NOTES

Relative Roles of Food Abundance and Cover in Determining the Habitat Distribution of Stream-Dwelling Cutthroat Trout (*Salmo clarki*)[1]

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Emigration of wild cutthroat trout (*Salmo clarki*) from laboratory channels over 1-wk trial periods was greater under conditions of low than high food abundance (5 vs. 15% of total trout biomass daily), irrespective of the amount of cover (simulated cover structures added vs. removed). When food abundance was high, emigration of trout was slightly greater under conditions of low than high cover. Cover had no effect on emigration rate when food abundance was low. Trout occurred in association with cover structures when food abundance was high, but not when food abundance was low. These experiments suggest that at summer temperatures, food abundance overrides cover in determining the abundance and microhabitat distribution of adult cutthroat trout within a stream.

L'émigration de la truite fardée (*Salmo clarki*) sauvage de bassins expérimentaux au cours d'expériences d'une semaine était plus élevée dans des conditions de faibles concentrations de nourriture qu'en présence de fortes concentrations (5 vs 15 % de la biomasse totale de truites quotidiennement), indépendamment de la quantité d'abri (couverture simulée ajoutée vs enlevée). Quand la quantité de nourriture était élevée, l'émigration des truites était légèrement plus élevée dans des conditions de faible couverture qu'en présence d'une couverture élevée. Par contre, la couverture n'avait aucune incidence sur le taux d'émigration quand la quantité de nourriture était faible. La truite était présente sous les abris quand la quantité de nourriture était élevée, mais non quand celle-ci était faible. Ces expériences portent à croire qu'aux températures estivales, la quantité de nourriture a plus d'importance que la couverture dans la détermination du nombre de truites fardées adultes présentes dans un cours d'eau et de leur répartition dans les micro-habitats.

Habitat features, including overhead shading and substrate complexity or associated crevices, have been demonstrated to reduce foraging efficiency of stream fishes, presumably by impairing detection of prey (Ware 1973; Wilzbach and Hall 1985). However, because these features also provide shelter from predation and/or physical disturbances, a trade-off may exist between potential benefits of cover and the cost in reduced foraging gain. Experimental elimination of substrate crevices, for example, increased foraging efficiency of cutthroat trout (*Salmo clarki*) relative to that found for trout in control pools, but probably resulted in an increased mortality (Wilzbach 1984). Dill (1983) reviewed considerable empirical evidence suggesting that fish may be able to adjust habitat use and foraging behavior so as to adaptively balance risks and rewards.

Difficulties in incorporating predation risk into models of foraging behavior or habitat use arise because the units of measurement (i.e. risk of mortality vs. energy or nutritional gain) are not comparable, and Dill (1983) has proposed that one possible solution may lie in observation of fish response to a variety of risk/reward combinations. The choices made by the fish provide a biologically relevant basis for weighting the two factors. In a recent experimental test that followed this approach, Werner et al. (1983) demonstrated that, in the presence of a predator (largemouth bass, *Micropterus salmoides*), small bluegill (*Lepomis macrochirus*) in artificial ponds grew more slowly and restricted their habitat use to areas of low foraging profitability.

Research findings that cutthroat trout are more numerous in cover-poor, logged streams of the Oregon Cascades than in forested streams with abundant cover (Aho 1977; Murphy and Hall 1981; Murphy et al. 1981; Hawkins et al. 1983), and that

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prey availability and foraging efficiency of the trout are likewise greater in logged streams (Wilzbach and Hall 1985), suggest that cover may be less important than prey abundance in determining habitat choice in these systems. The intensity of predation on the trout is not known, but from the documented loss of experimentally confined trout in several pools and the finding of a trout corpse that had evidently been killed by a predator (Wilzbach 1984), and from sightings of avian, reptilian, and mammalian predators at several study sites, at least some risk of predation may be inferred. In this study, to evaluate the relative contribution of food abundance and of cover in determining habitat distribution of cutthroat trout, I examined microhabitat use and emigration of wild cutthroat trout from laboratory channels under varying conditions of food abundance and cover.

Methods

The experiment was conducted in June and July 1984 in recirculating stream channels designed and constructed by Reeves et al. (1983). The channels were oval-shaped, approximately 18 m in total length, and had a water capacity of 5.9 m³. A 3-m section of each channel that contained a paddle wheel and heating and cooling elements was separated from the experimental area with screening. Escape traps were positioned at these upstream and downstream boundaries. The experimental portion of each channel consisted of an alternating series of riffles and pools, with water velocities ranging from 0 to 10 cm/s. The channel bottom was covered with sand and gravel in the pools, and with small rock (5–8 cm) in the riffles. Water temperature was maintained at 11°C throughout the experiment. The photoperiod was set for a 12-h day.

In trials of 1 wk duration, 10 adult cutthroat trout, ranging in size from 10 to 15 cm, were introduced into a channel. Wild trout were obtained from a resident (nonanadromous) population in Grasshopper Creek (Lane County, Oregon) with a barbless hook and line. The trout were obtained from the same stream in which previous studies of habitat influence on foraging efficiency and growth of the trout were conducted (Wilzbach and Hall 1985; Wilzbach 1984). Experimental fish were measured to the nearest millimetre, weighed to the nearest 0.1 g, and photographed for later identification (Bachman 1984). To acclimate the trout to the water supply and to allow time for recovery from handling stress, they were placed in a holding tank maintained at stream temperature for 48 h prior to introduction to the channel.

Treatment 1 consisted of high food (15% of the total trout biomass daily) and high cover. Fish were fed frozen brine shrimp (Artemia spp.) at dawn, noon, and dusk from a food delivery system that simulated natural drift by introducing the food from numerous ports along the entire length of the channel bottom (Reeves et al. 1983). Cover consisted of simulated undercut banks formed by wood shelters and large crevices formed by arrangements of bricks. Cover structures were added only to the upstream half of the channel to provide the trout with a choice in the use of cover. Differences in water velocity between sections of the channel with and without cover structures were insignificant.

Treatment 2 consisted of high food and low cover (no cover structures). Treatment 3 consisted of low food (5% of the total trout biomass daily) and high cover. From pilot experiments, this food level was sufficient to maintain short-term survival but not provide for growth. Treatment 4 consisted of low food and low cover.
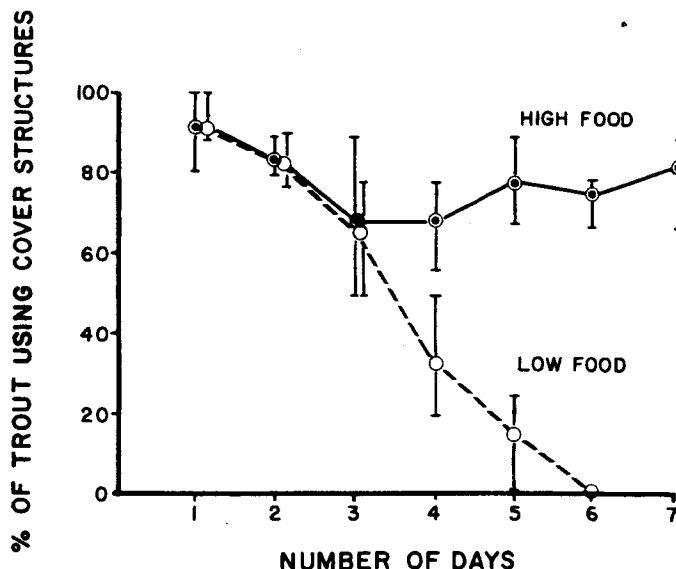
FIG. 1. Percentage of trout present in a channel on a given day that were using cover under conditions of high and low food abundance. Vertical bars represent range of values; n = 6 observations.

All treatments were repeated once. To simulate a predation risk and reinforce the use of cover, a battery-powered toy "scuba diver," 200 mm long, was made to swim through each channel at varying times each day. Although not in the legion of predators naturally encountered by the trout, the toy scuba diver effectively frightened the fish throughout the duration of the trial.

Trout use of microhabitat was monitored throughout each trial prior to feeding periods. Trout were observed from the center viewing area of the channels through openings in suspended black plastic curtains that covered the glass channel sides and allowed viewing of the fish without disturbing them (Reeves et al. 1983). Individual trout were identified from photographs by comparison of the lengths and spotting pattern on the body. The tops of the channels were covered with plastic sheets to prevent fish from jumping out. Escape traps were checked three times daily. Emigrants were measured, weighed, and removed from the channels.

Results and Discussion

At high food levels, trout showed strong preferences for cover structures. Little change in this preference occurred between the beginning and end of the trials (Fig. 1). Habitat distribution of the trout did not differ by time of day ($p > 0.10$, Kruskal–Wallis). Fausch (1984) found that trout fry chose cover sites that maximized potential energy gain in a stream aquarium in which predators were absent. In this study, use of cover by trout was likely related only to protection, as differences in water velocity and in prey availability between channel sections with and without cover structures were insignificant.

When food abundance was low, however, use of cover by trout steadily declined (Fig. 1). The percentages of trout that occurred in association with cover differed significantly between high and low food treatments ($p < 0.01$, Kolmogorov–Smirnov). The failure of trout to remain associated with cover structures when food abundance was low is consistent with the finding that, in the cover-rich, forested section of Grasshopper Creek, which has a low abundance of prey (Wilzbach 1984), no relationship existed between numbers of trout inhabiting a pool
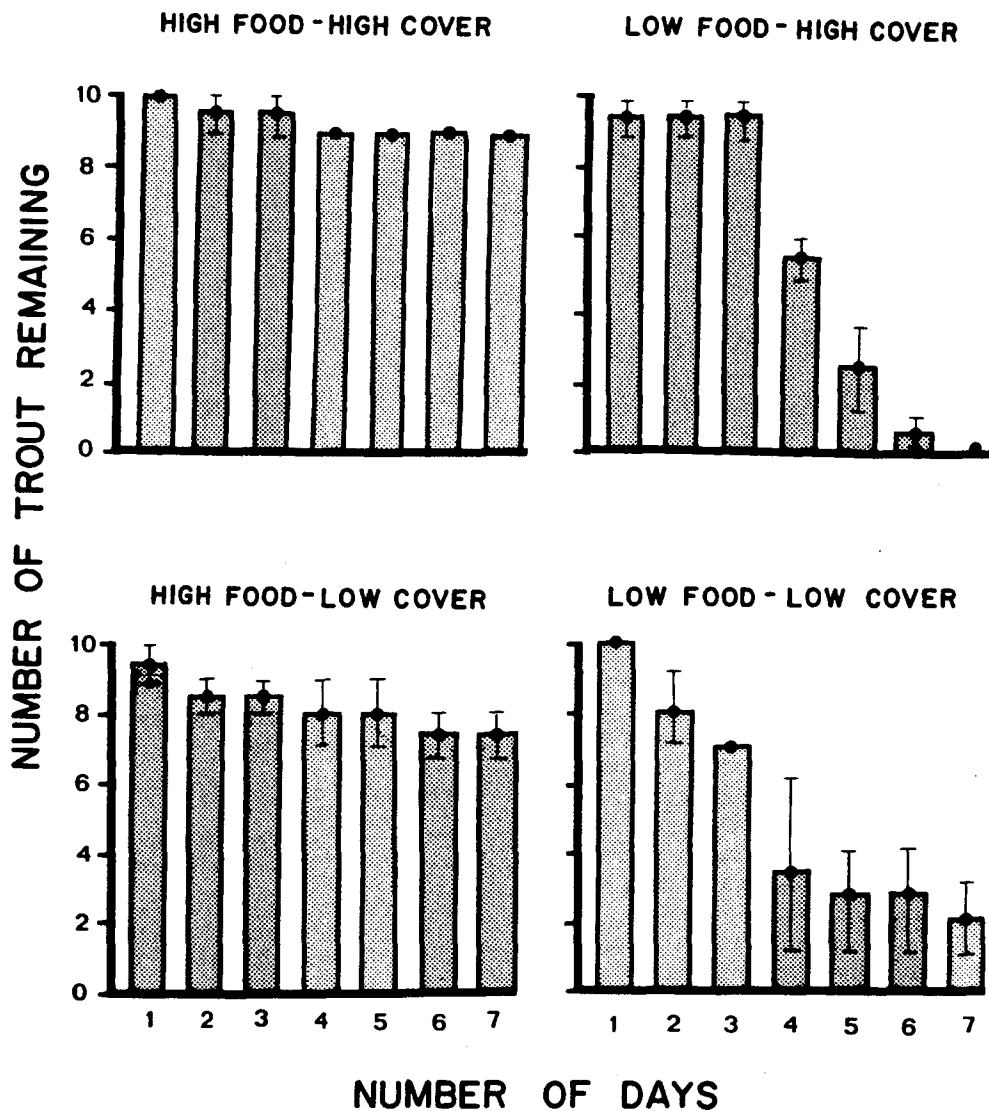
FIG. 2. Mean number of cutthroat trout remaining in channels on each day of a trial under different combinations of food abundance and cover. Vertical bars indicate range of values. All treatments were repeated once.

(1–18 trout per pool in 52 pools) and a qualitative ranking of cover (cumulative sum of a ranking from 0 to 3 of each of seven cover features) ($p > 0.05$, Kendall's rank correlation; unpubl. data).

In treatments lacking cover, cutthroat trout were dispersed throughout the channels, and individual trout changed locations frequently. Differences in the percentage of trout that were positioned in the upstream half of each channel were not significant between high and low food treatments ($p > 0.10$, Kolmogorov–Smirnov).

The numbers of trout remaining in a channel over the 1-wk trial period (Fig. 2) differed significantly between levels of high and low food abundance ($p < 0.01$, Kolmogorov–Smirnov) but not between amount of cover ($p > 0.05$). Classifications by food abundance and cover were associated ($p < 0.01$, 2 × 2 contingency table). When food abundance was low, however, the number of trout remaining in a channel at the end of a trial was slightly, but significantly, greater under conditions of high than low cover. When food abundance was low, however, the number of trout remaining did not significantly differ between

high and low cover. There was little variation between replicates within a treatment. Although decreased emigration of salmonids at high levels of food abundance has been established in previous studies (Symons 1971; Slaney and Northcote 1974; Mason 1976), the influence of a food–cover interaction on emigration has not been reported. Slaney and Northcote (1974) found that, compared with a situation in which trout fry were initially introduced to different food levels, emigration was not as rapid when prey level was reduced from an original level. Data from this study suggest the involvement of a fixed response pattern of trout to changing food availability that consists of use of cover at high food, followed by first movement out of cover, and then emigration at low food.

In all trials, at least one trout emigrated from the channel, suggesting that initial densities exceeded the carrying capacity. Stocking densities (approximately 3.4 trout/m^3 of pool), however, were slightly below densities of trout that were observed in the field (3.7 trout/m^2 in pool in the logged section of Grasshopper Creek). The majority (over 70%) of trout that emigrated from the laboratory channels exited into the downstream traps.

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TABLE 1. Weight change ± SD of cutthroat trout that emigrated from channels after 1–6 d and that remained in the channels throughout a 7-d trial. Weight change was measured as final minus initial weight, divided by initial weight, times 100.

No. of days	Weight change ± SD (% body weight)	n
1	−2.43±1.18	9
2	−5.50±3.00[a]	2
3	−5.57±2.50	17
4	−5.33±1.51	8
5	−5.20±3.19	5
6	−4.00±2.00[a]	2
7		
Low food	−2.50±2.38	4
High food	+2.94±4.14	33

[a]Range.

Displaced cutthroat trout may in general be more likely to attempt to relocate down rather than upstream because energy costs should be much less.

When provided with a high ration of food, the relative growth rate of trout was greater, but not significantly, in channels with high relative to low cover. However, when provided with a low ration of food, trout tended to lose a relatively greater amount of their body weight in channels with high cover. This may result from a decreased foraging efficiency associated with abundant cover (Wilzbach 1984), or from behavioral deterrents toward feeding in complex habitats (Glass 1971; Savino and Stein 1982). Overall, growth rates of the trout differed significantly between treatments that provided high and low food abundance ($p < 0.01$, Mann–Whitney), indicating that the differences in food rations were biologically meaningful to the trout. The relative growth rate ± SD of cutthroat trout remaining in channels at least 3 d is given below (sample size indicated in parentheses). Relative growth rate (final minus initial weight divided by mean weight, divided by number of days, times 100) is expressed as percent body weight per day:

	High food	Low food
High cover	0.39±0.41 (19)	−1.53±1.06 (19)
Low cover	0.24±0.34 (16)	−1.13±1.15 (14)

Trout emigrated from channels when weight loss approached a fairly narrow band of 2.5–5% of the body weight (Table 1). Trout that emigrated on the first day may have left the channels for reasons unrelated to food abundance (e.g. stress related to changed surroundings), and showed approximately the same weight loss as trout remaining in the channels after 7 d under low food abundance. Trout remaining in the channels after 7 d under conditions of high food abundance gained weight.

Previous studies that reported an increase in salmonid abundance when cover was increased (e.g. Hunt 1976) and a decline in abundance when cover was reduced (e.g. Boussu 1954) evidence the importance of cover (Reiser and Bjornn 1979). Food–cover relationships, however, are complex, and varying requirements of salmonids with species (e.g. Hanson 1977), size of fish (e.g. McCrimmon 1954; Chapman and Bjornn 1969), and season (e.g. Bustard and Narver 1975) may reflect,

in part, site-specific differences in disturbance regime, predation intensity, and prey availability. Results of this study corroborate field data suggesting that prey availability is relatively more important than cover in determining distribution and abundance of adult cutthroat trout at summer temperatures in the Oregon Cascades. Assuming that predation poses at least some risk of mortality to trout and that the amount of cover present affects predation risk, one implication is that the habitat response of trout to recent, man-made disturbances may be nonadaptive. Alternatively, trout populations in cover-poor and cover-rich streams may simply adopt different strategies for dealing with environmental uncertainty. Longer term studies, encompassing estimates of reproduction through several year classes, are necessary to determine which alternative may apply.

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Quadratic Discriminant Analysis with Covariance for Stock Delineation and Population Differentiation: A Study of Beaked Redfishes (*Sebastes mentella* and *S. fasciatus*)

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Stock delineation is of vital importance in fisheries management programs. Linear discriminant function (LDF) has been employed extensively in population differentiation studies but is of severely restricted usefulness when populations differ in their dispersion matrices. Quadratic discriminant function (QDF) is the appropriate analysis to employ in these situations. Here, I analyzed morphometric data of beaked redfishes (*Sebastes mentella* and *S. fasciatus*) by a recently developed conditional QDF.

L'identification des stocks revêt une importance vitale pour les programmes de gestion halieutique. Les études d'identification de populations font souvent appel à une fonction discriminante linéaire, mais l'utilité de cette dernière est grandement restreinte quand les matrices de dispersion des populations varient. Dans ces cas, l'analyse appropriée à utiliser est une fonction discriminante quadratique. L'auteur analyse des données morphométriques sur le sébaste (*Sebastes mentella* et *S. fasciatus*) à l'aide d'une fonction discriminante quadratique conditionnelle récemment mise au point.

Stock delineation is of vital importance in fisheries management programs. Effective management of a species depends on the reliability of our knowledge of distribution and biological characteristics of individual stocks. The distinction between deepwater redfish (*Sebastes mentella*) and Labrador redfish (*S. fasciatus*), although vital for the effective management of redfish resources in the Northwest Atlantic, has been less than clear for decades (Misra and Ni 1983; Ni 1981a, 1981b). Macdonald and Pitcher (1979) developed a method of analyzing distribution mixtures, at the univariate level, and applied it to estimate age-group parameters from size–frequency data. Morphometric measurements have frequently been used to differentiate populations in general (see e.g. Blackith and Reyment 1971; Ihssen et al. 1981; Misra and Ni 1983) and stocks of fish in particular (see e.g. Almeida 1982; Casselman et al. 1981; Davidson et al. 1982; Ihssen et al. 1981; Sharp et al. 1978). In a stock discrimination analysis of capelin in the Gulf of St. Lawrence, Sharp et al. (1978) noted that morphometrics offered greater potential in separating capelin (*Mallotus villosus*) stocks than meristics.

Fisher's discriminant function has been employed extensively, by the most conservative standards, in behavioral, biological, business, fisheries, medical, and social research (Goldstein and Dillon 1978). "Even when two similar species can be identified with a single measurement, a combined criterion of two or more may increase the separation between them" (Bliss 1970). The

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