

FORAGING OF INTRODUCED RAINBOW TROUT
ONCORHYNCHUS MYKISS IN RELATION TO BENTHIC
MACROINVERTEBRATES AND DRIFT IN THE GUADALUPE
RIVER TAILWATER BELOW CANYON RESERVOIR, TX

THESIS

Presented to the Graduate Council of
Southwest Texas State University
In Partial Fulfillment of the Requirements

For the Degree
Master of Science

By

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San Marcos, Texas
May, 2000

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ACKNOWLEDGEMENTS

I thank the faculty and graduate students of the Southwest Texas State University Aquatic Station that assisted me through this and many other studies. I thank my parents for their unwavering devotion. Only they know of the sacrifices leading up to the completion of this thesis. I would like to extend a special thanks to the Guadalupe River Chapter of Trout Unlimited (GRTU), particularly Alan Bray and Billy Trimble, for providing logistical and financial support during my work. Without the support of GRTU this work would not have been possible. I would like to thank the landowners at Whitewater Sports, Kanz Farms, Upper Rio Raft, Camp Beans, and Riverbank Outfitters. They allowed me almost unlimited access to their property during all times of the day. Finally, I dedicate this thesis to all the landowners who had their lives literally swept away in the flood of October 1998. We can only hope that our trout fishery will be as resilient as the people who rebuilt their lives following the devastation in the Fall of 1998.

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Introduction

The release of hypolimnetic water from impoundments, designed for purposes of flood control, water supply, and/or hydroelectric power has created a coldwater habitat downstream referred to as a tailwater (Ross 1997) which is suitable for coldwater fishes. Releases from dams have altered the typical seasonal patterns of water temperature, nutrient inputs, concentration of dissolved gases, sediment transport, and timing and volume of river flows (Baxter 1977; Bain et al. 1988; Ligon et al. 1995). Frequently, native warmwater fish populations decline or disappear entirely under these new conditions. To replace lost fisheries, hatchery-raised rainbow trout *Oncorhynchus mykiss* have been stocked into cold tailwaters in the southeast and south central United States since the late 1940's, thereby creating fisheries in conditions that would otherwise offer little fishing opportunity. The overall economic benefits associated with tailwater fisheries are from recreational

harvest (Axon 1974; Wiley and Dufek 1980), reproductive success (Baker 1959), and stocking methodologies (Boles 1968). However, little is known about the feeding preferences and foraging habits of introduced hatchery-reared rainbow trout in tailwaters.

The hatchery environment develops trout that exhibit greater fecundity, higher growth rates, and more genetic homogeneity (Vincent 1960) to insure greater yields both economically and recreationally (USFWS 1996). While these characteristics are ideally suited for the hatchery environment, they are sub-optimal for long-term survival following transplant into lotic systems (Cooper 1952; Miller 1953). Vincent (1960) found that hatchery trout have a low tolerance to high temperatures, poor predator recognition, a lack of wariness, and inferior stamina when compared to wild stocks. Moreover, hatchery-reared trout exhibit excessive activity and aggressiveness (Moyle 1969) and the inability to form feeding hierarchies (Chapman 1966) in the post-hatchery environment.

Ware (1971) tested the feeding responses of naturally-occurring rainbow trout in laboratory experiments and found that trout could begin to identify and subsequently feed on unfamiliar food items in just four days. Lord (1934) and Raney and Lachner (1942) found that hatchery trout are able to forage shortly after introduction in lotic systems. However, many times a rapid decline occurs in trout survivorship (Miller 1953) and condition (Ersbak and Haase 1983) shortly after release into streams and rivers. Partly, this may be due to a lack

of feeding sophistication following release. The foraging success of hatchery trout in tailwaters could be further limited due to their inability to forage effectively when faced with fluctuating flows, a limited range of suitable environmental conditions (particularly temperature regimes), availability of potential prey, and the bioenergetic demands required to maintain feeding positions and forage in lotic systems. These factors may influence the ability of hatchery-reared rainbow trout populations to make a successful transition from a hatchery diet of high protein pellets to foraging habits that will allow survival, growth, and reproduction for a long term carry-over fishery.

The diets and foraging strategies of many species of wild trout have been investigated in various lotic systems (Elliott 1967; Jenkins et al. 1970; Elliott 1973; Griffith 1974; Allan 1978; Pidgeon 1981; Huryn 1996). The three primary sources of food for native trout are: (1) benthic drift; (2) surficial insects (aquatic and terrestrial); and (3) epibenthic organisms. Benthic drift serves as the principal food source in the majority of rivers where the foraging strategies of wild populations of salmonids have been investigated (Waters 1969; Jenkins et al. 1970; Allan 1978, 1981; Thorp 1986; Metcalf et al. 1997). Wild trout populations forage actively for specific prey regardless of abundance of other prey available in the drift (Allan 1978; Tippets and Moyle 1978; Cada et al. 1987). The feeding strategies of wild trout populations are influenced by: (1) year class of trout (Elliott 1967; Tippets and Moyle 1978), (2) light intensity (Jenkins et al. 1970; Young et al. 1997), (3) prey size (Allan 1978), (4) seasonal

conditions (Elliott 1967; Allan 1981), (5) levels of allochthonous input (Chaston 1969; Cada et al. 1987), (6) stream type (Pidgeon 1981), and (7) competitive interactions with other species of trout (Griffith 1974).

Canyon Reservoir was completed in 1964 and is located 200 km below the north and south forks of the Guadalupe River. The reservoir is located on the southeastern portion of the Edwards Plateau in Comal County, TX and is classified as an oligomesotrophic deepwater reservoir (Hannan et al. 1979) that releases hypolimnetic water into the Guadalupe River. Trout have been stocked in the tailwater below the dam since 1966. Although temperatures in the tailwater are adequate to maintain a trout fishery, the status of other environmental conditions is uncertain. Questions associated with the structure and composition of the macroinvertebrate food base in relation to foraging abilities of stocked hatchery-reared trout appear critical to understanding the fishery and its potential. The objective of this study is to determine the macroinvertebrate benthic and drift composition and abundance in relation to the feeding habits and foraging selectivity of rainbow trout in the Guadalupe River at progressive intervals downstream from Canyon Reservoir.

Methods

Study Region

The geological composition of the substrate in the study section of the Guadalupe River is characterized by small-to-intermediate sized gravel,

cobble, and extended areas of exposed karstic bedrock. The riparian overstory along the river is comprised primarily of bald cypress *Taxodium distichum*, sycamore *Platanus occidentalis*, willow *Salix* sp., and cottonwood *Populus deltoides*. Mexican juniper *Juniperus mexicana*, live oak *Quercus virginiana*, and Texas oak *Quercus texana* are the most abundant plants in the understory and along the steep slopes bordering the river.

The wild fish population is comprised of the smallmouth bass *Micropterus dolomieu*, redbreast sunfish *Lepomis auritus*, spotted sunfish *Lepomis punctatus*, Texas shiner *Notropis amabilis*, blacktail shiner *Cyprinella venusta*, longear sunfish *Lepomis megalotis*, rock bass *Ambloplites rupestris*, Texas logperch *Percina carbonaria*, gray redhorse *Moxostoma congestum*, and mimic shiner *Notropis volucellus*.

Stocking Rates

Since 1980, Texas Parks and Wildlife Department (TPWD) has annually stocked rainbow trout in the tailwaters below Canyon Reservoir to provide a put-and-take fishery. The Guadalupe River Chapter of Trout Unlimited (GRTU) has also stocked trout in the Guadalupe River since 1970 (Tanner 1970). The tailwaters below the dam to Comal County Road 306, Comal County, TX, a distance of 6.4 km, are an unregulated fishery in which anglers may use live or artificial bait to catch trout. Texas Parks and Wildlife has designated a trophy trout zone from Comal County Road 306 to the second crossing on River Road,

Comal County, TX, a distance of 17 km. In this zone, only trout that are caught on artificial lures and measure \geq 7 cm total length can be harvested.

Over 15,000 catchable size rainbow trout were released at several locations in the Guadalupe River tailwater, both in the unregulated and trophy trout zones by TPWD during the winter of 1997 and the spring of 1998. Additionally, GRTU stocked about 7,800 rainbow trout over a five-month period beginning in November 1997. An undetermined number of brown trout *Salmo trutta* were also released by GRTU into the tailwater during 1997-1998 but none were obtained during this study.

Field Sites

A 17 km section of the Guadalupe River below Canyon Reservoir was surveyed to determine the composition of the benthic and drift macroinvertebrate community. Five locations, Whitewater Sports, Kanz Farms, Upper Rio Raft, Lower Camp Beans, and Riverbank Outfitters, were sampled to establish the invertebrate drift pattern and benthic composition from April through September 1998 (Figure 1). On each sampling date, invertebrate drift was determined at four locations.

The sample site nearest the dam, Whitewater Sports ($29^{\circ} 51' 42''$ N, $098^{\circ} 09' 69''$ W) is located 6.4 km below Canyon Reservoir. The drift net was placed 15 m upstream of Comal County Road 306. The riparian zone on the east bank is lined with concrete to accommodate recreational users and

contains over 50 campsites. Whitewater Sports site was sampled July through September 1998.

Kanz Farms ($29^{\circ} 51' 17''$ N, $098^{\circ} 09' 38''$ W) is 6.9 km below the dam. The drift net was placed about 26 m below a weir. The riparian zone along this section of the river is relatively undeveloped. Kanz Farms site was sampled April through May 1998.

Upper Rio Raft ($29^{\circ} 50' 37''$ N, $098^{\circ} 09' 56''$ W) is located 8.8 km below the dam. The drift net was placed 290 m upstream of River Road, Comal County, TX. The riparian zone to the northwest contains a series of cabins and campgrounds. Upper Rio Raft site was sampled from April through September 1998.

Lower Camp Beans ($29^{\circ} 48' 12''$ N, $098^{\circ} 09' 56''$ W) is 16.9 km below the dam. The drift net was placed 14 m downstream of the third crossing of River Road. The riparian zone is mostly undeveloped except for some seasonal campgrounds to the northeast. Lower Camp Beans site was sampled from April through September 1998.

The furthermost downstream sample site, Riverbank Outfitters ($29^{\circ} 46' 13''$ N, $098^{\circ} 09' 30''$ W) is 23.4 km below Canyon Reservoir. The drift net at this location was placed 18 m below a riffle across from the Riverbank Outfitters property. The riparian zone is relatively undeveloped except for the northeastern portion that contains a number of businesses and RV

campgrounds. Riverbank Outfitters site was sampled from April through September 1998.

Drift and Benthic Sampling

Drift was assessed by placing nets at Kanz Farms, Upper Rio Raft, Lower Camp Beans, and Riverbank Outfitters on 15 April and 30-31 May 1998. On 2-3 July, 11-12 August, and 11-12 September 1998, Whitewater Sports, Upper Rio Raft, Lower Camp Beans, and Riverbank Outfitters were used to determine the drift.

The drift nets were attached to the river bottom with two concrete blocks each weighing 18 kg and the bottom of each net was positioned at least 5 cm above the substrate. The nets (101.6 cm long with 363 μm mesh and an opening of 1371 cm^2) each had a dolphin bucket (363 μm mesh) at the terminal portion of the net. Substrate composition, current velocity, thalweg depth, and recreational activity necessitated nonrandom net placement. The bucket was changed about every 3.5 hours over a 24-h cycle except for 2-3 July, when the drift nets were changed about every four hours. The drift sample for 15 April was analyzed only for 1200 hours to 2100 hours because the remaining samples were lost.

The nets were positioned so that the top extended above the surface to include surficial organisms in the determination of the composition and pattern of the drift. On some sampling occasions there was fluctuation in the flow

pattern after the nets had been set up, resulting in partial or complete submersion of the net during a portion of the sampling regime.

Three benthic samples were taken at each site using a Hess sampler (surface area .086 m², 363 µm mesh) with a dolphin bucket (363 µm mesh). Three benthic samples were taken 50 m upstream of the drift net at the end of every 24-h sampling period.

Prior to placement in containers, samples were examined to remove debris, large leaves, and twigs that may have accumulated in the net. Samples were then placed in 75% ethanol. All aquatic invertebrate taxa obtained from the drift and benthos were identified to the lowest practical taxonomic level (usually genus) along with their respective stage of development (larva, pupa, or adult).

Trout Sampling

An electrofishing boat, using pulsed direct current, was used to collect 17 rainbow trout (range 247-462 mm; mean total length, 316 mm) on 12 April 1998. Five rainbow trout (range 280-401 mm; mean total length, 338 mm) were obtained on 1 August 1998 using a shore-based electrofishing apparatus comprised of an anode with a 30.5 m cable attached to a generator. Immediately after capture, the trout were placed in ice to reduce post-capture digestion. There was no evidence of regurgitation during collection or following placement into ice. Trout were weighed and measured to determine both

standard and total length for each fish. Stomachs were removed in accordance with the procedures outlined by Bowen (1996) and placed in 75% ethanol solution. All identifiable prey taxa found in the stomachs were identified to the lowest practical level (usually genus) along with their respective stage of development (larva, pupa, or adult).

Analysis of Stomach Contents

The relative abundance of invertebrates in the stomach contents were established and then compared with the relative abundance found in the drift using the linear index of food selection (Strauss 1979). The linear selection index (LSV), is a measure of electivity or degree of selection by a predator and is defined as:

$$LSV = r_i - p_i$$

where r_i is the relative abundance of prey item i in the gut and p_i is the relative abundance of that prey item i in the environment (Strauss 1979). The index has a range from -1 to +1. Positive values indicate active selection for a prey item while negative values indicate avoidance or inaccessibility of a prey item. Values near zero indicate random selection. Spearman rank correlation (r_s), (Zar 1996) was used to determine if a relationship existed between proportions of all invertebrate prey taxa present in the drift with proportions found in the trout diet. Because many genera were uncommon, they were combined into families for statistical analysis.

A coefficient of importance (CI) was used to estimate the relative importance of prey items found in the diet (Tusa 1968; Ersbak and Hasse 1983). The coefficient is defined as:

$$CI = (\sqrt{F}) \times (\sqrt{S})$$

where

$$\sqrt{F} = \frac{\text{number of individual prey items consumed per taxa}}{\text{total number of prey items consumed}} \times 100$$

$$\sqrt{S} = \frac{\text{number of stomachs containing a specific prey item}}{\text{total number of stomachs}} \times 100.$$

Prey items that occur with the highest frequency and in the greatest numbers result in the highest CI values (Ersbak and Haase 1983).

Analysis of the 1994 Survey

Spearman rank correlation and CI values were used to analyze data from Quiñonez's (1996) Guadalupe River study on benthic macroinvertebrate composition and feeding preferences of introduced hatchery trout in the tailwater.

Results

Composition of the Drift

Nineteen orders of invertebrates, including 42 families of benthic macroinvertebrates were identified in drift collections from April through September 1998 (Table 1). The most abundant benthic macroinvertebrates in the drift over the study period were: Hyalellidae (23.7 %), Chironomidae (19.2 %), Tricorythidae (16.9 %), Simuliidae (9.4 %), Helicopsychidae (6.5 %), Baetidae (6.4 %), and Hydroptilidae (3.4 %). Higher levels of drifting invertebrates at night was the only consistent invertebrate drift pattern over the six-month sampling period (Figure 2). The greatest number of drifting invertebrates occurred in May and September.

Amphipoda.—*Hyalella* (Hyalellidae), the most abundant invertebrate (Table 1), showed pronounced nocturnal activity throughout the six-month study (Figure 3).

Diptera.—Chironomidae larvae comprised a substantial portion ($\geq 13\%$) of the drift on all sample dates (Figure 4) however, no discernable drift pattern was observed (Figure 5). Chironomids were most abundant in the drift during September. *Simulium* (Simuliidae) larvae showed, in general, a monthly decline in abundance (Figure 4) and a variable drift pattern (Figure 6). Other dipterans present in the drift during the study were too low in abundance to establish a drift pattern (Table 1).

Trichoptera.—*Helicopsyche* (Helicopsychidae) larvae were relatively more abundant during April and August (Figure 4) and showed a late afternoon peak followed by a decline in drift abundance during the night (Figure 7). Conversely, *Helicopsyche* adults were relatively more abundant in May and July (Figure 4) and showed crepuscular drift activity (Figure 7). The remainder of trichopteran genera in the drift were too low in abundance to establish a drift pattern (Table 1).

Ephemeroptera.—The greatest generic diversity found in the drift were Baetidae mayflies, with seven genera (*Baetis*, *Baetodes*, *Callibaetis*, *Camelobaetidius*, *Centroptilium*, *Cloeon*, and *Fallceon*). Although *Baetis* was the most abundant baetid mayfly, its numbers were too low to determine a drift pattern (Figure 8). *Tricorythodes* (Tricorythidae) drift was variable during the early sample dates but showed a nocturnal peak during August and September (Figure 9). *Leptohyphes* (Tricorythidae) was found only in July and August and comprised < 1 % of the drift. Other mayflies were not collected in sufficient numbers to determine drift patterns (Table 1).

Terrestrial Taxa.—During the study, terrestrial invertebrates accounted for 4.1 % of the drift and were most abundant in July. The abundance of the most frequently occurring terrestrial insect, Formicidae, peaked during mid-summer and gradually declined over the study (Table 1).

Composition of the Benthos

Fifteen orders and 25 families of benthic macroinvertebrates were identified from collections in the benthos (Table 2). The most abundant benthic macroinvertebrates collected over the entire sampling period were: *Helicopsychidae* (19.3 %), *Tricorythidae* (11.5 %), *Tricladida* (9.0 %), *Hydropsychidae* (7.0 %), *Chironomidae* (6.8 %), *Hydroptilidae* (6.4 %), *Pleuroceridae* (5.5 %), *Physidae* (4.9 %), *Hyalellidae* (4.0 %), *Viviparidae* (3.3 %), and *Polycentropodidae* (2.9 %). *Corydalidae*, *Corbiculidae*, and *Tipulidae* were the only benthic macroinvertebrates collected in the benthos but not in the drift.

Trichoptera.—This was the most abundant order found in the benthos. The most abundant Trichoptera were *Helicopsyche* (*Helicopsychidae*), *Cheumatopsyche* (*Hydropsychidae*), *Hydropsyche* (*Hydropsychidae*), and *Hydroptila* (*Hydroptilidae*) (Table 2). *Helicopsyche* was the only caddisfly collected on every sampling date.

Ephemeroptera.—*Tricorythodes* was the most abundant mayfly in the benthos on all sampling dates except September. The only other mayfly that was found on all sample dates was *Stenonema* (*Heptageniidae*) (Table 2) and its abundance never exceeded 2.7 %.

Diptera.—None of the aquatic diptera were collected on every sample date and no dipterans were collected in July. *Chironomidae* was the most

abundant (Table 2). The other dipterans found in the collections were only collected during April.

Gastropoda.—Gastropods were collected from the benthos on every sample date and were most abundant in September. In July, *Elimia* (Pleuroceridae) was the most abundant invertebrate in the benthos and the only snail collected that month.

Composition of the Trout Diets

April 1998.—Twenty-two (18 aquatic; 4 terrestrial) invertebrate prey taxa were present in the stomachs and the median number of identifiable prey items was 31 (mean 43.4; range 3-181). The CI values based on consumed prey show that baetids, chironomids, helicopsychids, hydropsychids, and pleurocerids were the most important prey in the diet (Table 3).

The LSVs show that consumption for most drifting taxa was random. The LSVs indicate that *Simulium* larvae and *Hyalella* were underused. Baetids appeared to be the only preferentially consumed drifting prey (Table 4). The LSVs indicate that two taxa, *Helicopsyche* pupae and *Elimia*, were actively selected, though neither was obtained in the drift collections for this month.

Helicopsyche pupae were only found in the benthic collections and *Elimia* were absent from both the drift and benthic collections. The proportions of all prey items found in the drift and in the trout diet were positively correlated and significant ($r_s = 0.356$; $p < 0.05$).

August 1998. — Four invertebrate prey taxa (all aquatic) were present in the trout diet and the median number of identifiable prey items per stomach was two (mean 5.2; range 0-20). Five trout were sampled and 2 had no stomach contents. The CI values based on consumed prey in the trout diets indicate that *Hexagenia* (Ephemeridae), *Hyalella*, and *Elimia* were the most important food (Table 3). The only abundant drifting taxa consumed was *Hyalella*. The most preferred prey, *Hexagenia* larvae and pleurocerid snails, were among the most infrequent taxa available in the drift. The proportions of all prey items found in the drift and in the trout diet were not significantly correlated ($r_s = 0.210$; $p > 0.5$). Drifting invertebrates that were underused included *Tricorythodes*, *Hyalella*, and chironomid, taxa that comprised over 80 % of the drift (Table 5). The LSVs indicate that trout were not consuming the drifting food base in August relative to its abundance.

Comparison of April and August Foraging

The greatest number of drifting taxa in this study were consumed during April. Trout appeared to consume some drifting taxa (i.e. baetids, helicopsyhid larvae) but did not appear to actively select the most abundant aquatic invertebrates, amphipods and simuliid larvae. Drift feeding declined as the study progressed, though the number of drifting taxa increased during August. During August, the only drifting taxon found in the trout diets was *Hyalella*, despite the abundance of *Tricorythodes* and chironomids. The

presence of *Helicopsyche* pupae and pleurocerid snails in the trout diets suggest that foraging was occurring on the epibenthos during April. The abundance of some epibenthic taxa (e.g. ephemeralids and pleurocerid snails) in trout diets during August suggest that feeding habits had shifted primarily to the benthos.

Baetids were the most consumed drifting prey in April, but were underused in August even though their abundance during the two months was similar. There was no evidence (e.g. abrasions on the head) in April or August that trout were burrowing to obtain sub surface prey. Small amounts of indigestible material (filamentous algae, small pebbles, exuviae, and detritus) were found in the diets on both collection dates.

June 1994. —In the Quiñonez (1996) study, twenty invertebrate prey taxa were identified and the median number of identifiable prey items per stomach was 21 (mean 30.6; range 1-66). The CI values show that *Petrophila* (Pyralidae) larvae, *Hexagenia* larvae, chironomids, *Simulium* pupae, and *Isonychia* (Isonychiidae) larvae were the most important prey (Table 3). The proportions of all prey items found in the benthos were not significantly correlated with the proportions of prey items found in the trout diet ($r_s = 0.354$; $p > 0.10$).

Discussion

Drift Foraging

Presumably, consumption of the most abundant drifting prey should be the most efficient method of feeding in lotic systems. However, the LSVs in this study indicate that many of the most abundant drifting taxa (chironomids, *Tricorythodes*, *Similium*, and *Hyalella*) were underrepresented in the trout diet. Although *Hyalella* was the most abundant drifting invertebrate in the Guadalupe River tailwater, only baetids, chironomid pupae, and helicopsychid adults appear to have been actively pursued in the drift. In other tailwater trout fisheries, amphipods are among the most consumed prey (Weiland and Hayward 1997). The scarcity of amphipods in the trout diets in this study suggests poor use of the drift.

In August, the LSVs for prey collected in the drift suggest that trout foraging in the drift was random and there was no significant correlation between proportions of all taxa in the drift and in the trout diets. Cada et al. (1987) studied the foraging habits of rainbow trout in third- and fourth-order streams in the southern Appalachian Mountains of eastern Tennessee and western North Carolina and found that mayflies, stoneflies, and aquatic dipterans comprised a substantial portion of the diet. In this study, the drift declined during the summer months and foraging effort by trout appeared to be concentrated on the benthos.

Guadalupe River Tailwater

The lack of structural heterogeneity in portions of the Guadalupe River tailwater may not provide adequate habitat for the development of productive benthic macroinvertebrate communities. The tailwater includes sections of exposed limestone bedrock that lacks small gravel and has limited sediment. The level of biological richness in benthic macroinvertebrate assemblages has been related to the amount of available interstitial space in lotic systems (Flecker and Allan 1984). In a review of existing literature on diversity in streams, Vinson and Hawkins (1998) found that structurally complex substrate types (e.g. cobble, gravel, leafpacks, macrophytes) had higher levels of richness than simpler substrates such as sand and bedrock. The lack of a complex habitat in many portions of the Guadalupe River tailwater may limit the development of a productive benthic macroinvertebrate community.

The paucity of drifting invertebrates in the tailwater could also be influenced by coldwater discharges from Canyon Reservoir. Mayfly populations, an important food resource for both wild trout (Elliott 1973; Allan 1978, 1981) and stocked trout (Ersbak and Haase 1983) in many streams, were low in abundance in this study. There is evidence that some mayfly taxa with strict thermal requirements, for reproduction and growth, may be negatively impacted by coldwater discharges from impoundments (Lehmkuhl 1972). Spence and Hynes (1971) compared the macroinvertebrate content of riffles upstream and downstream of a dam to determine the effects of coldwater

on the benthic macroinvertebrate community and found that certain net-spinning caddisflies and amphipods appeared to benefit from increased detritus and coldwater but this study of the Guadalupe River tailwater shows that both caddisflies and amphipods were underutilized by the trout.

The structure of the benthic marcoinvertebrate community may also be influenced by the recreational use in the tailwater. An estimated 1.8 million people visited the Guadalupe River tailwater during the summer of 1998 for recreational purposes (rafting, tubing, angling, and camping) (Water Oriented Recreation District, personal communication). High levels of daytime recreational activity may impact trout by forcing some individuals to the least productive areas and also restrict the amount of available feeding space in the tailwater. Additionally, recreational traffic has also been found to adversely affect the densities of certain benthic macroinvertebrates (Wright and Li 1998). Trout foraging is highest during the daylight hours (Bisson 1978; Allan 1981) and the presence of so many people may prevent trout from exploiting daytime drift.

Drifting food resources found in the Guadalupe River tailwater do not favorably compare with levels found in other streams and rivers that support naturally-occurring trout populations. Griffith (1974) studied the foraging of invertebrate drift by wild trout in first- and second-order streams during the summer months and documented drift numbers two times greater than those found in the Guadalupe River tailwater. Additionally, the Guadalupe River

tailwater is impoverished when compared to at least one of its tributaries, Honey Creek. Bowles and Short (1988) found numbers of drifting *Hyalella* collected at a single site in Honey Creek in August in six non-consecutive hours during a 24-h period were more than double the number of *Hyalella* collected in this study at four sites over 24-h. In Cement Creek, CO, Allan (1981) found close to 100,000 drifting invertebrates in a 3-h period at a single site in a high mountain stream during June. By comparison, in this study's entire six-month sampling period about 3,100 invertebrates were collected from the drift over a monthly 24-h period at four sampling sites.

The composition of the drift in the Guadalupe River tailwater is also different from many trout fisheries. Plecoptera, a principal food source in many trout streams (Elliott 1967; Metcalf et al. 1997; Young et al. 1997) were not found in this study. Plecoptera are uncommon in warmer regions (Stewart and Stark 1988) and, when present, are generally restricted to high elevations and heavily shaded streams (Hynes 1976).

The number of drifting aquatic invertebrates in this study declined during the summer. In many trout streams, this decrease is offset by an increase in availability of terrestrial prey that will then comprise a considerable portion of the trout diet (Allan 1981; Cada et al. 1987). Although one terrestrial taxon, formicids, was more abundant than many aquatic taxa in the Guadalupe River drift during some of the summer months, this study did not find that terrestrial prey represented a substantial contribution to the trout diet. Contrary to

findings that trout in many streams switch to allochthonous prey during the late summer months (Chaston 1969; Jenkins et al. 1970), I found that trout in the Guadalupe River appeared to rely on the epibenthos.

Epibenthic Foraging

The occurrence of significant levels of infrequent drifters (e.g. snails, burrowing mayflies, and aquatic lepidopteran larvae) in the trout diets during this study and Quiñonez's study (1996) suggests that many trout were concentrating a substantial amount of foraging effort on the epibenthos. Significant use of infrequent epibenthic drifters has rarely been documented in wild trout populations. Elliott (1967) concluded that consumption of specific epibenthic macroinvertebrates, particularly large case-making caddisflies, by trout was to reduce competition between size classes of trout. The high occurrence of epibenthic invertebrates in the trout diets in this study suggests that the drift is inadequately utilized or is insufficient to support the introduced trout population. In conditions where trout are unable to obtain enough drifting prey, they may exploit other food sources to fulfill their nutritional demands.

The foraging behavior of hatchery trout could also be influenced by the rate of consumption. Ware (1972) found in laboratory experiments that wild rainbow trout initiate substrate-oriented foraging when drifting prey are not available for consumption at a certain rate. In situations where the drift is

inadequately utilized or is insufficient, trout may concentrate their foraging effort on epibenthic invertebrates.

Foraging for epibenthic taxa might be the result of a conditioned response learned in the hatchery. Ersbak and Haase (1983) concluded that stocked brook trout *Salvelinus fontinalis* may have mistaken saddle-case making caddisflies (Glossosomatidae larvae) for artificial pellets used for food in hatcheries. Pleurocerid snails, among the most abundant prey in this study, are somewhat similar in size, appearance, and coloration to artificial pellets. Consequently, inexperienced benthic foragers, such as hatchery-reared trout, might have mistaken them as pellets. However, it is not clear why other benthic macroinvertebrates--bivalves, helicopsychids, and other snails--which resemble pellets were not more frequent in the diet. Further, the consumption of certain epibenthic macroinvertebrates, particularly snails, may result in increased handling time and, consequently, offer a poor bioenergetic reward. Rainbow trout are unable to crush gastropod shells (most shells passed through the gut intact), because they lack pharyngeal teeth, and therefore consumption of gastropods may offer a limited nutritional benefit.

Stocking Rate

In 1997-98, the stocking rate of rainbow trout for the Guadalupe River tailwater was about 328 fish per hectare. The Fontenelle tailwater in Wyoming, which is about 49 times larger than the Guadalupe River tailwater, had a seven-

year stocking range of 200 to 440 trout per hectare (Wiley and Dufek 1980). The potential exists that the introduction of hatchery trout may cause a decline in the densities of benthic macroinvertebrate community. Thorp (1986) reviewed a number of experiments regarding the impact of predators on benthic macroinvertebrates densities and composition. He concluded that predators, including trout, have minimal influence on the structure of benthic systems. Weiland and Hayward (1997) found, however, that as the numbers of rainbow trout in the Lake Taneycomo tailwater declined, densities of the trout's most preferred prey, chironomids, increased. In tailwater fisheries the stocking of trout on a continuous or seasonal basis may significantly impair the benthic macroinvertebrate community.

Management and Research

A radiotelemetry study would be useful in determining the behavior of introduced trout. Radiotelemetry has been used to establish preferred habitats (Young 1995) and feeding activities (Young et al. 1997) of trout. It is relatively unobtrusive and can generate a large amount of information about fish behavior (Winter 1996). However, it can be expensive and is generally limited to a few individual fish.

It is unclear whether introduced trout have stocking site fidelity. Currently GRTU releases trout into the trophy trout zone of the tailwater but it is unclear if the fish remain in this section. It would be useful to examine the

distribution of the stocked trout after introduction. Radiotelemetry might also reveal the foraging patterns of trout in the tailwater and if individual trout attempt to establish feeding sites.

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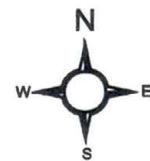
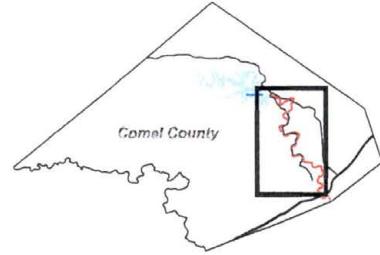
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Guadalupe River

River Road

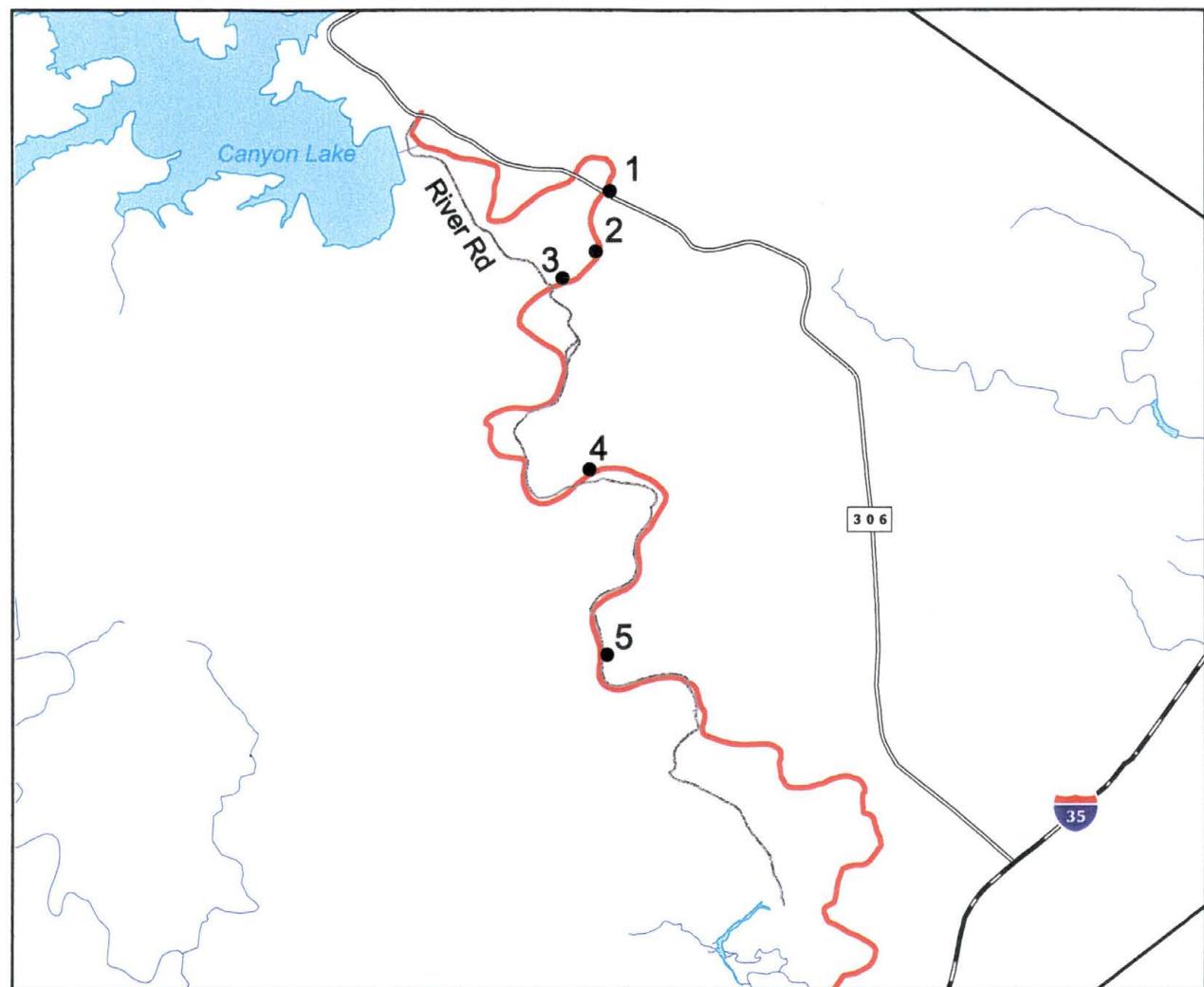


Figure 1. Map of the study area in Comal County, TX showing the five collecting stations:
1. Whitewater Sports 2. Kanz Farm 3. Upper Rio Raft 4. Lower Camp Beans 5. Riverbank Outfitters

Table 1.—Composition (%), total number, number of taxa, and Shannon-Wiener (S-W) diversity of macroinvertebrate drift for five dates in 1998 across all sample sites. The em-dash (--) indicates no individuals of that taxa were collected.

Taxon	15 Apr	30 May	2 July	11 Aug	11 Sept
Aquatic Taxa					
Ephemeroptera					
Baetidae					
<i>Baetis</i>	4.6	4.1	1.5	6.9	6.3
<i>Baetodes</i>	1.5	1.4	0.5	1.1	1.1
<i>Callibaetis</i>	--	--	0.2	--	--
<i>Camelobaetidius</i>	--	--	0.2	--	0.4
<i>Centroptilum</i>	0.4	--	--	--	--
<i>Cloeon</i>	0.4	0.1	--	--	--
<i>Fallceon</i>	--	0.1	0.7	--	0.5
Caenidae					
<i>Caenis</i>	0.4	--	--	--	--
Ephemeridae					
<i>Hexagenia</i>	--	--	--	0.2	0.4
Heptageniidae					
<i>Stenonema</i>	--	0.5	--	--	--
Isonychiidae					
<i>Isonychia</i>	0.8	0.1	0.9	0.2	--
Tricorythidae					
<i>Leptohyphes</i>	--	--	0.4	0.4	--
<i>Tricorythodes</i>	9.3	9.8	7.1	22.5	30.5
Odonata					
Calopterygidae					
<i>Hetaerina</i>	--	--	--	--	0.1
Coenagrionidae					
<i>Argia</i>	--	--	0.2	--	0.1
Corduliidae					
<i>Epitheca</i>	--	--	--	--	0.1
Gomphidae					
<i>Hagenius</i>	--	--	--	0.2	--
Libellulidae					
<i>Sympetrum</i>	0.4	0.1	--	--	--

Table 1.—(cont.).

Taxon	15 Apr	30 May	2 July	11 Aug	11 Sept
Hemiptera					
Belostomatidae	--	--	--	0.2	--
Gerridae					
<i>Metrobates</i>	--	--	1.3	1.4	--
Naucoridae					0.1
<i>Pelocoris</i>	--	--	0.2	--	--
Veliidae					
<i>Rhagovelia</i>	0.8	0.6	1.1	0.5	--
Coleoptera					
Curculionidae	--	--	--	0.2	--
Dryopidae					
<i>Helichus</i>	--	0.1	2.0	0.7	--
Dytiscidae					
<i>Brachyvatus</i>	--	0.3	--	--	--
<i>Hydrovatus</i>	--	--	1.8	--	0.3
Elmidae					
<i>Microcylloepus</i>	1.2	--	--	--	--
<i>Stenelmis</i>	0.8	--	0.7	0.9	0.3
Haliplidae					
<i>Peltodytes</i>	--	--	0.2	--	0.4
Hydrophilidae					
<i>Enochrus</i>	--	0.1	--	--	--
<i>Berosus</i>	--	--	--	--	0.1
Psephenidae					
<i>Psephenus</i>	--	0.1	0.2	--	--
Diptera					
Chironomidae	13.0	18.2	14.3	17.0	27.3
Ceratopogonidae					
<i>Bezzia</i>	--	0.1	0.2	--	0.1
Chaoboridae					
<i>Chaoborus</i>	--	--	--	--	1.0
Culicidae					
Simuliidae					
<i>Simulium</i>	25.0	19.0	6.5	0.9	1.0
Stratiomyidae					
<i>Myxosargus</i>	--	--	0.4	--	--

Table 1.—(cont.).

Taxon	15 Apr	30 May	2 July	11 Aug	11 Sept
Trichoptera					
<i>Helicopsychidae</i>					
<i>Helicopsyche</i>	10.8	8.6	11.6	4.6	0.4
<i>Hydrobiosidae</i>					
<i>Atopsyche</i>	--	0.1	2.0	0.7	0.4
<i>Hydropsychidae</i>					
<i>Cheumatopsyche</i>	1.2	0.2	--	0.4	0.1
<i>Hydropsyche</i>	--	0.8	--	0.7	0.3
<i>Hydroptilidae</i>					
<i>Hydroptila</i>	1.9	4.4	2.4	2.9	1.1
<i>Ochrotrichia</i>	--	--	4.1	--	--
<i>Oxyethira</i>	--	--	--	0.2	--
<i>Leptoceridae</i>					
<i>Nectopsyche</i>	1.2	0.2	0.9	0.5	--
<i>Oecetis</i>	0.8	0.1	--	--	--
<i>Philopotamidae</i>					
<i>Chimarra</i>	--	0.1	--	--	--
<i>Polycentropodidae</i>					
<i>Cyrnellus</i>	1.5	--	--	--	0.1
<i>Polycentropus</i>	--	0.5	0.7	1.9	--
<i>Polyplectropus</i>	--	--	--	--	0.5
Lepidoptera					
<i>Pyralidae</i>					
<i>Petrophila</i>	0.4	--	1.4	0.5	0.6
Turbellaria					
<i>Tricladida</i>					
<i>Dugesia</i>	2.3	--	0.4	--	0.1
Hirudinea					
	--	--	0.2	0.2	--
Bivalvia					
<i>Sphaeriidae</i>	--	--	--	--	0.1

Table 1.—(cont.).

Taxon	15 Apr	30 May	2 July	11 Aug	11 Sept
Gastropoda					
Physidae					
<i>Physa</i>	--	1.0	1.4	--	--
Viviparidae	0.4	--	--	--	--
Hydracarina	0.4	0.8	0.5	0.5	0.6
Amphipoda					
Halellidae					
<i>Halella</i>	18.8	23.5	23.8	28.0	22.6
Decapoda					
Cambaridae					
<i>Procambarus</i>	0.4	0.2	0.2	--	--
Ostracoda	--	0.3	0.9	1.4	1.5
Terrestrial Taxa					
Araneae	--	0.6	1.1	0.2	0.1
Coleoptera	--	--	--	0.4	--
Hemiptera	--	--	--	--	0.1
Homoptera	--	--	--	--	0.1
Hymenoptera	0.8	0.2	0.7	0.4	--
Formicidae	1.5	3.0	7.7	2.7	0.8
Lepidoptera	--	0.2	--	--	--
Orthoptera	--	0.2	--	--	--
Total number	260	932	560	565	789
Total number of taxa	27	35	38	33	34
S-W diversity	2.47	2.42	2.71	2.25	1.87

Table 2.—Composition (%), total number, number of taxa, and Shannon-Wiener (S-W) diversity found in the benthos for five dates in 1998 across all sample sites. The em-dash (--) indicates no individuals of that taxa were collected.

Taxon	15 Apr	30 May	2 July	11 Aug	11 Sept
Aquatic Taxa					
Ephemeroptera					
Baetidae					
<i>Baetis</i>	--	--	--	--	4.5
<i>Centroptilum</i>	1.9	--	--	--	
<i>Falceon</i>	--	--	--	--	2.3
Heptageniidae					
<i>Stenonema</i>	1.9	1.0	2.7	0.7	2.3
Tricorythidae					
<i>Leptohyphes</i>	--	--	--	0.7	--
<i>Tricorythodes</i>	9.7	5.2	8.1	22.4	2.3
Odonata					
Coenagrionidae					
<i>Argia</i>	1.0	1.0	10.8	0.7	3.4
Gomphidae					
<i>Erpetogomphus</i>	--	--	--	0.7	--
Libellulidae					
<i>Libellula</i>	1.0	--	--	--	--
Coleoptera					
Dytiscidae					
<i>Hydrovatus</i>	1.0	--	--	--	--
Elmidae					
<i>Stenelmis</i>	--	--	--	--	1.1
Psephenidae					
<i>Psephenus</i>	6.8	1.0	5.4	3.4	--
Megaloptera					
Corydalidae					
<i>Corydalus</i>	--	--	2.7	--	--

Table 2.—(cont.).

Taxon	15 Apr	30 May	2 July	11 Aug	11 Sept
Diptera					
Chironomidae	2.9	10.4	--	8.2	8.0
Simuliidae					
<i>Simulium</i>	3.0	--	--	--	--
Tipulidae					
<i>Tipula</i>	1.0	--	--	--	--
Trichoptera					
Helicopsychidae					
<i>Helicopsyche</i>	44.7	7.3	18.9	8.2	21.5
Hydropsychidae					
<i>Cheumatopsyche</i>	--	--	--	8.2	1.1
<i>Hydropsyche</i>	1.0	19.8	--	--	--
Hydroptilidae					
<i>Hydroptila</i>	--	16.7	--	4.8	5.7
<i>Ochrotrichia</i>	--	--	--	1.4	--
Leptoceridae					
<i>Nectopsyche</i>	--	--	5.4	--	1.1
<i>Oecetis</i>	1.0	--	--	2.0	--
Polycentropodidae					
<i>Polycentropus</i>	--	3.1	2.7	5.4	2.3
Lepidoptera					
Pyralidae					
<i>Petrophila</i>	--	--	--	6.1	--
Turbellaria					
Tricladida					
<i>Dugesia</i>	16.5	1.0	8.1	10.9	5.7
Hirudinea					
Oligochaeta					
Bivalvia					
Corbiculidae					
<i>Corbicula</i>	1.9	11.5	--	--	1.1

Table 2.—(cont.).

Taxon	15 Apr	30 May	2 July	11 Aug	11 Sept
Gastropoda					
Physidae					
<i>Physa</i>	1.9	5.2	--	2.7	13.6
Pleuroceridae					
<i>Elimia</i>	--	3.1	24.3	6.8	4.5
Viviparidae	1.0	3.1	--	--	13.6
Hydracarina	--	1.0	--	--	--
Amphipoda					
Hyalellidae					
<i>Hyalella</i>	1.0	8.3	5.4	3.4	3.4
Ostracoda	--	--	--	2.0	2.3
Total number	103	96	37	147	88
Total number of taxa	18	17	12	20	19
S-W diversity	1.94	2.41	2.06	2.51	2.55

Table 3.—Ranking of coefficients of importance (CI) for prey items consumed by stocked rainbow trout in the Guadalupe River. The em-dash (--) indicates prey item not present. Rankings based on number of trout diets sampled.

Food item	June	1994	April	1998	Aug	1998
	Rank	CI	Rank	CI	Rank	CI
Araneae	14	3.3	13	0.7	--	--
Baetidae	6	8.2	1	59.7	--	--
Cambaridae	9	5.7	--	--	--	--
Chironomidae	3	27.9	3	23.6	--	--
Coenagrionidae	14	3.3	--	--	--	--
Curculionidae	--	--	13	0.7	--	--
Dytiscidae	--	--	13	0.7	--	--
Ephemeridae	2	28.7	--	--	1	48.0
Formicidae	12	4.9	10	4.3	--	--
Helicopsychidae	6	8.2	2	52.6	--	--
Heptageniidae	--	--	13	0.7	--	--
Homoptera	--	--	13	0.7	--	--
Hyalellidae	--	--	7	9.2	2	30.3
Hydrobiosidae	9	5.7	--	--	--	--
Hydropsychidae	11	5.3	4	15.5	--	--
Hydroptilidae	19	1.6	13	0.7	--	--
Isonychiidae	5	22.2	--	--	--	--
Isopoda	12	4.9	--	--	--	--
Leptoceridae	--	--	9	4.7	--	--
Libellulidae	--	--	--	--	4	8.7
Notonectidae	18	2.3	--	--	--	--
Oligochaeta	--	--	13	0.7	--	--
Orthoptera	--	--	13	0.7	--	--
Ostracoda	--	--	13	0.7	--	--
Physidae	--	--	13	0.7	--	--
Pleuroceridae	--	--	5	14.7	3	24.8
Polycentropodidae	14	3.3	--	--	--	--
Pyralidae	1	58.2	11	2.9	--	--
Simuliidae	4	24.3	6	10.3	--	--
Tricorythidae	8	6.1	12	1.3	--	--
Viviparidae	--	--	8	7.9	--	--

Table 4.—Relative abundance of macroinvertebrates in the stomachs of captured rainbow trout (T) and in the drift (D) for April 1988. Linear selection values (L) range from -1 to +1 and (--) indicates no individuals of that taxa were collected.

Taxon	T	D	L
Aquatic Taxa			
Ephemeroptera			
Baetidae			
larvae	.434	.069	+0.4
adults	.001	--	0
Caenidae			
larvae	--	.004	0
Isonychiidae			
larvae	--	.008	0
Heptageniidae			
larvae	.001	--	0
Tricorythidae			
larvae	.003	.093	-0.1
Odonata			
Libellulidae			
larvae	--	.004	0
Hemiptera			
Dytiscidae	.001	--	0
Veliidae	--	.008	0
Coleoptera			
Curculionidae			
adults	.001	--	0
Elmidae			
larvae	--	.012	0
	--	.008	0

Table 4.—(cont.).

Taxon	T	D	L
Diptera			
Chironomidae			
larvae	.011	.088	-0.1
pupae	.054	.027	0
adults	.003	.015	0
Simuliidae			
larvae	.012	.173	-0.2
pupae	.004	.042	0
adults	.007	.035	0
Trichoptera			
Helicopsychidae			
larvae	.104	.108	0
pupae	.190	--	+0.2
Hydropsychidae			
larvae	.004	.012	0
adults	.037	--	0
Hydroptilidae			
larvae	.005	.019	0
adults	.001	--	0
Leptoceridae			
larvae	.005	.020	0
adults	.001	--	0
Polycentropodidae			
larvae	--	.015	0
Lepidoptera			
Pyralidae			
larvae	.005	.004	0
Turbellaria			
Tricladida	--	.023	0

Table 4.—(cont.).

Taxon	T	D	L
Oligochaeta	.003	--	0
Gastropoda			
Physidae	.001	--	0
Pleuroceridae	.061	--	+0.1
Viviparidae	.018	.004	0
Hydracarina	--	.004	0
Amphipoda			
Hyalellidae	.018	.188	-0.2
Decapoda			
Cambaridae	--	.004	0
Ostracoda	.003	--	0
Terrestrial Taxa			
Araneae	.002	--	0
Homoptera	.002	--	0
Hymenoptera	--	.008	0
Formicidae	.007	.015	0
Orthoptera	.001	--	0

Table 5.—Relative abundance of macroinvertebrates in the stomachs of captured rainbow trout (T) and in the drift (D) for August 1998. Linear selection values (L) range from (1) to (-1) and (--) indicates no individuals of that taxa were collected.

Taxon	T	D	L
Aquatic Taxa			
Ephemeroptera			
Baetidae			
larvae	--	.080	-0.1
Ephemeridae			
larvae	.580	.002	+0.6
Isonychiidae			
larvae	--	.002	0
Tricorythidae			
larvae	--	.229	-0.2
Odonata			
Gomphidae			
larvae	--	.002	0
Libellulidae			
larvae	.038	--	0
Hemiptera			
Belostomatidae	--	.002	0
Gerridae	--	.014	0
Veliidae	--	.005	0
Coleoptera			
Curculionidae			
adults	--	.002	0
Dryopidae			
adults	--	.007	0

Table 5.—(cont.).

Taxon	T	D	L
Elmidae adults	--	.009	0
Diptera			
Chironomidae			
larvae	--	.103	-0.1
pupae	--	.067	-0.1
Culicidae			
adults	--	.002	0
Simuliidae			
larvae	--	.005	0
adults	--	.004	0
Trichoptera			
Helicopsychidae			
larvae	--	.044	0
pupae	--	.002	0
Hydrobiosidae			
larvae	--	.002	0
pupae	--	.005	0
Hydropsychidae			
larvae	--	.011	0
Hydroptilidae			
larvae	--	.011	0
pupae	--	.004	0
adults	--	.016	0
Leptoceridae			
larvae	--	.005	0
Polycentropodidae			
larvae	--	.019	0

Table 5.—(cont.).

Taxon	T	D	L
Lepidoptera			
Pyralidae			
larvae	--	.005	0
Hirudinea	--	.002	0
Gastropoda			
Pleuroceridae	.154	--	+0.2
Hydracarina	--	.005	0
Amphipoda			
Hyalellidae	.230	.280	-0.1
Ostracoda	--	.014	0
Terrestrial Taxa			
Araneae	--	.002	0
Coleoptera	--	.004	0
Hymenoptera	--	.004	0
Formicidae	--	.027	0