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Diel Food Selection by Two Sizes of Rainbow Trout (*Salmo gairdneri*) in an Experimental Stream

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The food selected by small (~3 g) and large (~45 g) hatchery rainbow trout (*Salmo gairdneri*), studied over a 28-h period, showed that the fish fed selectively, but often on different prey organisms. Feeding activity was highest during daylight hours but was only loosely associated with increases in invertebrate drift density. The majority of large trout exploited adult chironomids on the surface, whereas small trout fed primarily on midwater drift. At night when drift densities were low the limited feeding that took place apparently shifted to bottom foraging. Prey size was the most important factor affecting vulnerability to predation at all hours. Both large and small fish rarely consumed invertebrates <2 mm long. Selection of larger individuals among certain prey taxa occurred, and in two important groups (Trichoptera and Chironomidae) large trout ate significantly larger prey than did small trout. By being size selective, the trout lost the opportunity to exploit smaller organisms, particularly Collembola, which constituted the bulk of the total drift.

Key words: diel habits, drift, predation, rainbow trout, size selection

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Les habitudes alimentaires de petites (~3 g) et de grandes (~45 g) truites arc-en-ciel (*Salmo gairdneri*) de pisciculture ont été étudiées sur une période de 28 h. Les truites des deux tailles exercent un choix dans leur nourriture et on observe une grande variation dans la sélection des proies parmi les membres de chaque groupe. L'alimentation se poursuit plus activement pendant les heures de clarté, mais elle n'est que vaguement associée à des augmentations de densité des invertébrés en dérive. La plupart des grandes truites se nourrissent de chironomidés adultes à la surface, alors que les petites truites se nourrissent surtout d'organismes dérivant entre deux eaux. La nuit, quand la densité des organismes dérivants est faible, le peu d'alimentation qui se produit consiste à fourrager sur le fond. A toute heure, la taille des proies est le facteur qui influe le plus sur la vulnérabilité à la prédation. Les grandes truites, tout comme les petites, consomment rarement des invertébrés de longueur <2 mm. Il se fait un choix de grands individus parmi certains taxons de proies, et dans deux groupes importants (Tricoptera et Chironomidae), les grandes truites mangent un nombre nettement supérieur de grosses proies que ne le font les petites truites. En exerçant un choix de taille, les truites ne profitent pas de l'occasion d'utiliser les petits organismes, en particulier Collembola, qui constituent la majeure partie de la dérive totale.

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STREAM-DWELLING salmonid fishes are believed to feed selectively (Allen 1941; Hynes 1970; Waters 1972), but the basis of selection is not well understood. Studies of lake-dwelling salmonids, which actively search for food, have shown prey size, visibility, and relative abundance to be important factors influencing predation intensity on different prey species. In streams, however, where trout often adopt stationary territories and intercept prey passing downstream in the drift, the determinants of diet and the relationship between food availability and feeding activity remain controversial.

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Maciolek and Needham (1952), Elliot (1967, 1970), and Metz (1974) showed increased feeding rates to be associated with increased invertebrate drift, while Chaston (1969), Tusa (1969), Mundie (1969, 1971), and Bisson (1976) found that a poor correlation often existed between the abundance of potential prey organisms and their utilization by drift feeders. Further, the relative importance of drift feeding and bottom foraging varies greatly among different populations, seasonally and with time of day (Allen 1969) as well as age of fish (Waters 1972). The existence of food selection has been questioned by Egglishaw (1967), who suggested that instances of apparent selectivity may be governed by the type of habitat in which fish feed and by the localized distributions of benthic organisms.

In early spring 1976 I studied the changes in diel food selection by two sizes of rainbow trout (*Salmo gairdneri*) in a spring-fed experimental stream. The objectives of the experiment were to establish whether or not the trout were feeding selectively from available food organisms, and to trace patterns in feeding activity as related to food abundance over a diel cycle.

Materials and Methods

The study was conducted in a single riffle-pool unit of an experimental stream channel located near the Kalama River in southwestern Washington. Surface areas of the riffle and pool were 13.0 and 3.7 m^2, respectively. Flow was 1.5 $m^3 \cdot min^{-1}$ and velocity over the riffle was 54 $cm \cdot s^{-1}$. Water temperature remained at 6°C throughout the diel cycle.

The experiment began at 0800 on 11 March 1976 and ended at 1200 on the following day. Sunset occurred at 1801 and sunrise was at 0620. Light levels exceeded 16 000 lx around midday and dropped below 0.1 lx at night. The stream water was very clear (<0.2 FTU) and visual detection of prey by trout during daylight was hindered neither by low light levels nor by excessive turbidity.

Rainbow trout were obtained from a commercial trout farm; the mean wet weight of "large" fish was 45.40 g (SD = 10.67) and the mean wet weight of "small" fish was 2.82 g(SD = 0.66). All fish were acclimated to the experimental stream for 1 mo prior to the study. They appeared to be well adapted to the stream and to exhibit high growth rates during their preliminary residence. Two days before the experiment the trout were removed from the stream and placed in holding tanks where they were deprived of food. At 6°C this time was sufficient for nearly complete gastric evacuation (Windell et al. 1976). During the experiment five individuals of each size were placed in the stream and allowed to feed for 4 h; they were then collected by electrofishing and replaced with 10 new, unfed fish. Immediately after recovery each trout was anesthetized and its stomach thoroughly flushed with water injected through the mouth with a blunted hypodermic needle. The stomach contents of each fish were retained separately. With the exception of turbellarians and oligochaetes, food organisms were usually intact and in excellent condition. The trout were weighed immediately following removal of stomach contents.

Drift samples were taken for 5 min at hourly intervals within each feeding period. The 210-μm mesh nylon drift net spanned the width of the stream at the downstream end of the riffle and extended several centimetres above the water to capture winged adults and terrestrial organisms floating on the surface. At the end of a 4-h feeding period, drift samples were combined to give an average estimate of the abundance of drifting invertebrates. All samples were sorted manually under magnification and lengths of specimens were determined to the nearest 0.5 mm. Biomasses of various taxa were computed with the aid of known length–weight relationships (R. N. Thut unpublished data) and results of drift sampling were expressed as drift densities (micrograms dry weight per cubic metre) passing the downstream end of the riffle and entering the pool in which most of the trout resided.

TABLE 1. Diel variation in invertebrate drift density and trout feeding intensity, which was calculated according to the formula of Manzer (1976), where feeding intensity = (total food weight ÷ estimated body dry weight) × 100.

Time interval	Drift density $\mu g \cdot m^{-3}$	Mean feeding intensity	
		Small trout	Large trout
0800–1200	12570	0.79	0.39
1200–1600	15096	0.72	0.19
1600–2000	3557	0.59	0.06
2000–2400	3027	0.21	0.04
2400–0400	7434	0.12	0.02
0400–0800	4751	0.37	0.13
0800–1200	14040	0.25	0.24

Results

The density of drifting invertebrates varied widely over the day and night (Table 1). In contrast to many natural streams, total drift density in the experimental stream was much higher at midday than it was at dusk, night, or dawn. It was not surprising, therefore, to find that trout feeding activity was highest during the day (Table 1), although the correlation between feeding intensity and drift density was not significant ($r = +0.54$ for large fish and $+0.17$ for small fish). One reason for the poor correlation was that proportionately more feeding relative to drift density took place at dusk and dawn, particularly among small trout. A second reason was that the abundance of certain preferred food organisms in the drift did not always follow the pattern of total density over the diel cycle.

Frequencies of various invertebrate taxa in trout stomachs, when compared with frequencies of those taxa in the drift (Table 2), indicated that both sizes of trout fed selectively. In general, individuals tended to favor only a few taxa during a 4-h interval. Considerable differences existed not only between large and small trout, but also between the food habits of fish within size-groups — a factor that made generalization difficult.

Collembola (mostly *Isotoma subaequalis*) and Chironomidae dominated the midday drift (0800–1600); all other taxa made up only 7% by weight of the total drift density. Very few Collembola were eaten by small and large trout, which instead relied heavily on other organisms. Small trout often preferred chironomid larvae and caddisfly larvae (*Rhyacophila* spp.), which were observed in the midwater drift and on or next to the bottom. Ovipositing and emerging chironomid adults made up the majority of food of most large trout, thus indicating that large fish had been exploiting the surface drift to a much greater extent than had the smaller trout. Neveu and Thibault (1977) have recently documented a similar increase in surface feeding by older members of a stream-dwelling brown trout (*S. trutta*) population.

TABLE 2. Changes in the mean relative frequencies (% by weight) of the most important invertebrate taxa in drift samples (D), and in stomach contents of small (S) and large (L) trout during 4-h intervals throughout one 28-h period.

Organisms	0800–1200			1200–1600			1600–2000			2000–2400			2400–0400			0400–0800			0800–1200		
	D	S	L	D	S	L	D	S	L	D	S	L	D	S	L	D	S	L	D	S	L
Turbellaria	1	0	1	1	3	0	4	10	27	10	15	17	25	36	8	28	0	41	3	0	0
Oligochaeta	1	0	0	1	4	1	6	4	2	3	0	0	2	0	0	2	0	0	1	8	1
Gastropoda	2	0	2	1	5	0	1	6	9	0	24	79	5	28	40	3	35	19	1	0	0
Ostracoda	1	1	0	1	1	1	3	1	1	3	3	1	2	7	1	3	7	2	1	0	1
Collembola	77	1	1	72	0	0	62	0	1	47	0	0	46	0	0	25	0	0	82	0	0
Ephemeroptera	1	0	0	1	16	3	1	11	2	3	28	0	1	0	2	2	0	0	1	10	2
Trichoptera	1	33	5	1	11	4	2	14	19	2	7	3	1	6	45	4	24	27	2	23	21
Chironomidae																					
larvae	6	59	3	8	20	3	9	10	7	12	0	0	6	0	3	19	28	10	6	52	17
pupae	2	1	3	1	5	3	1	10	3	1	0	0	1	0	0	1	0	0	1	0	16
adults	8	3	86	12	31	86	1	26	26	0	0	0	1	0	0	0	0	0	2	0	39
Simuliidae	1	3	1	1	5	0	8	8	1	19	22	1	12	24	1	12	5	2	1	8	1

Both the composition of the drift and food habits of trout changed markedly at dusk (1600–2000) and dawn (0400–0800). Collembola still dominated the drift, but were usually not consumed by either fish size. Densities of adult and pupal chironomids were much lower than daytime levels, while turbellarians (*Polycelis* sp.) and simuliids (*Twinnia nova*) exhibited relative frequency increases. As was the case during the day, trout diet was a poor reflection of drift composition. Small trout generally did not show a marked preference for any particular prey. Large trout fed chiefly on turbellarians, caddisfly larvae, and snails (*Gyraulus* sp.), plus a few chironomid adults only at dusk. Although snails and caddisfly larvae figured prominently in the food of both fish sizes, these taxa made up very low fractions of the drift during dusk and dawn.

Collembola dominated the night drift (2000–0400) to a lesser extent, with Turbellaria and Simuliidae being the other important taxa. What little night feeding there was by trout was restricted mostly to snails, turbellarians, simuliid larvae, and caddisfly larvae. Chironomid larvae, which were usually well represented in fish stomachs during daylight hours, were rarely consumed at night.

The diet of large trout tended toward greater dominance by a single type of food (chironomid adults during midday, turbellarians at dusk and dawn, snails at night) than did the diet of small trout, which as a whole tended to consume several taxa in similar quantities. Large trout had apparently become more specialized in their prey selection than had the smaller fish.

Both sizes of trout were size selective. Although small invertebrates made up the greatest percentages of the drift, they were generally ignored by the fish at all hours. This was especially true during the midday peak in drift density, when very few organisms <3 mm were taken.

All taxa that were rarely or never eaten by trout were represented in the drift by individuals <2.0 mm. Included in this group were Hydracarina, Ostracoda, Copepoda, and Collembola. Taxa that were more frequently preyed upon were represented by larger organisms that possessed a broader size distribution; included in this group were Turbellaria, Gastropoda, Ephemeroptera, Trichoptera, Chironomidae, and Simuliidae. There was also evidence that the larger members of certain taxa were being differentially cropped (Table 3). Both sizes of trout consumed significantly larger larval Chironomidae, Trichoptera, and Ephemeroptera from among those available. In addition, large trout ate significantly larger chironomid and caddisfly larvae than did small trout. These results complement recent evidence of size selectivity by *S. trutta* (Neveu and Thibault 1977) and *S. clarki* (Aho 1976) in streams.

TABLE 3. Average lengths of three groups of invertebrates in the drift and in the stomachs of small and large trout over the 28-h period. * indicates significant ($P < 0.05$) difference from drift; ** indicates significant difference from both drift and small trout as tested by analysis of variance.

Organisms	Avg length (mm) in		
	Drift	Small trout	Large trout
Ephemeroptera larvae	2	5*	5*
Trichoptera larvae	2	4*	5.5**
Chironomidae larvae	3	4*	5.5**

Discussion

Although feeding behavior was not observed directly, I inferred that some of the food ingested by large and small fish was taken from the stream bottom during certain times of the day. Species of invertebrates were occasionally found in fish stomachs that did not occur at all in the drift samples. In other instances certain sizes of various taxa, e.g. large caddisfly larvae, which were not present in the drift, were eaten by trout. More often, however, invertebrates whose presence on the upper surface of stones made them especially conspicuous were sometimes consumed in comparatively large quantities by the fish. The most important of such taxa were *Gyraulus* sp., *Polycelis* sp., *Twinnia nova*, and *Ecclisomyia maculosa* (Trichoptera: Limnephilidae). While these taxa did occur at low levels in the drift, their occasional heavy exploitation by trout suggested that most were being foraged from the bottom.

Comparisons of the availability of different prey taxa (drift density and size distribution, conspicuousness on the bottom) with the composition and size distribution of food items in fish stomachs suggested that both sizes of trout were almost exclusively drift feeders during the midday hours of 0800–1600. At dusk there was no consistency among the preferred feeding modes. At dawn bottom foraging predominated, although a few individuals fed on both benthos and drift. During the darkness hours of 2000–0400 the fish appeared to feed exclusively off the bottom, and more trout were captured on the riffle than at other times. A few large trout did not eat anything during the 2400–0400 period. In general, drift feeding was associated with periods of highest illumination and food abundance. Bottom foraging occurred at low levels of light and drift density.

Although application of these findings to rainbow trout populations in natural streams is constrained by the experimental design (starved fish at high densities, with a relatively short time for acclimation), the results clearly indicated that both sizes of rainbow trout were selective in their food habits and that much of the selectivity was due to size differences among prey organisms. Selection, i.e. nonconsumption of small prey, was apparent at all hours and included periods when both drift feeding and bottom foraging predominated. The fish were size selective despite having been deprived of food for 2 d — an observation similarly noted in planktivorous rainbow trout by Ware (1971). I did not determine whether small prey were actively rejected by the trout or were simply not perceived as available food. Ware (1972) showed that size selectivity among rainbow trout held in laboratory aquaria was due to differences in food visibility. In this study it was also possible that the trout were unable to distinguish small invertebrates from other fine particulate material (algae and organic detritus) in the drift, or, in the case of the Collembola, from terrestrial debris floating on the surface.

Bioenergetic considerations are often given as the underlying reasons for food selectivity by foraging predators; whether or not a particular prey will be eaten depends upon the relative metabolic cost of search, pursuit, capture, and handling vs. the energy reward of capture. Salmonids in streams presumably expend relatively more energy maintaining a feeding position and relatively less energy in the active pursuit of prey than their lake-dwelling counterparts. Consequently, the advantages of size specialization to drift feeders would appear to be reduced because even small prey items might repay the cost of capture. Therefore, unless the great majority of tiny invertebrates sampled in this study were not recognized by either size of trout, it seems surprising that organisms comprising size fractions (1–2 mm) that held the bulk of the total drift density were not more fully exploited by the fish.

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