

FEEDING BY BROWN TROUT (SALMO TRUTTA) AND  
ARIZONA TROUT (SALMO APACHE) AT VARIOUS LIGHT LEVELS

by

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## ABSTRACT

Brown trout (Salmo trutta) fed on brine shrimp in starlight ( $10^{-4}$  ftL). Arizona trout (Salmo apache) required light levels  $\geq$  to moonlight to feed. Brown trout (presumably using chemosenses) fed more effectively than Arizona trout in total dark. The greater visual and possibly chemosensory capabilities of brown trout would enable them to feed later in the evening and earlier in the morning than Arizona trout.

In high light ( $9.5 \times 10^1$  ftL) brown trout appeared more inhibited from feeding than Arizona trout, suggesting that Arizona trout are more active daytime feeders. Data from stomachs and fly-fishing supported this contention.

Brown trout utilized cover to a much greater degree than Arizona trout under daylight (50 ftL). This would minimize habitat overlap, and adds further support to the contention that Arizona trout are more active daytime feeders than brown trout.

Proof for partitioning of food and habitat between brown and Arizona trout is provided by this study, but the partitioning has been insufficient for the co-existence of these two species in many areas.

## CHAPTER 1

### INTRODUCTION

Different species that evolved together have adapted to partition their environment and reduce competition with each other (Nillson, 1963, 1965; Werner and Hall, 1976, 1977; Andrusak and Northcote, 1971). If species that did not evolve together come into contact with each other they may lack some or all of the adaptations for partitioning, resulting in severe competition and the possible displacement of one species. Fishery management practices have often involved combining different species that did not evolve together. In this paper, I am concerned with one such case history, the introduction of brown trout (Salmo trutta) into waters occupied by native Arizona trout (Salmo apache).

Until 1920 the Arizona trout was the only trout species in the White Mountains of Arizona and was common throughout the upper Salt and Little Colorado River drainages (Miller, 1972). Currently, the Arizona trout is mostly restricted to areas above 2500 m in the headwaters of the Salt River drainage (Harper, 1976); some of this

displacement could be the result of competition with brown trout (Behnke and Zarn, 1976).

Brown trout feed mostly from dusk through dawn (Brynildson, Hacker, and Klick, 1963). My preliminary observations and those of Harper (1976) indicate that the Arizona trout is very active during the day, which if true, could enable it and brown trout to partition their environment and lessen competition.

In this study I experimentally evaluated one of the potentials for competition between the Arizona and brown trouts by measuring their feeding efficiencies at different light levels. Further, in field studies, I corroborated my experimental results with data from stomach samples, fly-fishing, diurnal observations of trout feeding activity, and invertebrate drift samples.

## CHAPTER 2

### MATERIALS AND METHODS

#### Feeding at Various Light Levels

The experimental equipment was the same as described by Holonov and Tash (in press) with the following exceptions:

(1) 433 liters of water were used in the test tank; (2) plastic diaganols were removed from the corners; (3) two vinyl hoses leading into the test tank were cut and glued to the back wall of the tank 7 cm below the water surface and 35 cm from the corners; and, (4) several 1 mm holes were cut in the upper walls of these hoses (to release trapped air).

Twenty-six brown trout (13.2-17.7 cm TL,  $\bar{X}$ =14.5 cm), were captured on June 18, 1977 by electrofishing from the Big Bonito Creek study area (Harper, 1976) and taken to The University of Arizona. Twenty-six Arizona trout (12.0-15.9 cm TL,  $\bar{X}$ =14.6 cm) were taken from the same area on October 15, 1977. Between experiments, trout were kept in a refrigerated 490 l Living Stream Unit (Frigid Units Inc.). The unit was divided into three compartments (55x48x19 cm) with bricks arranged in each compartment to provide hiding places, to minimize fright, and to prevent fighting between

fish. A maximum of thirteen fish were held in a single compartment at one time. Trout were fed frozen brine shrimp once per day. During tests, water temperature in the Unit ranged from  $10^{\circ}$  to  $12^{\circ}\text{C}$ . A 40W fluorescent light 0.6 m above the Unit provided a 12 L:12 D hr photoperiod. Prior to testing, brown trout were acclimated for 24 days and Arizona trout for 17 days. A total of 80 experiments were conducted for brown (49) and Arizona trout (31) at light levels of  $9.5 \times 10^1$ ,  $9.5 \times 10^{-1}$ ,  $9.5 \times 10^{-3}$ ,  $9.5 \times 10^{-5}$ , and  $3.2 \times 10^{-5}$  ftL (foot-Lamberts). For comparative purposes, foot-Lamberts = foot-candles (Hunter, 1968).

Fish were not fed for 22-26 hours before testing. Fresh water was used for each experiment. Experiments were conducted in water kept at  $13^{\circ}\text{C} \pm 1.0^{\circ}\text{C}$ . A fish, selected randomly from the holding compartment, was acclimated for two hours in the test tank. In each experiment, 100 active adult brine shrimp (3.5-10.0 mm,  $\bar{X}=7.3$  mm body length) were flushed with one liter of water into the test tank containing the test fish. Fish had two minutes to feed on shrimp, then they were removed and transferred to the Living Stream Unit. No fish was tested more than once at the same light level (except at the highest level), and no fish was tested more than three times. To determine the number of shrimp eaten by test fish, at the end of each experiment, the remaining shrimp were counted and subtracted from 100.

I used the same methods in fourteen tests (eight with browns and six with Arizona trout) run in the dark (Of+L) except that the trout were left in with the shrimp for one hour instead of two minutes. Also in the dark, one test for each species was run with fish given thirteen hours to feed on shrimp. Counting error was determined by running trials without fish.

#### Concealment and Vertical Distribution

Twelve each of Arizona and brown trout (12-17 cm TL), taken on November 19, 1976 from the Big Bonito Creek study area, were kept in a plywood tank (185 x 54 x 61 cm) for seven days prior to tests. Experiments were conducted in the Living Stream Unit. Water temperature in both tanks was kept at 7<sup>o</sup>-9<sup>o</sup>C. The Living Stream was illuminated from 0800-2000 hour MST with a 40W fluorescent light suspended 0.7 m above the water surface that provided approximately 50 ftL in the Living Stream. Between tests, fish were fed brine shrimp daily; during tests, fish were fed only after observations. Observations were made from a blind that concealed the observer.

Three metal cans (17x9 cm) with blackened interiors were placed in each of two of the Living Stream compartments. Three brown trout were put into one compartment and three Arizona trout in the other. After a 24 hour acclimation period, the trout were observed for 0.5 hour periods at

3.5 hour intervals from 0800 to 1900 hours for two days, and the time each species of trout stayed in the cans was recorded.

Four horizontal lines were drawn on the window of the Living Stream to mark off five water levels: (1) from the bottom to 3.8 cm; (2) 3.8 to 10.2 cm; (3) 10.2 to 16.5 cm; (4) 16.5 to 22.8 cm; and (5) 22.8 cm to the surface. The water depth was kept at 29.2 cm. Ten brown trout were put into one compartment and ten Arizona trout into another. After 24 hours acclimation, thirteen observations were made  $\geq$  two hours apart during the daylight period of the ensuing three days. The number of fish of each species that occurred at each level was recorded for each observation.

#### Diurnal Feeding Activity

Three areas (Bull Cienega on Ord Creek, the Big Bonito Creek study area, and an area approximately two miles downstream from the study area) were fly-fished for brown and Arizona trout on three separate days. Two fishermen fished two separate 150 m sections in each of the three areas using 2.4 m fly rods, floating line, and muddler minnows on #8 barbless hooks. The number of fish strikes and the number of each species caught were recorded; all fish caught were released. The Big Bonito Creek study area was fished from 1130-1230, 1530-1630, and 1900-1930

hours on July 28, 1976, and from 0630-0730 hours on July 29, 1976. The stream two miles below the study area was fished from 0630-0730, 1100-1200, 1500-1600, and 1830-1930 hours on August 16, 1976. Ord Creek was fished from 0600-0700, 1030-1130, 1500-1600, and 1830-1900 hours on August 10, 1976.

#### Stomach Samples

On June 17, 1977, five brown and five Arizona trout (12.3-18.1 cm TL) were collected by electrofishing at 0600 and again at 1800 hours from the Big Bonito Creek study area. Stomachs from these fish were preserved in 10% formalin. Twenty stomachs were taken from brown trout that were collected by Harper during the afternoon of October 11, 1975. Aquatic insects in stomachs were identified to family using Usinger (1973). All winged organisms were classified as terrestrials. Only items that had undergone relatively little digestion were counted. Based on digestion rates determined by Elliot, (1972), items in stomachs that were still identifiable were considered to have been eaten in the twelve hours preceding collection.

#### Invertebrate Drift

At 0600 hour on June 16, 1977, two drift nets (constructed by McClain, 1976) were set in a riffle at the lower end of the Big Bonito Creek study area. The nets were emptied at four hour intervals during a 24 hour period.

One net was again set in the same riffle on the afternoon of July 1, 1977 and was emptied every 0.5 hours from 1745-2115 hours and again from 0400-0600 hours. A light reading was taken every 0.5 hours over the same periods using a meter described by Holonov and Tash (in press). Drift samples were preserved in 70% ethanol and their contents were identified in the same manner described above for stomach contents.

## CHAPTER 3

### RESULTS

#### Feeding at Various Light Levels

Brine shrimp eaten by brown and Arizona trout in 80 two minute tests are shown in Table 3.1. The greatest range in shrimp eaten occurred in both species at  $9.5 \times 10^1$  ftL. Since behavioral patterns could be modified by conditioning in the laboratory, I ran linear regressions on both species relating feeding rates to the number of days the fish were in the laboratory prior to tests (Figure 3.1); the correlation was significant for brown trout ( $r=0.799$ ;  $p>0.005$ ), indicating a behavioral change, but the correlation was not significant for Arizona trout ( $r=0.327$ ;  $p>0.05$ ). The most rapid feeding rates for both species occurred at  $9.5 \times 10^1$  ftL, and, at this level, both species were able to feed at approximately equal rates.

Brown and Arizona trout were equally as efficient in eating at all light levels down to  $9.5 \times 10^{-3}$  ftL, below which brown trout fed more efficiently (Table 3.1 and Figure 3.2). Although the average feeding rate of Arizona trout at  $9.5 \times 10^{-1}$  ftL was higher than for browns, the difference was not significant at the 0.05 level ( $LSD_{df(36)}=6.7$ ).

Table 3.1 Brine shrimp eaten in two minutes by brown and Arizona trout at five light intensities.

(Note) Experimental error in counts ranged from -1 to +2; all counts less than 1 are considered as 0.

Light Level (ftL)	Tests		Eaten ( $\bar{X}$ )		Range		Standard Error s	
	Browns	Arizona	Browns	Arizona	Browns	Arizona	Browns	Arizona
$9.5 \times 10^1$	15	13	28.1	34.9	0-62	0-74	24.5	22.7
$9.5 \times 10^{-1}$	6	6	33.3	38.3	30-46	29-48	6.3	7.4
$9.5 \times 10^{-3}$	7	6	22.1	22.4	16-28	13-29	4.1	6.3
$9.5 \times 10^{-5}$	11	6	7.8	.33	0-21	0-2	6.8	1.4
$3.2 \times 10^{-5}$	10	-	0.0	-	0-1	-	1.3	-

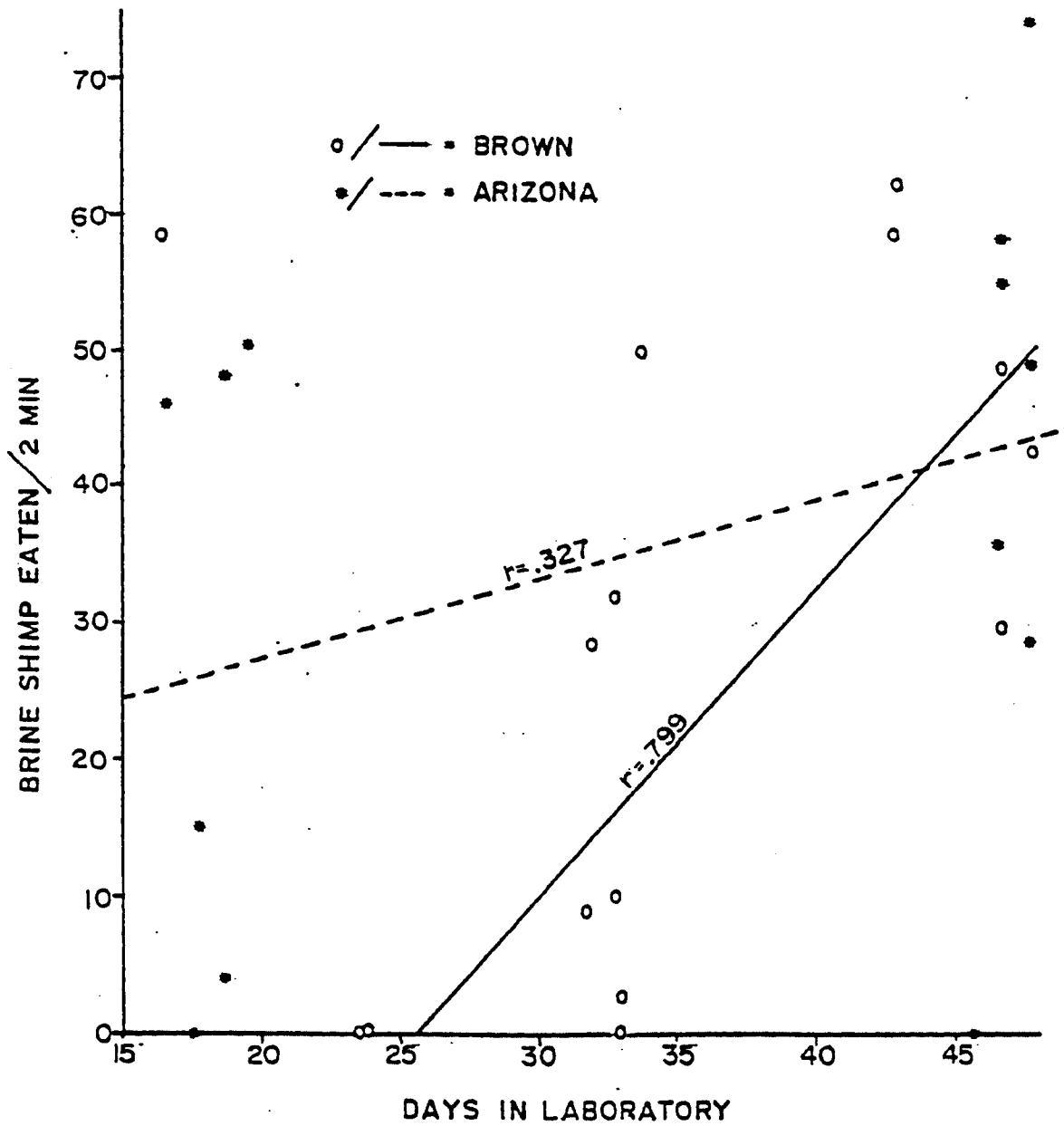


Figure 3.1 Variation in feeding rates with days in laboratory of brown and Arizona trout tested at a light intensity of  $9.5 \times 10^4$  ftL.

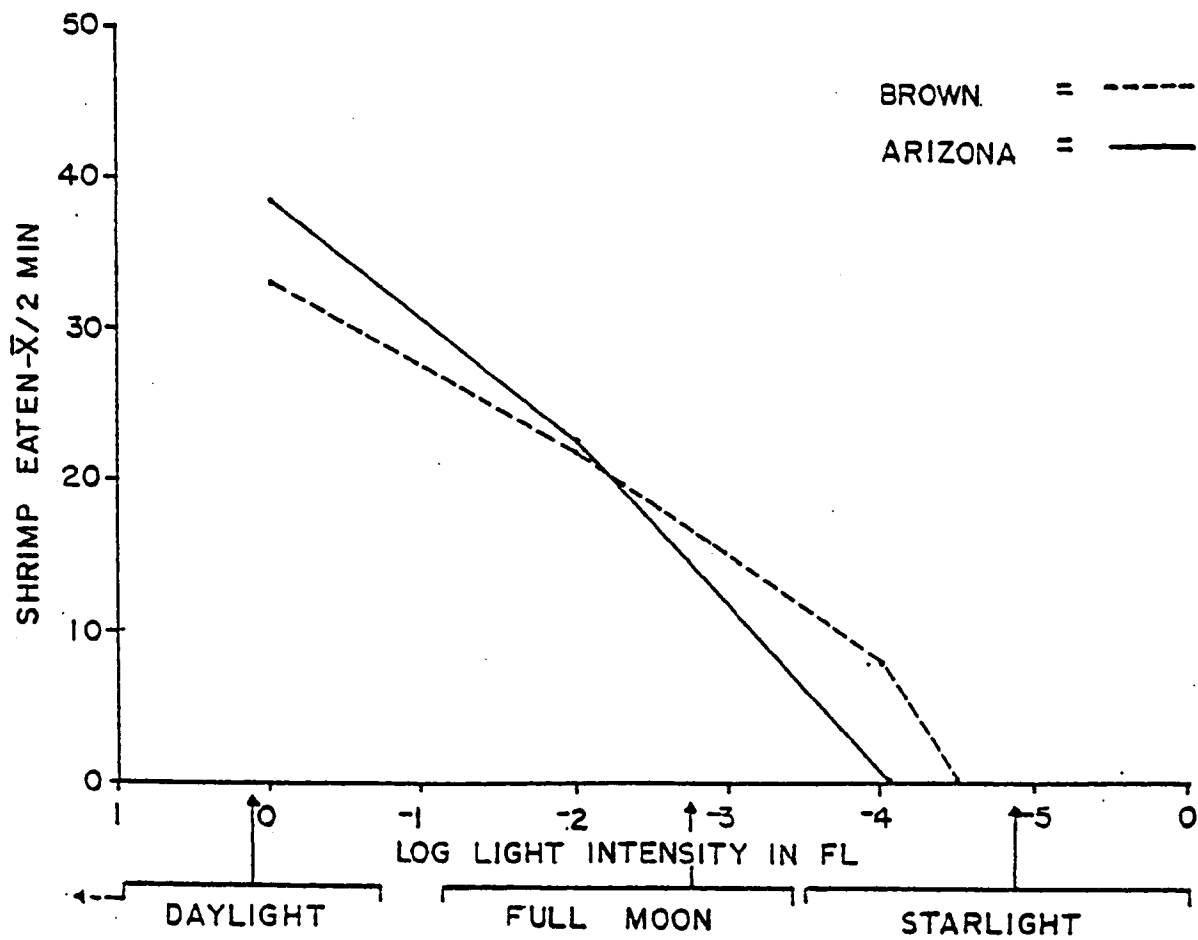


Figure 3.2 Mean feeding rates of brown and Arizona trout at various light intensities in the field.

Arizona trout apparently could not feed at  $9.5 \times 10^{-3}$  and  $9.5 \times 10^{-5}$  ftL. Brown trout did not feed at  $3.2 \times 10^{-5}$  ftL, indicating that the minimum amount of light required for visual feeding in this species is between  $9.5 \times 10^{-5}$  and  $3.2 \times 10^{-5}$  ftL.

There was a significant difference between the slopes of the two lines shown in Figure 3.2 (ANOVA test-F ratio value  $df(2,36) = 4.0; p=0.027$ ). However, an obvious difference in feeding rates between the two species only occurred at  $9.5 \times 10^{-5}$  ftL.

Neither species ate shrimp in the dark (0 ftL) during two minute tests, but in eight 60 minute tests brown trout ate an average of 21 (Range = 3-43) out of 100 shrimp. During six 60 minute tests with Arizona trout, no feeding occurred. During two 13 hour tests in the dark, the browns ate 91 and the Arizona trout ate 85 out of 100 shrimp.

#### Concealment and Vertical Distribution

Three brown trout hid inside cans for 88% of 720 minutes, and three Arizona trout spent 6% of 720 minutes in cans. The occurrence of each species in each of five different water levels during thirteen observations of ten trout of each species are illustrated in Figure 3.3. In water level experiments, both species oriented themselves against the current produced in the Living Stream but brown trout usually rested on the tank bottom, and were

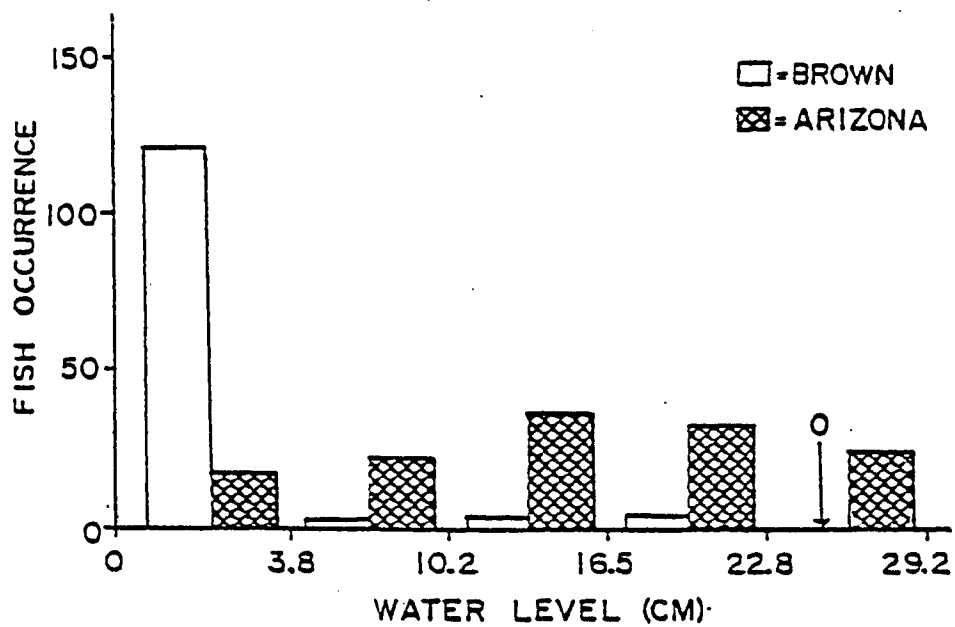


Figure 3.3 Total number of times individuals of brown and Arizona trout were observed in each of five water levels in thirteen observations on ten trout of each species.

rarely observed in the four upper water levels. Resting brown trout usually touched bottom with at least their ventral fins and sometimes their bellies. When an Arizona trout occurred in the bottom area, it did not actually rest on the bottom, but hovered above it.

#### Diurnal Feeding Activity

From a total of 99 fish strikes, 39 Arizona and one brown trout were caught in seven man-hours of daytime fly-fishing on the study area at Big Bonito Creek (Harper, 1976, found Arizona trout outnumber brown trout in this area 10:1). In a lower section of Big Bonito Creek (this author in preliminary observations found that brown trout outnumbered Arizona trout 4:1 in the area fished) twelve Arizona trout and three brown trout were caught out of a total of 45 strikes that occurred in eight man-hours of daytime fly-fishing.

Nineteen brook trout (Salvelinus fontinalis), four Arizona trout and no brown trout were caught from a total of 59 strikes that occurred in seven man-hours of daytime fly-fishing on Ord Creek (John Rinne, Rocky Mountain Forestry and Range Experiment Station, Arizona State U., Tempe, Arizona, personal communication, found the ratio brook: brown:Arizona trout to be 45:20:1 in the area fished).

### Stomach Samples

Numbers of food items that were in five Arizona and five brown trout stomachs from fish taken at 1800 hours on June 17, 1977 in the Big Bonito Creek study area were respectively 335 and 54. Five Arizona and five brown trout stomachs from fish taken at 0600 hours on June 17, 1977 in the study area contained 67 and 51 food items respectively.

Nine stomachs from Arizona trout taken from the study area by Harper (1976) during the afternoon of October 15, 1977 contained (by number) 14% trichopterans and 45% terrestrial insects; twenty stomachs from brown trout taken at the same time contained 84% trichopterans and 13% terrestrial insects.

### Invertebrate Drift

Insects caught in drift nets during June 16 and 17, 1977 are shown in Figure 3.4. Total drift was relatively constant during the day, but increased markedly from 1800 to 0200 hours and then decreased. During the day terrestrial drift was constant and in about the same abundance as aquatic drift. A peak in terrestrial drift did occur during 1800-2200 hour.

Aquatic invertebrate drift increased dramatically during the evening of July 1, 1977, when light intensity decreased to about  $1.4 \times 10^{-2}$  ftL and then decreased the

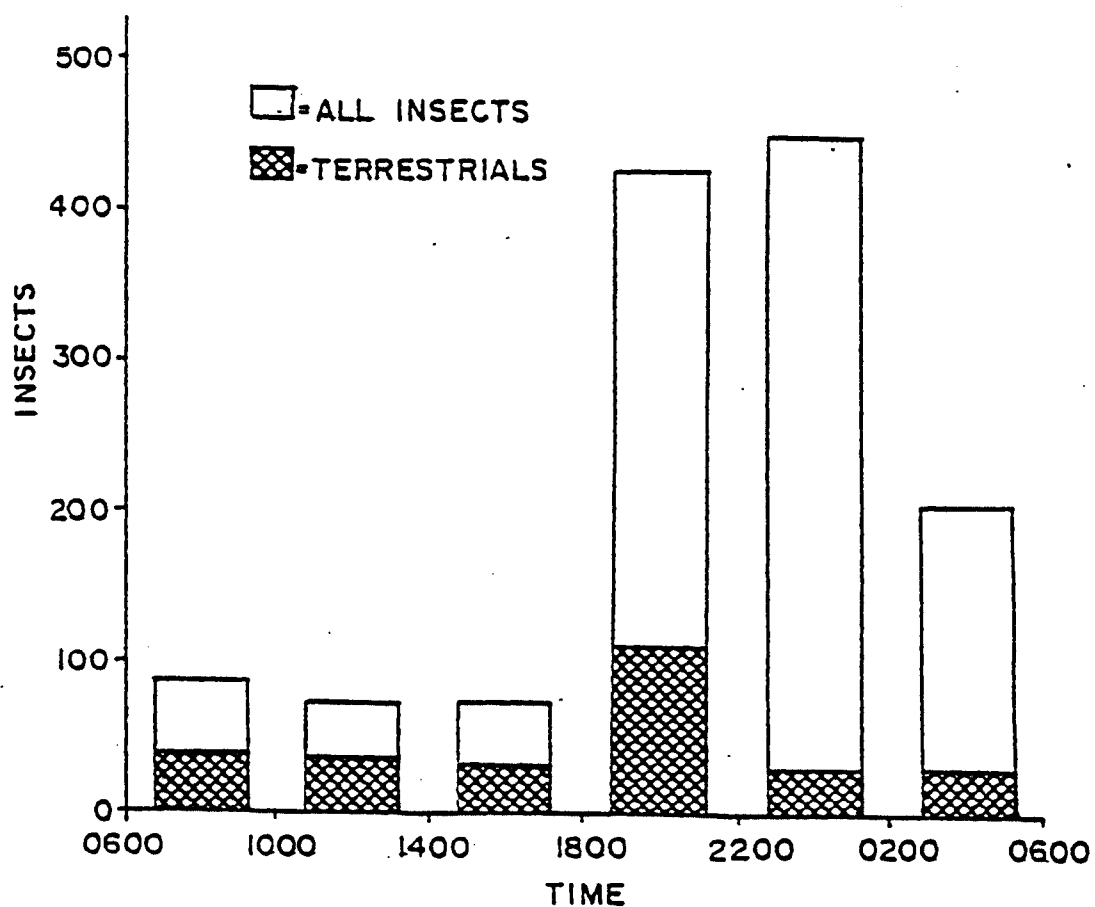


Figure 3.4 Total numbers of aquatic and terrestrial insects taken from Big Bonito Creek on June 16-17, 1977 during different time intervals.

next morning when light intensity increased to  $1.2 \times 10^{-3}$  ftL (Figure 3.5). The highest drift rates occurred in the evening, when the light intensity was decreasing from  $4 \times 10^{-4}$  to  $1.6 \times 10^{-5}$  ftL.

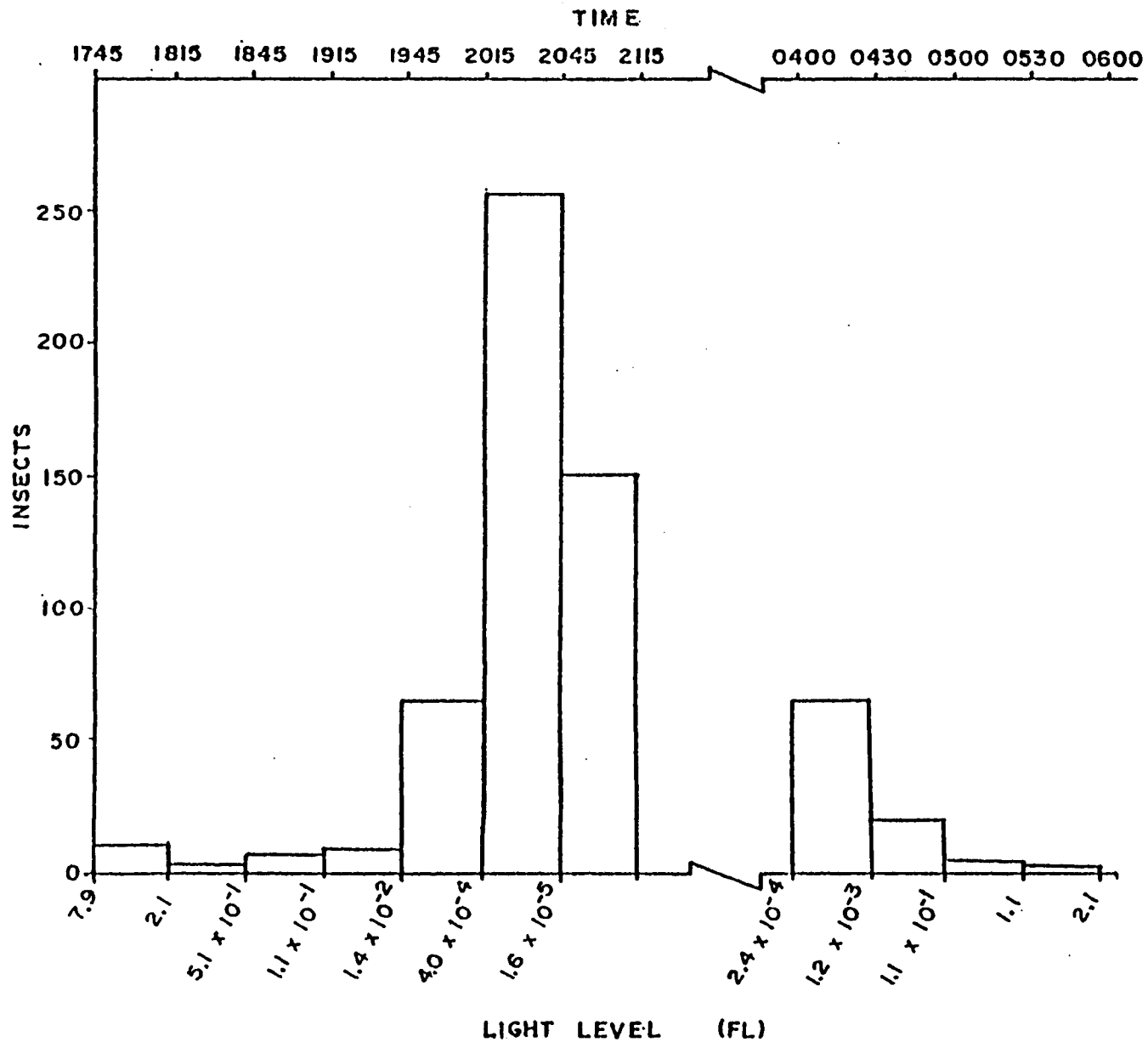


Figure 3.5 Total numbers of aquatic insects taken from Big Bonito Creek on July 1-2, 1977 at different light intensities.

## CHAPTER 4

### DISCUSSION

Salmonids are primarily visual feeders (Kalleberg, 1958; Ware, 1972), but they also feed by use of chemosensory adaptations (Hoar, 1942; McBride et al., 1962). There are two general considerations to be accounted for when analyzing the feeding abilities of trout, one being the mechanical limitations (the physical limitations of the visual and chemosensory adaptations of each species) and the other being behavioral traits (innate and conditioned) of each species. In general, the feeding pattern in any individual of a trout species is the result of the combination of its behavioral responses acting within the limitations of its physical abilities.

The general feeding patterns of both brown and Arizona trout are comparable to the feeding patterns found for other salmonids (Needham, 1969; Harper, 1976). Within these patterns, I will first discuss the impact of visual feeding. A few studies are available on the variations in visual capabilities at different light levels between salmonid species (Ali, 1959; Schutz and Northcote, 1972). Variations between species are most noticeable at lower

light intensities and have been attributed to differences in the retinomotor responses rather than ocular structure. Minor variations in the ability to see at various light intensities between trout species could allow them to partition food in their environment and thereby reduce competition.

Prior to my study, the visual capabilities of neither brown nor Arizona trout had ever been investigated at exact light levels. I found that brown trout have very sensitive vision, even enabling them to feed on brine shrimp in starlight ( $10^{-4}$  ftL). However, Arizona trout required light levels  $\geq$  moonlight to feed. This difference in visual feeding may cause partitioning of food between these two species by enabling brown trout to feed more actively than Arizona trout later in the evening and earlier in the morning (or even throughout moonless nights when skies are cloudless).

The salmonid eye has been found to be highly adapted to function over a wide range of light intensities and bright light does not hinder vision (Brett and Groot, 1962). I found that brown trout and Arizona trout fed actively in bright light ( $9.5 \times 10^1$  ftL), and brown trout fed as rapidly as Arizona trout. Therefore, if based only on their physical limits to feed visually, the only partitioning of food that could occur between brown and Arizona trout would

occur at low light levels. However, salmonids also have chemosensory feeding abilities (Hoar, 1942; McBride et al. 1962). I found that brown trout ate as many as 43 ( $\bar{X}=21$ ) out of 100 shrimp in 60 minutes in total dark, strongly suggesting that they were using chemosenses to locate shrimp. Arizona trout ate no shrimp in total dark during 60 minutes, but in 13 hours ate 85 of 100. These tests showed that brown trout have greater chemosensory abilities than Arizona trout, suggesting the possible presence of another mechanism for partitioning of food and thereby for decreasing competition.

Both innate and conditioned behavior can contribute to the observed feeding characteristics of fish. Hoar (1942) found that bright sunlight depressed feeding activity in brook trout and Atlantic salmon. This could be due to shade seeking and fright responses to high light which have been observed in brown, brook, and rainbow trout (Newman, 1956; Ritter and MacCrimmon, 1973; MacCrimmon and Kwain, 1966). I observed that both brown and Arizona trout were more easily frightened by movement or noise under bright light (50 ftL), and quickly began to seek cover. During feeding tests, both brown and Arizona trout showed their greatest variations in feeding rates at the highest light level tested ( $9.5 \times 10^1$  ftL). Although both species showed some feeding inhibition and greater fright responses

at the highest light level, the inhibition was more prevalent in the browns. This data suggests that brown trout would feed less actively than Arizona trout during the day. Even more support for daily partitioning of food between brown and Arizona trout was provided by data from fly-fishing, from stomach analysis, and from field and laboratory observations on habitat utilization.

Mostly Arizona trout were caught during 22 man-hours of daytime fly-fishing on two streams containing both brown and Arizona trout. The ratio of Arizona trout to brown trout was 55:4, despite the fact that the browns outnumbered Arizona trout in two of the three areas fished by ratios of 20:1 and 4:1. Further evidence for this feeding pattern is that, in fish captured at 1800 hours, stomachs of Arizona trout contained many more items (335) than those of brown trout (54). These data offer strong support to the contention that there is a daily partitioning of food between these two species with Arizona trout eating more during the day.

The manner in which fish utilize habitat can greatly modify their daily feeding patterns. Species that seek cover during periods of high light greatly reduce their feeding area and thereby reduce competition for food with other species that feed in the open during these periods. In the field, Arizona trout were often observed

out in shallow riffles during bright sunlight, but brown trout were rarely observed in this situation. In laboratory experiments under high light (50 ftL), brown trout spent 88% of the time hidden in cans, but Arizona trout hid only 6% of the time. Interspecific differences in daytime use of cover have also been found between Atlantic salmon and brook trout (Gibson and Keenleyside; 1966) and brown trout have been found to use cover more than both rainbow and brook trout (Lewis, 1969; Jenkins and Klain, 1969; Butler and Hawthorne, 1968). In addition to browns using cover more than Arizona trout, in experiments (also at 50 ftL) to determine vertical distribution I observed that brown trout usually stayed on the bottom, as if hiding, whereas Arizona trout usually occurred relatively high in the water column. Further evidence showing a tendency for greater secretiveness in brown trout than in Arizona trout under high light intensities is that most of the browns and none of the Arizona trout captured in the field had mottled coloration. Mottled coloration has been observed as a characteristic of trout that hide on the bottom (Jenkins, 1969). These observations show that there is little competition for cover during the day between these two species, and supports the contention that brown trout are less active daytime feeders than Arizona trout.

These physical and behavioral differences between brown and Arizona trout are important in view of what is known about the diel invertebrate drift cycles. Aquatic invertebrates increase in stream drift at night (Hynes, 1970; Waters, 1969; and present study) in conjunction with changes in light intensity; the threshold light intensity which initiates high aquatic insect drift rates has been found to range from  $10^{-1}$ - $10^{-4}$  foot-candles (Holt and Waters, 1967; Bishop, 1969). I found a threshold value between  $10^{-1}$ - $10^{-2}$  ftL. These threshold values coincide well with the light level at which brown trout surpass Arizona trout in their ability to feed, indicating that night drifting insects are more vulnerable to predation by brown trout than by Arizona trout. Previous studies have shown that brown trout feed effectively on nighttime drift (Elliot, 1967; Jenkins, Feldmeth, and Elliot, 1970). Arizona trout, however, could still capture as much food as brown trout by feeding more actively during the day when visual acuity is maximum.

In conclusion, I have shown that partitioning of food and habitat occurs between brown and Arizona trout by: (1) their having different absolute visual and chemosensory capabilities with the greater visual and chemosensory acuity of brown trout in low light enabling them to feed more effectively than Arizona trout later at

night and earlier in the morning; and (2) their differences in behavior causing them to use the habitat in ways wherein they have little over-lapping use at the same time. These partitionings undoubtedly reduced any competition for food or space that may have occurred between these two species, but, apparently the reduction was insufficient, as brown trout have displaced Arizona trout from many areas.

Further research on the causes for this displacement are required in order to understand the many complex interactions occurring between these two species.

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