hayes and Shonkwiler 2001).

Spatial overlap in the estuarine distributions of juvenile *C. asper* and *C. aleuticus* appeared to be more frequent than has been reported for these two species in other study systems (Ringstad and Narver 1973; White and Harvey 1999). White and Harvey (1999) reported that these species were separated in streams primarily along gradients of depth and current speed, with *C. asper* occurring primarily in slower, deeper microhabitats and *C. aleuticus* occurring in shallow, fast stream riffles. Ringstad and Narver (1973) reported similar associations that extended into the mixohaline portion of a tidal creek. My upstream census data showed no overlap between these two species and *C. asper* was only found in very deep microhabitats, which is consistent with White and

Harvey's (1999) finding, but there was considerable overlap with *C. aleuticus* in some estuarine census stations. Thus, microhabitat segregation based solely on physical properties is not sufficient to explain the coexistence of these two species in estuaries.

I conducted the competition experiments in a microhabitat that was intermediate to the reported associations of the two species in other systems (Ringstad and Narver 1973; White and Harvey 1999) and where they were known to overlap. If the reported associations with physical properties of stream microhabitats favor the dominant species in them, then I would expect the effect of *C. asper* on *C. aleuticus* to be reduced if this experiment were conducted in a shallow, fast-flowing microhabitat and possibly enhanced if it were conducted in a deep, slow-flowing pool within the estuary. In the intermediate microhabitats, *C. asper* showed a much stronger effect on the average individual growth of *C. aleuticus* than was observed in intraspecific competition treatments. Although long-term census data show that resource availability for benthic estuarine cottids was substantially higher in the year, this experiment was conducted (2000) than in the year of the density manipulation (1998), I would expect that the observed competitive effects of *C. asper* on *C. aleuticus* would be exacerbated in years of lower productivity. I did not observe strong intraspecific competition during the course of either experiment but also did not observe marked differences in the abundance of *C. aleuticus* across years where productivity differed severalfold. Patch-scale interspecific competition resulted in a strong effect of *C. asper* on the ability of *C. aleuticus* to respond to estuarine resources, which might be alleviated if microhabitat partitioning were more complete in the estuarine habitat. Competition may act synergistically with other possible mechanisms such as perceptual limitation (Abrahams 1986; Spencer et al. 1995, 1996) and other costs of habitat selection such as predation risk (Grand and Dill 1999). Nevertheless, the outcome of competition usually favors one species and similar studies have shown that competition among fish can have serious negative effects on growth and development in the weaker competitor including age-class "bottlenecks" (Persson and Greenberg 1990). My results support the further pursuit of long-term demographic consequences of competition in estuarine habitats.

Spatial and temporal variation in the use of estuaries by both fishes and invertebrates has been attributed to variable physical conditions in estuaries (Weinstein 1979; Rogers et al. 1984; Allen and Barker 1990) where temperature (Frank and Leggett 1982) and freshwater flow (Crecco and Savoy 1987) strongly influence the intraannual survival of juvenile fish that successfully enter these habitats. Species that have adapted to the physically variable estuarine environment generally benefit from high growth rates (e.g., Kneib 1984; Gray et al. 1996). Temperature varied with the influx of seawater in the estuarine system studied here, which generally affects fish growth rate (e.g., Brett 1979), but many nearshore species have wide ranges of temperature (4–6 °C) under which growth rates are optimal (e.g., Imsland et al. 1996; Jonassen et al. 1999). My in situ measurements of growth in experimental enclosures incorporated natural variation in temperature and salinity in the estuary where growth was still shown to be higher.

Population-level mechanisms may constrain the ability of estuarine-opportunist fishes such as *C. aleuticus* to match resources independently of interspecific interactions. Source-sink dynamics or bet-hedging dispersal strategies might result in a relatively consistent proportion of a population to be found in a particular habitat type. *Cottus aleuticus* juveniles were found in two habitat types that differed widely in productivity, whereas *C. asper* juveniles were exclusively found in the estuary. Disproportionate use of poor habitats is fairly common (e.g., Van Horne 1983; Grand and Dill 1997) and evolutionarily stable in some circumstances (Holt 1997; Schmidt et al. 2000; Holt and Barfield 2001); my work suggests that interspecific competition might have resulted in a habitat selection pattern for *C. aleuticus* consistent with an estuarine-opportunist strategy, but details of the broader evolutionary significance of such strategies (e.g., Pulliam 1988, 1996; Pulliam and Danielson 1991) to estuarine-opportunist species remain poorly understood. Bet-hedging by allocating a consistent proportion of individuals to estuarine or marine habitats has been proposed as a mechanism leading to anadromy in freshwater cutthroat trout (Northcote 1997), but whether this was also responsible for estuarine habitat use among the freshwater cottids in this study system is beyond the scope of the work reported here.

Deviations from the predictions of resource matching models such as the IFD may result from the forager's lack of perfect knowledge of the environment (Abrahams 1986; Kennedy and Gray 1993), which typically occurs when the spatial scale of resource heterogeneity exceeds the typical movement patterns of the forager (Tyler and Hargrove 1997) and are especially important when perceptual limits vary among individuals in a population (Spencer et al. 1996). In this study system, it is difficult to identify the extent to which individual *C. aleuticus* are able to detect differences in average resource availability across the riverine/intertidal ecotone (a violation of the "ideal" assumption of the IFD), but active habitat selection is apparent from the movement of marked individuals (K.M. Polivka, unpublished data) and differential depletion of resources on patches that vary in predation risk (K.M. Polivka, unpublished data).

Here, I showed with observational and experimental evidence that estuarine habitat selection by the euryhaline freshwater cottid *C. aleuticus* is driven in part by resources, resulting in high growth rates for a portion of the population, but limited by interspecific competition, likely contributing to underutilization of the estuary as indicated by failure to meet the predictions of simple resource matching models. Alternative models incorporate the effects of competitive differences between individuals (e.g., Hugie and Grand 1998), predation risk (e.g., Grand and Dill 1999), or local physical factors of the environment (e.g., Hill and Grossman 1993; Tyler and Gilliam 1995) on the ability of animals to match resource availability; however, relatively few of them consider the effects of interspecific competition (but see Grand 2002; Morris 2003). A forager's perceptual limits in terms of either habitat or patch-scale variation in resource availability are difficult to determine, but measurement of the effects of competition at patch scales is both tractable and valuable in resource matching studies. Identification of such costs and how they interact with other mechanisms to limit the profitability of estuaries will facilitate the evalua-

tion of habitat selection theory and provide clues about whether and how aquatic species can respond to the variation in resources that characterize their environments.

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