

# Microhabitat-scale influences of resources and refuge on habitat selection by an estuarine opportunist fish

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**ABSTRACT:** We examined how the marine cottid fish *Clinocottus acuticeps* used vegetated microhabitats within an estuarine system in the Pacific Northwest, USA. *C. acuticeps* was more abundant and grew faster in microhabitats in algal beds compared with open microhabitats. Furthermore, the condition index (CI) increased in vegetated microhabitats and decreased in open habitats which, combined with the variability in growth measured in both habitats, suggests that fish may regulate their growth more narrowly when food resources and protective cover provided by the algal bed function as complementary resources. Reduced growth in open microhabitats may be a physiological response to increased predation risk. Additionally, giving-up densities (GUDs) were similar in both habitats, in both field and laboratory experiments, where fish foraged in the presence of predators and under different levels of protection by algae. These results, combined with the implications of the growth experiments, suggest that *C. acuticeps* utilizes a risk-reckless strategy in the face of a trade-off between food and safety by maximizing food intake despite predation risk. Nevertheless, we maintain that the increased growth and lower predation risk associated with algae microhabitats imply that, ultimately, fitness may be higher in individuals that primarily use vegetated habitats.

**KEY WORDS:** Habitat selection · Prey · Refuge · *Clinocottus acuticeps* · Giving-up density (GUD) · Risk-reckless

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## INTRODUCTION

Organisms are often faced with a trade-off between obtaining food and remaining safe from predators, and this conflict can be resolved through shifts in activity levels and habitat selection (Lima & Dill 1990, Peckarsky 1993, Werner & Anholt 1993, Anholt & Werner 1995, 1998, Halpin 2000, and reviewed in Gotthard 2000). Foraging habits and patch use are critical aspects of behavior that directly influence an organism's fitness (Brown 1988). Individuals will benefit from foraging directly through energy input and indirectly through growth (Roff 1984). These benefits are represented by harvest rate and are balanced by the

metabolic cost of foraging, risk of predation, and missed opportunity costs, or the value of alternative activities. Brown et al. (1994) suggest that the ratio between the benefits and costs of foraging defines foraging efficiency. Further, individuals will maximize fitness by exploiting a resource patch until benefits from resources obtained exactly match the costs of foraging. At this point, the forager should leave that patch and the giving-up density (GUD), or the amount of prey or resource available after the forager has quit, is a measure of optimal foraging efficiency. In patches that offer higher harvest rates or lower foraging costs, benefits will match costs at a lower resource density which will be represented by a lower GUD, indicating more

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efficient foraging (Brown et al. 1994). GUDs have been estimated for a variety of organisms as a way of understanding how these organisms perceive and react to varying risks throughout their natural habitats (Bowers et al. 1993, Brown et al. 1994, 1997). Examination of GUDs suggests that food and safety are complementary resources and that in heterogeneous landscapes foragers use patches which offer each resource in such a way that they may maximize fitness (e.g. Brown 1988). Complementary resources, when used in pairs, also offer the opportunity to reduce variability in important fitness-related traits (e.g. Clark 1994, Sirot & Berenstein 1996). In some cases, exploitation of complementary resources results in higher fitness than exclusive use of the individual resources in a complementary pair (Rapport 1980). Use of complementary resources may cause deviation from the expectation that a forager will always select the most productive habitat (e.g. Polivka 2002).

Due to their high productivity (e.g. Schelske & Odum 1962), estuaries are often vital rearing habitats for marine and freshwater fishes (e.g. Kneib 1984, Sogard 1992, Kneib & Knowlton 1995, Gray et al. 1996, Limburg et al. 1997). Sogard (1992) suggests that rapid growth, providing a selective advantage by increasing both survival and fecundity, is key to the utilization of estuaries as nurseries for fishes. Fish utilizing estuaries often benefit from higher growth rates compared to other habitats such as upstream areas of tidal creeks (Kneib 1984, Polivka in press), but must adapt to a physically variable environment. They are often susceptible to increased predation and other biotic interactions that might reduce growth and survivorship (Kneib 1987, Crowder et al. 1997, K. M. Polivka unpubl.). These biotic interactions often combine with physical variation in substrate and cover, causing the specialization of fish to certain microhabitats (Sogard 1992), but Beck et al. (2001) urge the use of a more comprehensive set of criteria in determining whether microhabitats can be considered as nurseries. Where growth provides a selective advantage and also varies between microhabitats, it is expected that fish will choose habitats that support the highest growth rates, unless such habitats also present higher predation risk (e.g. Lima & Dill 1990). In this research, we examined both the growth and prey consumption of an estuarine fish and show that it exploits vegetated microhabitats offering both high food availability and the best refuge from predation risk, such that individuals adopt an unusual pattern of behavior relative to risks and resources.

Vegetated habitats within estuaries often support greater densities of fish species than non-vegetated habitats (Sogard 1992). Both increased food availability and refuge from predation are benefits of vegetated habitats for juvenile fishes (Rozas & Odum 1988, Sogard

1992). However, this seems to be a species-dependent relationship because preferred vegetated microhabitats provide lower foraging return rates and support weaker growth rates in some study systems (Werner et al. 1983, Sogard 1992). Some species demonstrate behavioral patterns and cryptic coloration that enable them to utilize open unvegetated habitats with no trade-off in predation risk (Sogard 1992).

*Clinocottus acuticeps*, the marine sharpnose sculpin (Cottidae), is commonly found in intertidal habitats including estuarine vegetation and has evolved a unique cryptic green coloration, which makes the interaction between *C. acuticeps* and algal patches dominated by green algae of the genus *Enteromorpha* particularly interesting. The patchy distribution of algal beds throughout estuaries makes both vegetated and open microhabitats available to *C. acuticeps* as well as its competitors and predators, and has prompted an experimental examination of why and how *C. acuticeps* utilizes these algae patches. We hypothesized that vegetated microhabitats would (1) harbor higher densities of *C. acuticeps* than unvegetated microhabitats, (2) yield higher performance and less overall variability in fitness-related responses (such as growth and condition) for fish, and (3) provide patches that offered fish the opportunity to utilize both food and safety as complementary resources. Therefore, we expected to observe lower GUDs in vegetated habitats if vegetation reduced the cost of predation risk, and lower variation in growth and condition if vegetation provided a refuge that complemented foraging opportunities in such patches.

## MATERIALS AND METHODS

**Study system.** This research was conducted at the University of Washington Big Beef Creek Research Station in Seabeck, Washington from July through September, 2000 to 2001, although most of the experimental work took place in 2001. Big Beef Creek is a low-order stream draining into Hood Canal, a fjord off the Strait of Juan de Fuca. The lower 0.8 to 1 km of Big Beef Creek receives semi-diurnal tidal inundation resulting in salinity fluctuations on a gradient from 10 to 28 ppt and temperature increases of 3 to 5°C. *Clinocottus acuticeps* is found in the lower estuary and shares this habitat with several freshwater species (including other cottids) and marine species including the Pacific staghorn sculpin *Leptocottus armatus* (Anderson & Chew 1972, Polivka 2002). Although *L. armatus* is primarily a generalist predator, it opportunistically feeds on small fish (e.g. Mace 1984) including *C. acuticeps* (K.M.P. pers. obs.). *L. armatus* influences the habitat selection and foraging behavior of

marine invertebrates (Fernandez et al. 1993) and other estuarine fish (Polivka 2002, K. M. Polivka unpubl.). Invertebrates present in the estuary are primarily gammarid amphipods *Eogammarus confervicolus* and *Corophium spinicorne* and the marine isopod *Gnori-mosphaeroma oregonense*. All of these species were present in the guts of *C. acuticeps* collected at the site (K.M.A. pers. obs.). We studied the occurrence of *C. acuticeps* and its prey resources in vegetated microhabitat which consist exclusively of algae. *Enteromorpha* sp. is the dominant alga in Big Beef Creek, with *Ulva* and *Fucus* also occasionally present, particularly in the lower intertidal zone.

**Factors characterizing the distribution of *Clinocottus acuticeps*.** In 2000 and 2001 we surveyed fish abundance between June and September to determine the distribution of *C. acuticeps* and assess the correlated biotic and abiotic features of the microhabitats where fish densities were highest. A total of 55 samples were taken at locations representing the range of microhabitats available throughout the estuary at low tide. We sampled the active creek channel during maximum low tides, which generally occur between 09:00 and 12:00 h during the summer months. Fish were collected at each sample by seining twice through a surface area of approximately 6.25 m<sup>2</sup> using a 2 × 1.2 m seine with 3 mm mesh (sensu Polivka in press). The temperature, depth, salinity, substrate and percent algal coverage of each sample area were measured along with the abundance, standard length (SL) to the nearest mm, and mass to the nearest 0.1 g of all fish captured. Substrate was given a classification based on visual identification of predominantly fine (sand or mud), coarse (gravel/small pebbles), or mixed (fine and coarse present) bottom substrate. All vegetated microhabitats sampled consisted exclusively of *Enteromorpha*, which was found to vary spatio-temporally in the active channel in Big Beef Creek. It occurred throughout the entire intertidal zone during the course of the summer, usually spreading upstream as rainfall and freshwater input decreased. Thus, we estimated percentage vegetative coverage based on the density of algae in each area, and used 2 sets of categories to account for heterogeneous distributions of algae within microhabitat patches. Relatively uniform areas were scored in categories of 0–25, 25–50, 50–75 and 75–100% coverage. Heterogeneous areas where relatively dense algae patches (75 to 100% coverage) abutted open microhabitats (0 to 25% coverage) were categorized as 'edge habitats'. We used multiple regression analyses to assess the affects of temperature, salinity, and depth on fish distributions and analyzed categorical variables such as vegetative cover and substrate type with ANOVA.

**Growth of *Clinocottus acuticeps* in different microhabitats.** To identify differences in growth of juvenile

*C. acuticeps* in vegetated vs. unvegetated microhabitats, we collected individuals, measured their initial standard length (SL) and mass, and placed them together in multiple enclosures with ('vegetated') and without algae ('open'). All enclosures were closed on the bottom, but were covered with 1 to 2 cm of substrate from the microhabitats in which they were placed. Enclosures consisted of 6 sides of galvanized hardware cloth and measured 61 × 61 × 31 cm, with 3.25 mm mesh, which prevented fish from escaping, but was large enough for prey to colonize substrate in the enclosure at stable densities for each microhabitat. To prevent limitations on fish growth due to density dependence, only 2 individuals were placed in each enclosure. The assays were conducted for 3 wk (3 July through 24 July 2001) after which the fish were removed and we re-measured their SL and mass. Due to limitations on the number of enclosures, and to increase sample size, we repeated the assay between 18 August and 7 September 2001 to obtain a total of 9 vegetated and 8 open replicates. We calculated the Fulton condition index (CI) for each fish as an indicator of differential change in mass or length (Anderson & Neumann 1996). This index was  $\text{mass} \times \text{SL}^{-3.71} \times 10^6$ , with the exponent estimated from surveys taken throughout the season at Big Beef Creek. The mean and coefficient of variation (CV) for growth, in mass and SL, and overall change in CI were calculated as an average per enclosure. We confirmed the effect of microhabitat type by comparing final mass at the end of the growth period with ANCOVA, using SL as a covariate, and confirmed the use of a single exponent in the Fulton index with a test of parallelism for the slopes of the length-mass regression produced for fish in each habitat type. Finally we compared individual growth responses (SL, mass, change in CI) using multivariate ANOVA.

**Field test of prey consumption in vegetated and unvegetated microhabitats.** To examine the influence of algal beds on foraging by *Clinocottus acuticeps* facing predation risk, we used a field technique that approximated a giving-up density (GUD) for benthic fish in experimental arenas. In vegetated and open microhabitats, we allowed the crustacean prey of *C. acuticeps* to colonize a known volume of substrate, and then compared a set of treatments in which fish were excluded from foraging on the prey with a set in which fish reduced prey density through both foraging and non-lethal effects. We placed substrate obtained directly from the habitats used by *C. acuticeps* in shallow circular plastic trays 10 cm in diameter (approx. 80 ml) and placed the trays in enclosures to permit stabilization of prey populations in the absence of fish predation. Trays that were intended to estimate foraging in vegetated microhabitats were

also supplemented with a patch of algae to more accurately simulate the effects of structural complexity in patch productivity and fish-amphipod relationships. Following incubation of a set of trays in each microhabitat type, we moved the trays into the experimental enclosures ( $31 \times 31 \times 16$  cm, 3.25 mm mesh galvanized hardware cloth on 6 sides) and added 6 *C. acuticeps* with total biomass between 2.3 and 2.8 g, or no fish in the case of control replicates. These enclosures were then placed in the larger,  $61 \times 61 \times 31$  cm enclosures and a single *Leptocottus armatus* (SL > 80 mm) was allowed to occupy the area of the larger enclosure that surrounded the smaller enclosure. Although the density of *C. acuticeps* in the smaller enclosures was substantially greater than that in the growth experiments, we needed to have measurable depletion of prey on a short time scale (1 wk) to minimize the effects of migration, death and recruitment on invertebrate dynamics. We do not know whether the overall fish density in enclosures affects individual *C. acuticeps* behavior, but our design allowed us to examine the invertebrate prey response in a short time-frame without compromising the survivorship of *C. acuticeps* or *L. armatus*. We expected to observe higher total prey consumption (lower GUDs) on trays in vegetated microhabitats, where we assumed that vegetation provided an apparent refuge from predation risk. Because the total number of enclosures was limited, we conducted the experiment in 2 sessions, where each session involved 5 replicates containing *C. acuticeps* and 5 control replicates in each microhabitat for a total of 10 experimental replicates of each microhabitat type.

After 1 wk, 'prey trays' were removed from the enclosures and all of the amphipods remaining on trays were collected, preserved, and sorted by size. Dry biomass of the entire assemblage of invertebrates from each tray was measured to the nearest 0.0001 g using an analytical balance. Individuals of each amphipod species >4 mm were considered too large for consumption by *Clinocottus acuticeps* based on their absence in the gut contents of fish examined prior to this experiment (K.M.A. pers. obs.). We reweighed the smaller amphipods from both microhabitats and compared the biomass of GUDs left by fish foraging on both the complete prey assemblage and on the smaller amphipods, relative to those same groupings on control (fishless) trays, with 2-way ANOVA.

**Algal density and prey consumption with predation risk.** In order to examine the effects of algal density and distribution on the cost of predation, we simulated the estuarine environment in experimental mesocosms that facilitated the control of algal distribution and the number of available prey on small spatial scales. We established experimental arenas in

8 cylindrical fiberglass tanks, 75 cm in diameter, and filled with water at a salinity of 25 ppt, prepared by pumping seawater from Hood Canal (approx. 28 ppt) and diluting it as necessary to reach a total depth of ca. 50 cm. To each tank, we added substrate consistent with that found in the microhabitats where *Clinocottus acuticeps* was distributed, and 4 roughly equal clumps of algae attached to rock. We cleansed the algal clumps of amphipods by rinsing with a mixture of club soda and water, enabling an accurate accounting of amphipods added as potential prey for *C. acuticeps*. We then prepared a 'prey tray' of the same size as those used in the field experiment with substrate from *C. acuticeps*' habitat. We collected amphipods from trays incubated in *C. acuticeps*' habitat and added 20 amphipods of total length between 1 and 3 mm to each experimental 'prey tray'. Roughly 75% of the added amphipods were *Corophium spini-corne* and 25% were *Eogammarus confervicolus*, proportions relatively consistent with their proportions in this region of the estuary (K. M. Polivka unpubl. data).

We captured both *Leptocottus armatus* predators (>80 mm SL) and *Clinocottus acuticeps* (28 to 34 mm SL) 2 d prior to the start of experimental trials at low tides in relatively fresh water, and acclimated them to 25 ppt seawater in captivity using a species and size-specific acclimation regime (*L. armatus*: increase in salinity by 5 ppt every 30 min; *C. acuticeps* increase 5 ppt every 15 min). Predators and *C. acuticeps* occupied separate holding tanks at 25 ppt without feeding until the start of the experiment.

The response variable was the relative prey consumption by *Clinocottus acuticeps* in treatments that varied by the arrangement of algal masses; in a 'clumped' distribution, all 4 masses were arranged in a single patch around the 'prey tray,' whereas in the 'dispersed' distribution, the 'prey tray' was placed in 1 of 2 patches, each including 2 algal masses. Eight control replicates were set up without *C. acuticeps* in order to estimate the baseline mortality of amphipods and/or incidental consumption by *Leptocottus armatus*. Each treatment was replicated 8 times with 5 *C. acuticeps* and one *L. armatus* in each tank. After 2 d, we removed all fish from the tank and recorded the number of amphipods remaining on the trays, algae, and in the substrate.

We defined the total number of amphipods remaining in each tank as the total GUD, and the number of amphipods remaining in the tray or the algae nearest the tray as a partial GUD, which represents *Clinocottus acuticeps*' foraging within the patch we established. We compared partial and total GUDs with a *t*-test. Similarly, we compared the proportion of partial:total GUDs between treatments to examine the effect of amphipod dispersal throughout the tanks in order to confirm the validity of the partial GUD.

## RESULTS

Factors characterizing the distribution of *Clinocottus acuticeps*

*Clinocottus acuticeps* was found most often in areas divided between 0 to 25% and 75 to 100% algal coverage, and least often in areas of 0 to 25% coverage only. While the differences in abundance between varying categories of algal coverage were not statistically significant (1-way ANOVA;  $F_{4,50} = 1.75$ ,  $p = 0.155$ ), *C. acuticeps* was nearly 3 times as abundant in algae (averaging abundance in all categories with 25 to 100% coverage) than in open (0 to 25% coverage alone) microhabitats (Fig. 1;  $t = 2.37$ ,  $df = 54$ ,  $p = 0.022$ ).

*Clinocottus acuticeps* was found at a variety of temperatures, salinities and depths, and there was no significant relationship in its habitat selection based on these factors, nor did any of these physical properties explain a great deal of the variation in fish abundance (temperature:  $R^2 = 0.003$ ,  $N = 50$ ; salinity:  $R^2 = 0.001$ ,  $N = 50$ ; depth:  $R^2 = 0.001$ ,  $N = 51$ ). There was also no significant difference in the abundance of *C. acuticeps* between substrate types ( $F_{2,47} = 2.38$ ,  $p = 0.103$ ).

Growth of *Clinocottus acuticeps* in different microhabitats

Growth of *Clinocottus acuticeps* was significantly greater in vegetated compared with open microhabitats, at 0.62 versus 0.083 mm  $wk^{-1}$  (Fig. 2a, multivariate ANOVA;  $F_{1,13} = 14.5$ ,  $p = 0.002$ ). Similarly, *C. acuticeps*

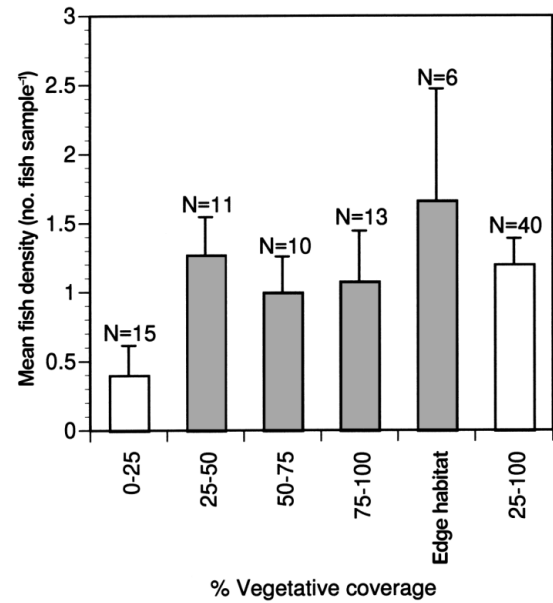


Fig. 1. *Clinocottus acuticeps*. Mean (+SE) density (no. fish sample<sup>-1</sup>) in field surveys in each category of vegetative coverage. Edge habitat is defined as areas of 25 to 100% coverage bordering open areas. One-way ANOVA for all categories:  $F_{4,50} = 1.75$ ,  $p = 0.155$  (shaded bars). Open bars demonstrate significant differences in fish abundance for comparison of sites in algal beds with moderate to heavy coverage with those in areas with little or no coverage ( $t = 2.37$ ,  $df = 54$ ,  $p = 0.022$ )

gained an average of 0.056 g  $wk^{-1}$  in vegetated microhabitats and lost an average of 0.013 g  $wk^{-1}$  in open microhabitats (Fig. 2b, multivariate ANOVA;  $F_{1,13} = 22.8$ ,  $p < 0.001$ ). In several cases, one or both fish from

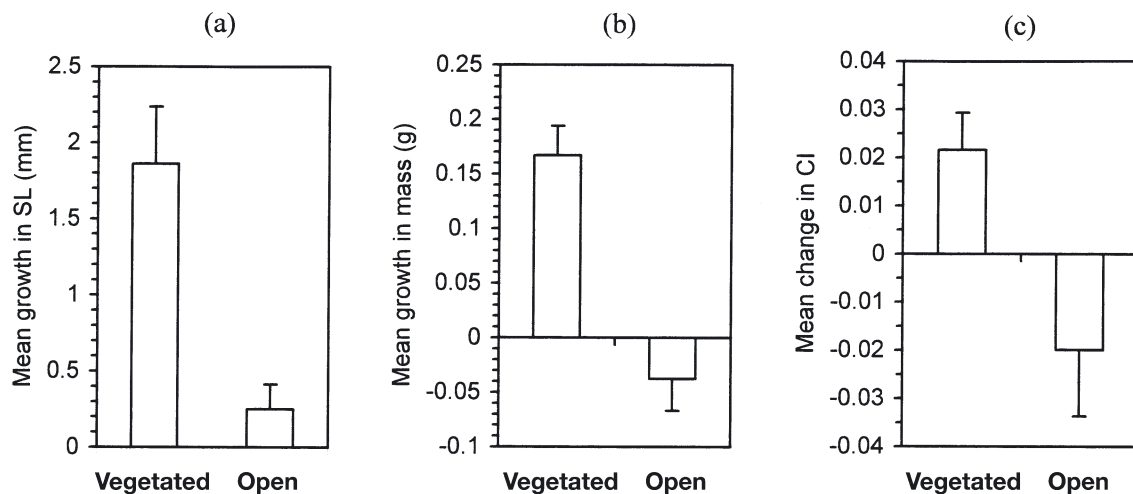


Fig. 2. *Clinocottus acuticeps*. Mean (+SE) total growth over a 3 wk experimental period in terms of (a) standard length (SL) and (b) mass, and (c) change in condition index (CI) in open and vegetated microhabitats. Responses were heterogeneous by multivariate ANOVA (SL:  $F_{1,13} = 14.5$ ,  $p = 0.002$ ; mass:  $F_{1,13} = 22.8$ ,  $p < 0.001$ ; change in CI:  $F_{1,13} = 6.83$ ,  $p = 0.021$ )

a replicate were missing due to small tears in the mesh enclosures. Enclosures with no remaining fish were excluded, and the average growth per cage was calculated for the remaining enclosures. The number of fish remaining in each enclosure did not have a significant effect on growth in SL (multivariate ANOVA;  $F_{1,13} = 1.13$ ,  $p = 0.306$ ) or mass (multivariate ANOVA;  $F_{1,13} = 1.96$ ,  $p = 0.185$ ). Treatment period also showed no significant effect on growth in SL (multivariate ANOVA;  $F_{1,13} = 2.89$ ,  $p = 0.113$ ) or mass (multivariate ANOVA;  $F_{1,13} = 0.018$ ,  $p = 0.895$ ).

Analysis of the final, average-per-cage mass across microhabitats with SL as a covariate suggests that *Clinocottus acuticeps* in vegetated microhabitats have a greater mass at any given length than those in open microhabitats (ANCOVA;  $F_{1,14} = 16.8$ ,  $p = 0.001$ ). The linear relationships between final mass and SL of *C. acuticeps* in each microhabitat type produced parallel slopes (test of parallelism,  $F_{1,13} = 0.541$ ,  $p = 0.475$ ). Thus the exponent in the Fulton CI calculated above ( $-3.71$ ) was justified for fish in both treatments. A second ANCOVA revealed that the effect of experimental period had a marginal effect on the change in CI ( $F_{1,13} = 4.45$ ,  $p = 0.055$ ), whereas number of fish remaining in each enclosure at the end of the period had no significant effect on change in CI ( $F_{1,14} = 1.28$ ,  $p = 0.278$ ). Regardless of the interpretation of the effect of period, change in CI was significantly more positive in vegetated microhabitats (Fig. 2c;  $F_{1,13} = 6.83$ ,  $p = 0.021$ ).

Finally, estimates of performance were consistently less variable in vegetated microhabitats. In all cases (growth in mass and SL and change in CI) the CV was greater in open than in vegetated microhabitats (Table 1). The CV for growth in SL in open microhabitats was more than 3 times that of vegetated microhabitats, while the CV for growth in mass in open microhabitats was almost 5 times that of vegetated microhabitats.

#### Field test of prey consumption in vegetated and unvegetated microhabitats

In the analysis of small size-class invertebrates ( $\leq 4$  mm) we found no significant difference between vegetated and open microhabitats in the density of prey considered consumable by *Clinocottus acuticeps* (Fig. 3, 2-way ANOVA;  $F_{1,36} = 0.091$ ,  $p = 0.765$ ). The exclusion of invertebrates  $>4$  mm is supported by the lack of a significant difference in the dry biomass of large invertebrates removed from control versus experimental samples in both vegetated ( $t = -0.456$ ,  $df = 18$ ,  $p = 0.654$ ) and open microhabitats ( $t = 1.48$ ,  $df = 18$ ,  $p = 0.156$ ). This indicates that larger invertebrates were neither

Table 1. *Clinocottus acuticeps*. Coefficient of variation (CV) for growth in standard length (SL) and mass, and change in Fulton condition index (CI) in experimental enclosures placed in vegetated vs. unvegetated estuarine microhabitats

Habitat	Growth in SL	Growth in mass	Change in CI
Unvegetated	188	227	199
Vegetated	71	53	106

influenced nor eaten by *C. acuticeps*. The 2-way ANOVA of remaining smaller invertebrate biomasses (GUDs) supports the conclusion that the fish were eating a measurable amount through significance in the effect of the presence of fish (Fig. 3,  $F_{1,36} = 6.09$ ,  $p = 0.018$ ). However, this analysis shows no significant interaction of fish and microhabitat effects, meaning that there was no significant difference in feeding among microhabitats (Fig. 3,  $F_{1,36} = 0.625$ ,  $p = 0.435$ ).

#### Algal density and prey consumption with predation risk

The partial GUD, representing *Clinocottus acuticeps*' foraging in a patch composed of the tray and algae nearest the tray, was nearly twice as high in clumped versus dispersed distributions of algae (Fig. 4,  $t = 3.70$ ,  $df = 14$ ,  $p = 0.002$ ). Amphipods dispersed throughout the tank in both treatments, but there was

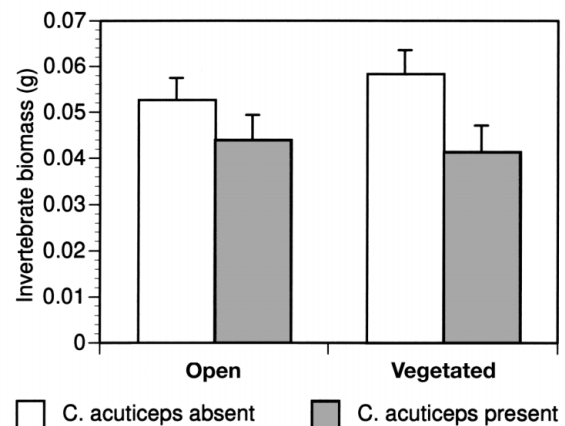


Fig. 3. Mean (+SE) biomass (g) of amphipods ( $\leq 4$  mm) remaining on trays in open and vegetated microhabitats in the presence or absence of *Clinocottus acuticeps* individuals ( $N = 6$ ) under predation risk. Two-way ANOVA was used to identify effects of *C. acuticeps*:  $F_{1,36} = 6.09$ ,  $p = 0.018$ ; algal presence:  $F_{1,36} = 0.091$ ,  $p = 0.765$ ; and fish  $\times$  vegetation:  $F_{1,36} = 0.625$ ,  $p = 0.435$

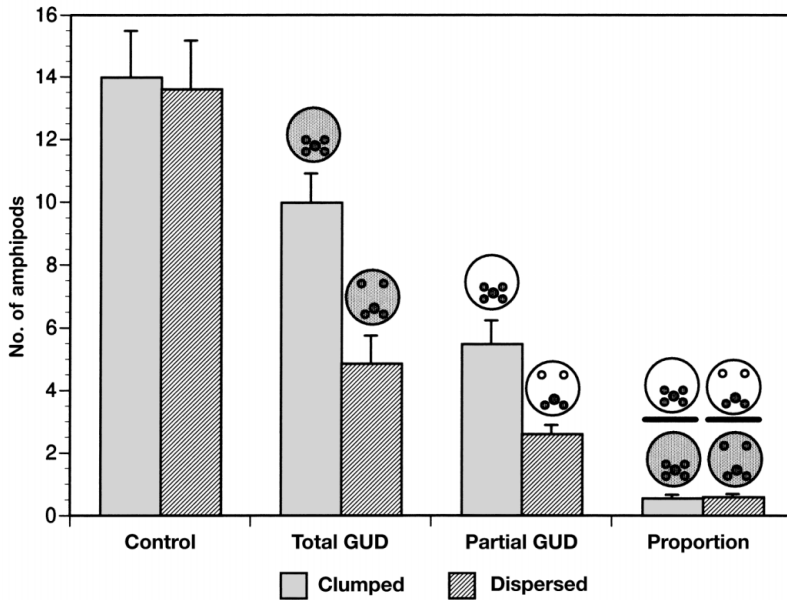


Fig. 4. Mean (+SE) number of amphipods remaining after consumption (GUD) by *Clinocottus acuticeps* ( $N = 5$ ) on trays in experimental mesocosms compared with control trays and for 2 categories of algal dispersal. Trays are represented by circular diagrams, with algal clump configuration indicated by open dots and foraging patch represented by closed dots. Total GUD ( $t = 4.07$ ,  $df = 14$ ,  $p = 0.001$ ; shaded diagrams) and partial GUD ( $t = 3.70$ ,  $df = 14$ ,  $p = 0.002$ ; white diagrams; calculations described in 'Materials and methods') differed significantly for clumped versus dispersed algal treatments, but the proportion of amphipods remaining on the tray or in algae nearest the tray did not ( $t = -0.035$ ,  $df = 14$ ,  $p = 0.730$ )

no significant difference between treatments in the proportion of remaining amphipods that were found in the tray or in the algae nearest to the tray (Fig. 4,  $t = -0.035$ ,  $df = 14$ ,  $p = 0.730$ ). This suggests that amphipods dispersed throughout the tank in equal proportions for each treatment, and that differences in a partial GUD accurately reflect significant differences in feeding efficiency and not differences in amphipod dispersal.

At the end of the foraging period, 4 *Clinocottus acuticeps* were missing from tanks with dispersed algae, with 2 of those being from a single tank, while all *C. acuticeps* were present in clumped algae treatments. These *C. acuticeps* were presumably eaten by *L. armatus* although we did not sacrifice the predators to confirm this. A  $t$ -test of the number of *C. acuticeps* remaining in each replicate, equivalent to the GUD or predatory efficiency for *L. armatus*, did not show a significant difference between treatments ( $t = 1.87$ ,  $df = 14$ ,  $p = 0.082$ ). However, the power associated with this comparison is only 0.38, assuming that the observed effect size is true; therefore the probability of a Type II error is 0.62. Thus, a more powerful test of the effect of algal density on the susceptibility of *C. acuticeps* to predation would require increased replication and encounters with *L. armatus*.

## DISCUSSION

Highly productive habitats such as estuaries may offer fitness-enhancing foraging opportunities, but often at the cost of increased exposure to predators (Lima & Dill 1990). We attempted to match distributional patterns in the abundance of *Clinocottus acuticeps* with important correlates of fitness such as growth, condition and predator-sensitive foraging behavior. The distribution of this species is consistent with a preference for algal cover, apparently because these microhabitats provide fish with both food and refuge. We hypothesized that this distribution was driven by predation risk which has been shown to partially influence habitat selection and foraging in other species in this study system (K. M. Polivka unpubl.). We expected that predation risk would reduce food intake and growth rate (Lima & Dill 1990, Peckarsky 1993, Werner & Anholt 1993, Anholt & Werner 1995, 1998, and reviewed in Gotthard 2000). Sublethal effects of predators can reduce fitness, despite the lack of mortality (reviewed by Peckarsky 1993), and are particularly important in aquatic systems that often include organisms with indeterminate growth and complex life cycles (Dill 1987).

In our system, growth and foraging were not congruent between microhabitats. Growth and condition index improved in enclosures that simulated vegetated microhabitats (Fig. 2), which may allow *Clinocottus acuticeps* to maximize fitness through increased survival and fecundity, as has been previously shown for other fish foraging in submerged vegetation (e.g. Crowder & Cooper 1982, Grand & Dill 1997, Rozas & Odum 1988, but see Sogard 1992). However, overall prey availability and consumption did not differ between microhabitats, although we expected lower GUDs in areas with algae (Fig. 3). Ordinarily, increased growth within vegetated microhabitats suggests an increase in foraging efficiency which, in turn, is expected with higher densities of prey and/or lower foraging costs due to less difficult extraction of prey from algae than open sediment (Mittelbach 1981). The sparse structure of open habitats may provide more efficient foraging, whereas vegetation may introduce structural complexity and make foraging more difficult (Crowder & Cooper 1982). It may not be possible to detect differences in prey consumption across a range

of algal densities, but such a study might enable us to more accurately assess the ways in which the cover present in algal microhabitats interacts with predation risk to determine foraging effort in this study system.

Possible explanations for our results, which are not mutually exclusive, include: (1) Prey consumption is equal among both microhabitat types, but predation risk induces different growth patterns as a result of stress. (2) *Clinocottus acuticeps* uses a 'risk-reckless' foraging strategy, either due to the inability to detect predation risk or a lack of response. The results from our mesocosm experiment support this alternative. (3) Microhabitats that offer safety in addition to food facilitate reduced variability in fish condition, which increases the average fitness among individuals in the population.

Given that *Clinocottus acuticeps* does not change its apparent foraging effort but experiences decreased growth and condition in open microhabitats, we expect that other predator-induced stress (e.g. energy allocated to other predation-avoidance behaviors) might interact with resource productivity. The presence of a predator has been shown to reduce the growth rate of damselflies through stress effects, without reducing food uptake, which may lower assimilation efficiency and/or increase metabolic rate (Stoks 2001) and differences among 2 damselfly genera in this stress response might facilitate coexistence (McPeck et al. 2001).

Our mesocosm experiments, in which we estimated the GUDs of *Clinocottus acuticeps* under predation risk and with varying distributions of algae, supported the relatively rare 'risk-reckless' foraging strategy (Fraser & Huntingford 1986; Fig. 4). Initially, the lower GUDs of *C. acuticeps* suggested higher foraging efficiency in algae with a dispersed distribution, which could be attributed to lower foraging costs resulting from easier prey detection or extraction. Indeed, some fish show faster growth and higher prey consumption at intermediate macrophyte densities in habitats where dense structure inhibits foraging but holds highly profitable prey, whereas sparse structure allows efficient foraging but yields few profitable prey (Crowder & Cooper 1982). Alternatively, our results may demonstrate that the predation risk associated with moving to another available patch may increase the total foraging costs, and thus require a much higher harvest rate from the new patch. If the current patch has features that reduce foraging costs (i.e. predation risk), foragers will remain in that patch longer and we would expect to observe lower GUDs. Patch residence times may be a function of several variables, including patch productivity, the number of individuals foraging at the patch, and the search time to find new patches (Giraldeau & Caraco 2000). Although we did not document patch residence times directly, we did observe a

trend toward increased risk of predation mortality in the tanks with dispersed algae distributions, indicating that costs would be reduced by longer residence times. However, lack of statistical power made conclusions about *C. acuticeps*' survivorship in dispersed algal distributions ambiguous.

Whereas our experimental design made it difficult to distinguish among different hypotheses, our results were consistent with field experiments. When the partial GUDs are compared to the density of algae nearest the prey tray, the density of remaining prey over algae was nearly equal in both clumped and dispersed algal configurations. That is, in the dispersed treatment, half as many amphipods remained within an algae patch that was half the volume of the clumped patch (consisting of 2 rather than 4 bunches of algae nearest the prey tray). When we consider that this patch was harvested to approximately the same density of prey over algae in each treatment, we conclude that prey consumption was similar in each treatment, regardless of the risk that might be associated with lower densities of algae. This result is consistent with that of the field GUD experiment, suggesting that *Clinocottus acuticeps* may not lower its apparent foraging effort when faced with the risk of predation. Such a 'risk-reckless' strategy conflicts with the expectation that an individual will minimize risk by lowering activity when faced with the trade-off between food and safety, but may allow *C. acuticeps* to obtain prey resources when algal densities vary in time. Estuarine algae such as *Enteromorpha* appear to show large, rapid fluctuations in density in estuarine systems, depending on the level of freshwater input and its associated nutrient ratios and effects on salinity (Martins et al. 2001). In our study system, we observed sparse coverage in the spring, with rapid growth to dense coverage in mid-summer, then thinning again by early autumn.

One possible explanation for a 'risk reckless' foraging strategy involves theoretical predictions about how individual condition affects the amount of risk a foraging animal might be expected to take in a heterogeneous landscape (Mangel & Clark 1988, McNamara & Houston 1990, Houston et al. 1993). The patterns of variation in growth and condition observed in *Clinocottus acuticeps* between microhabitats suggest that the availability of some protection from predation risk in vegetated habitats reduces variability in these parameters, though the mechanism is unclear. According to the 'asset-protection principle' (Clark 1994), individuals in poor or highly variable states have lower reproductive values and are therefore more likely to accept a greater level of risk, whereas individuals in better condition might take fewer risks in order to 'protect' future reproductive opportunities (Clark 1994). A strong trade-off between food and safety or other com-



plementary resources can result in narrower regulation of individual condition and, ultimately, higher fitness (Rapport 1980, Sirot & Bernstein 1996, but see Bernays & Minkenberg 1997). Individual *C. acuticeps* in vegetated microhabitats demonstrated both higher CIs (Fig. 2) and lower variation in condition (Table 1). This suggests that, in vegetated microhabitats, a complementary relationship between prey and refuge led to lower variation in the condition of individuals by decreasing susceptibility to predation and dependence on the variability of food resources alone. Prey availability was similar between microhabitats, so the structural advantage of vegetation likely complements food resources to facilitate the maintenance of a narrower range of growth and condition. This mechanism warrants testing to determine whether individuals move into open habitats when prey or algal densities fluctuate, reducing condition and necessitating greater risk taking (Clark 1994). At the population level and on longer time scales, higher variation in condition can be corrected, as those individuals that take more risks ultimately succumb to predators (Sinclair & Arcese 1995). Our mesocosm experiment was of short duration and the individuals caught by *L. armatus* were not likely to be in poorer condition than the others, because starting condition and pre-experimental starvation regimes were controlled as much as possible. Finally, behavioral decisions influenced by the 'asset-protection principle' may depend upon the effects of environmental parameters and correlated life-history traits on condition (e.g. Reinhardt & Healey 1999).

Algal beds in the intertidal zone of estuarine habitats offer species such as *Clinocottus acuticeps* the opportunity to maximize fitness through growth, and appear to offer some protection from predation. Brown (1999) suggests that patch choice most often necessitates a trade-off between feeding rate and predation risk. GUDs suggest that in riskier open habitats, *C. acuticeps* does not lower activity levels, or change food intake in the face of increased predation risk, thus utilizing a risk-reckless strategy (Fraser & Huntingford 1986). Regardless of the mechanism that resulted in the lack of a difference in foraging activity, clearly there are some fitness-related benefits to selection of algal microhabitats in the intertidal ecology of this species. Our results warrant further investigation of the effects of condition variability on foraging behavior in this and other estuarine species (Polivka 2002), to determine the implications of risk-reckless foraging strategies, and identify those that are more predation-sensitive for overall community and food-web dynamics.

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