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A QUALITATIVE AND QUANTITATIVE STUDY OF TROUT FOOD IN CASTLE LAKE, CALIFORNIA[1]

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Trout in Castle Lake were studied, using stomach content analysis and calorimetry, to delineate their diets and energy supply. A qualitative difference exists between foods of the eastern brook trout, *Salvelinus fontinalis*, and rainbow trout, *Salmo gairdnerii*, with the brook trout feeding primarily on benthic organisms and the rainbow trout feeding primarily on terrestrial organisms. Zooplankton is eaten equally by both species. Based on the energy content of the food items and their proportions in the diet, 40% of the total energy consumed by the trout is benthic in origin, about 10% is pelagic, and about 50% is terrestrial.

INTRODUCTION

Despite advances in trout management, one cannot predict with certainty how a fish population will adapt to its environment. Successful management of fish populations requires a sound knowledge of food availability and utilization. The examination of stomach contents provides a means of studying both these parameters.

This study was carried out at Castle Lake, California, with populations of eastern brook and rainbow trout. The objectives of the study were (i) to determine what organisms made up the trout diet, (ii) to determine the caloric value of each food item, and (iii) to calculate the relative importance of each food item in the diet of the two trout populations.

STUDY AREA

Castle Lake is located about 10 miles southwest of the city of Mount Shasta in Siskiyou County, California. It is a cirque lake bounded by steep cliffs on the south, by high ridges on the east and west, and by a terminal moraine on the north. It is fed by snowmelt in the spring and by underwater springs throughout the year. The single outflow is through the moraine at the north end. The lake lies at an elevation of 1,707 m (5,600 ft) and has an area of 20.1 ha (49.6 acres). The northern half of the lake averages about 3 m in depth and the southern end drops steeply to 37 m. Ice covers the lake from December to mid-April or May. Strong thermal statification occurs in the summer, with the thermocline usually at about 9 meters. Surface temperatures in August reach 22 C. The lake has a self-sustaining population of brook trout ; rainbow trout, which do not reproduce in the lake, are maintained by an August plant of 10,000 fingerlings. The Castle Lake fishery has been studied since 1938 by the California Department of Fish and Game (Wales, 1946; Wales and German, 1950, 1956; Wales and Borgeson, 1961). Limnological studies were begun in 1959 and

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TABLE 1

Food of Eastern Brook Trout in Castle Lake, Averages for 1963, 1964, and 1965 *

	May			June			July			August			September			October		
	N	V	P	N	V	P	N	V	P	N	V	P	N	V	P	N	V	P
Aquatic organisms																		
Odonata																		
Dragonfly n	188	64.3	**33.0**	66	17.3	**14.6**	9	2.8	**9.6**	3	0.5	**11.6**	44	18	**30.2**	19	11.7	**53.8**
Damselfly n	33	9.0	**5.0**	6	1.5	**1.4**	1	1.0	**0.6**	--	--	--	0.7	Tr	**0.1**	2	0.4	**2.3**
Ephemeroptera																		
Mayfly n	2	0.2	**0.1**	--	--	--	6	0.2	**0.5**	--	--	--	--	--	--	1	0.5	**0.4**
Trichoptera																		
Caddisfly l	86	9.0	**4.0**	206	16.0	**14.9**	30	1.4	**3.3**	4	0.05	**0.2**	9	0.6	**0.7**	13	1.2	**4.4**
Diptera																		
Chironomidae	130	1.5	**0.7**	1500	6.1	**6.4**	424	3.1	**10.3**	16	0.1	**2.5**	153	1.1	**1.8**	1.3	Tr	Tr
Heleidae p				1334	3.0	**2.7**	--	--	--	--	--	--	--	--	--	--	--	--
Heleidae l	21	0.1	**0.1**	350	7.5	**2.6**	7	0.2	**0.4**	33	0.3	**1.6**						
Neuroptera																		
Sialidae	4	2.0	**1.2**	2	0.6	**0.4**	0.3	Tr	Tr			--						
Acarina																		
Water mites				1	Tr	Tr	--	--	--	--	--	--	--	--	--	--	--	--
Cladocera																		
Daphnia	400	0.3	**0.1**	4389	11.4	9.6	737	3.1	**8.4**	1415	5.7	**52.7**	2227	12.1	**18.0**	464	1.8	**9.2**
Eurycercus							24	0.8	**0.3**	242	0.8	**4.8**	74	0.2	**0.3**	308	0.9	**3.2**
Oligochaeta				1	Tr	Tr	--	--	--	--	--	--	--	--	--	--	--	--
Mollusca																		
Snails	12	1.0	**0.4**	16	1.6	**1.2**	6	0.7	**3.2**	3.3	0.2	**8.6**	4	0.2	**0.2**	3.7	0.2	**1.0**
Clams	8	0.4	**0.2**	16	0.6	**0.4**	1	Tr	Tr	2.7	Tr	**0.2**	0.7	Tr	Tr	0.7	0.7	**1.3**

Terrestrial organisms																		
Diptera	1.3	Tr	Tr	24	1.1	1.0	22	1.7	4.8				1.3	Tr	Tr			
Hymenoptera																		
Ants										0.3	Tr	1.0	282	8.6	9.1			
Others	21	2.4	0.9	15	0.2	0.3	0.3	Tr	Tr							0.3	Tr	Tr
Coleoptera	17	1.8	0.8	3	0.2	0.1	0.6	Tr	0.2									
Neuroptera							0.3	0.2	0.6									
Hornoptera	42	0.1	Tr	14	0.1	0.1	7	0.5	1.3				8	0.4	0.7			
Hemiptera	0.3	0.1	0.1	52	0.6	0.8							1.3	Tr	Tr			
Lepidoptera																		
Odonata																		
Damselflies							2	1.0	2.0									
Arachnida				8.7	0.1	0.1											Tr	
Frog																0.3	4.3	Tr
Worms		0.3	0.2		1.2	0.8		0.5	2.0		0.2	0.8						26.6
Debris and unidentifiable material		38.5	19.2		41.7	40.1		15.7	42.4		0.5	16.3		25.5	37.7			
Total volume	133.2			106.8			33.8			8.4			67.3			20.6		
Number of stomachs	74			43			18			3			21			16		

*N = number, V = volume (ml), P = % of the total volume, Tr = less than 0.05 (ml or %), l = larvae, n = nymphs, p = pupae.

TABLE 2

Food of Rainbow Trout in Castle Lake, Averages for 1963, 1964, and 1965 *

	May (1963,1964)			June			July			August			September			October		
	N	V	P	N	V	P	N	V	P	N	V	P	N	V	P	N	V	P
Aquatic organisms																		
Odonata																		
Dragonfly n	32	12.7	**10.0**	0.3	0.2	**0.1**	16	10.7	**10.7**	20	12.3	**11.5**	23	14.3	**6.6**	4	4.0	**5.6**
Damselfly n	0.7	0.1	**0.1**	9	1.6	**0.9**	0.7	Tr	**0.1**	6	1.0	**1.1**	22	1.3	**0.8**	4	0.7	**1.1**
Ephemeroptera																		
Mayfly n	2.7	0.1	**0.1**	4	0.4	**0.7**	28	0.1	**0.4**	1	0.2	Tr	11	0.2	**0.1**	4	Tr	Tr
Plecoptera																		
Stonefly n									--	--	--	--	12	0.2	Tr	--	—	--
Trichoptera																		
Caddisfly l	72	5.2	**4.5**	47	4.0	**5.0**	26	2.0	**2.7**	18	0.1	**0.1**	26	1.8	**0.7**	58	4.2	**2.0**
Diptera																		
Chironomidae	156	1.6	**1.2**	324	3.0	**2.6**	253	2.1	**1.9**	122	0.5	**0.9**	2224	9.2	**2.6**	13	0.1	**0.1**
Heleidae p ----------------				5577	14.2	**7.4**	23	0.1	**0.1**	--	--	--	--	--	--	--	--	--
Heleidae l	134	0.7	**1.5**	502	3.3	**3.0**	4.7	Tr	Tr	9	0.1	**0.1**	25	0.2	**0.1**	--	--	--
Neuroptera																		
Sialidae											--	--	0.3	0.1	Tr	--	--	--
Cladocera																		
Daphnia ---------------	1583	6.3	**3.9**	4666	13.4	**10.5**	2154	8.9	**8.4**	5346	22.0	**26.1**	17367	75.0	**24.5**	20944	51.6	**29.3**
Eurycercus --------------							81	0.3	**0.3**	37	0.3	**0.2**	537	2.0	**0.4**	352	1.0	**0.7**
Oligochaeta	65	0.6	**0.4**		--	--	--	--	--	--	--	--	--	--	--	--	--	--
Copepoda							2	Tr	Tr	--	--	--	--	--	--	--	--	--
Mollusca																		
Snail	2	Tr	Tr	6	0.4	**0.2**	2.3	0.2	**0.2**	7	0.1	**0.1**	21	0.4	**0.1**	12	0.2	**0.2**
Clam	3	0.4	**0.4**	1	Tr	**0.1**	--	--	--	--	--	--	--	--	--	32	0.4	**0.1**
Fish	0.3	0.3	**0.4**	--	--	--	0.3	0.2	Tr	0.3	0.7	**0.8**	--		--	0.3	0.8	**0.3**

Terrestrial organisms																		
Diptera	71	4.4	5.4	61	3.8	1.9	88	3.0	2.7	58	2.5	2.6	173	2.2	4.3	204	5.7	5.0
Hymenoptera																		
Ants				3	2.0	3.0	18	0.6	0.5	175	8.0	70	2041	70.2	21.0	119	9.2	4.2
Others	61	6.3	4.2	52.3	10.1	4.8	37	1.8	1.6	12	3.0	3.3	9	1.0	0.6	206	6.6	4.3
Coleoptera	42.9	2.0	1.8	48	3.8	2.7	55	5.0	4.4	38	1.4	1.4	4	0.4	0.2	41	1.7	1.0
Neuroptera							0.3	Tr	Tr		0.1	0.3	0.3	Tr	Tr			
Homoptera	51	0.9	0.7	19	2.2	1.0	36	2.5	2.2	6	0.4	0.5	134	2.3	0.6	122	4.3	2.7
Hemiptera	2	0.1	0.5	8	0.1	0.2	2	0.1	0.1	209	2.5	4.6	1481	12.8	4.3	126	2.3	1.6
Lepidoptera													0.3	Tr	Tr			
Odonata																		
Dragonflies							0.7	0.7	0.6									
Damselflies							10.3	4.7	4.1				2	0.6	0.5	5	4.0	1.4
Orthoptera																		
Acrididae							0.3	0.7	0.6							0.3	0.3	0.2
Arachnida		0.1	0.1	14	0.3	0.3	11	0.2	0.1	7	0.3	0.4	1	Tr	Tr	64	1.5	0.7
Salmon eggs				20	10.0	4.4	22	13.3	18.2	15	10.3	4.7	0.3	0.1	Tr	0.7	2.0	0.1
Worms								1.0	1.6		4.0	2.9		2.0	0.8		0.8	0.5
Debris and unidentifiable material		39.5	31.8		80.4	55.7		36.4	36.0		25.1	31.8		78.9	34.1		63.9	33.3
Total volume	85.0			149.9			97.3			88.9			267.4			159.8		
Number of stomachs	27			45			38			26			67			72		

* N = number, V = volume (ml) P = % of the total vol me Tr = less than 0.05 (ml or %), l = larvae, n = nymphs, p = pupae.

have continued on a year-round basis. They include nutrient limiting factors and primary productivity (Goldman, 1960, 1963, 1967), zooplankton population dynamics (Carlson, 1968), and benthos communities (Beatty, 1968).

METHODS AND MATERIALS

All stomachs examined were from fish caught by anglers at Castle Lake. Samples from the 1963, 1964, and 1965 fishing seasons were collected and preserved in formalin following the method of Borgeson (1963). These samples were pooled by fish species each month. Samples taken during the summer of 1966 and winter of 1966-67 were preserved in formalin until counted. From May 1967 to May 1968 the whole stomach was taken and frozen before counting. Individual food items were picked out of these samples and dried at 50 C at least 48 hr for calorimetric determination. During the winter, fish were taken through the ice using a handline. Rainbow trout stomachs were sampled by year class (I, II, III, IV) using a fin clip code. The brook trout stomachs were sampled according to arbitrary size classes (<6, 6–8, 8-10, >10 inches).

Food items were counted in a petri dish using a 10X binocular dissecting microscope. For the 1966 samples, number and frequency of occurrence were recorded, while number and volume were measured for each food item during 1967-68. Volumes were determined by water displacement in a graduated centrifuge tube. The 1963-65 samples were counted using the method of Borgeson (1963) to obtain number and volume.

Caloric values were determined using a nonadiabatic Phillipson microbomb calorimeter calibrated with benzoic acid. Individual food items, keyed to family or genus, were pooled from several samples, dried, pulverized, made into pellets, and combusted. Five determinations were made for each food item and the mean taken as the caloric value.

For convenience, the various stomach contents were divided into four categories: terrestrial food, pelagic food, benthic food, and debris or unidentifiable material. Terrestrial food included any food item originating outside the lake. Pelagic food included the zooplankton (*Daphnia, Holopedium,* and *Diaptomus*) and fish. The benthic component included those organisms that spend the majority of their time on the bottom of the lake. This included the permanent bottom dwellers (snails, clams, and oligochaetes) and the transient population of juvenile aquatic insects. Debris included cigarette filters, rocks, insect wings, pine needles, etc. These categories were chosen to show the source of the trout food. Aquatic nymphs and larvae were considered to be benthic in origin, although they may often be found in the pelagic zone or at the surface.

RESULTS

Insects, both terrestrial and aquatic, were the major part of the food eaten by both brook and rainbow trout throughout the year (Tables 1 and 2). Zooplankton was a moderately important food item for brook trout, but made up a larger proportion of the rainbow trout food. *Daphnia rosea* was the major zooplankter eaten by both species.

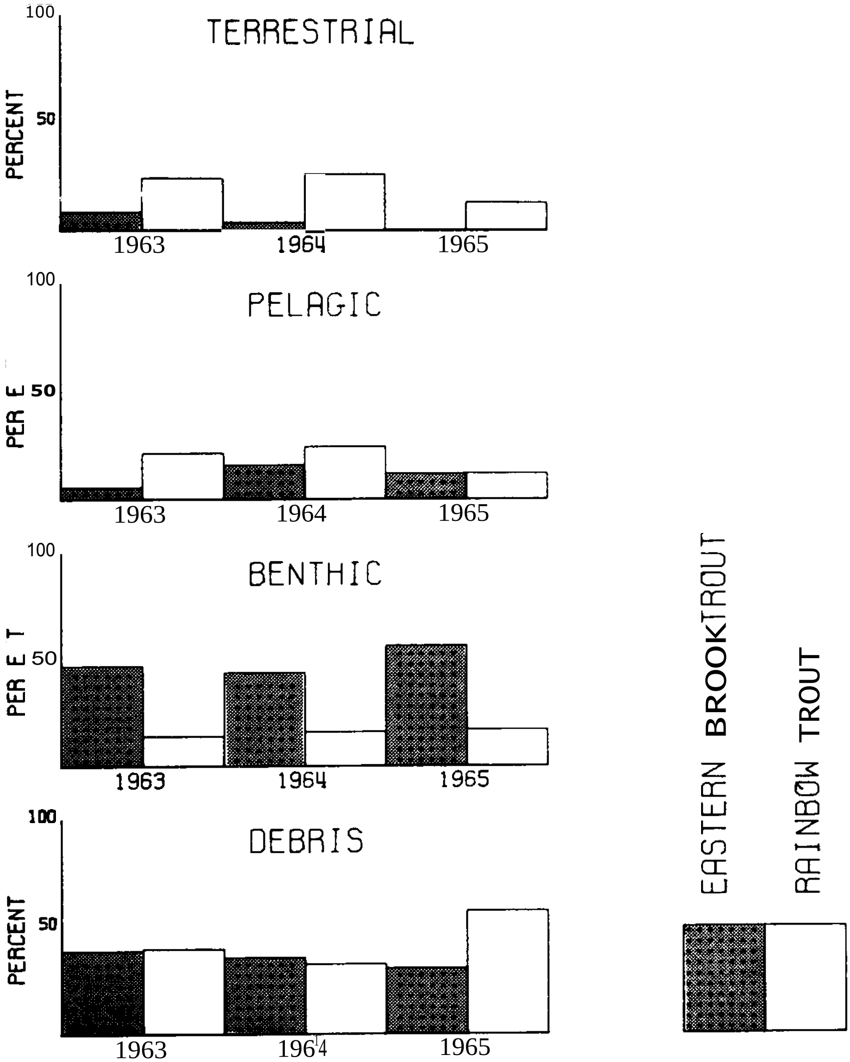

FIGURE 1—Food of eastern brook and rainbow trout in Castle Lake; percentage of the total volume of stomach contents by category, 1963, 1964, and 1965.

Rainhow and brook trout less than 5 inches were not adequately sampled. However, stomachs of fingerling rainbow trout taken after planting in 1964, 1966, and 1967 contained small terrestrial insects and cladocerans. Occasional small rainbow trout caught in the winter contained copepods (probably *Diaptomus novamexicanus).* No data on the food of brook trout fry and fingerlings are available.

Brook trout and rainbow trout had different diets (Figure 1). Rainbow trout ate three times more terrestrial food than brook trout, while brook trout ate three times more benthic food than rainbow trout. Pelagic food was about evenly split between the two species, while debris formed a relatively constant 40 to 60% of the stomach contents. The same data were analyzed on a monthly basis (Figure 2). Pelagic food reached its maximum during the late summer when the *Daphnia* population was at its peak. Both rainbow and brook trout fed on zooplankton during this period.

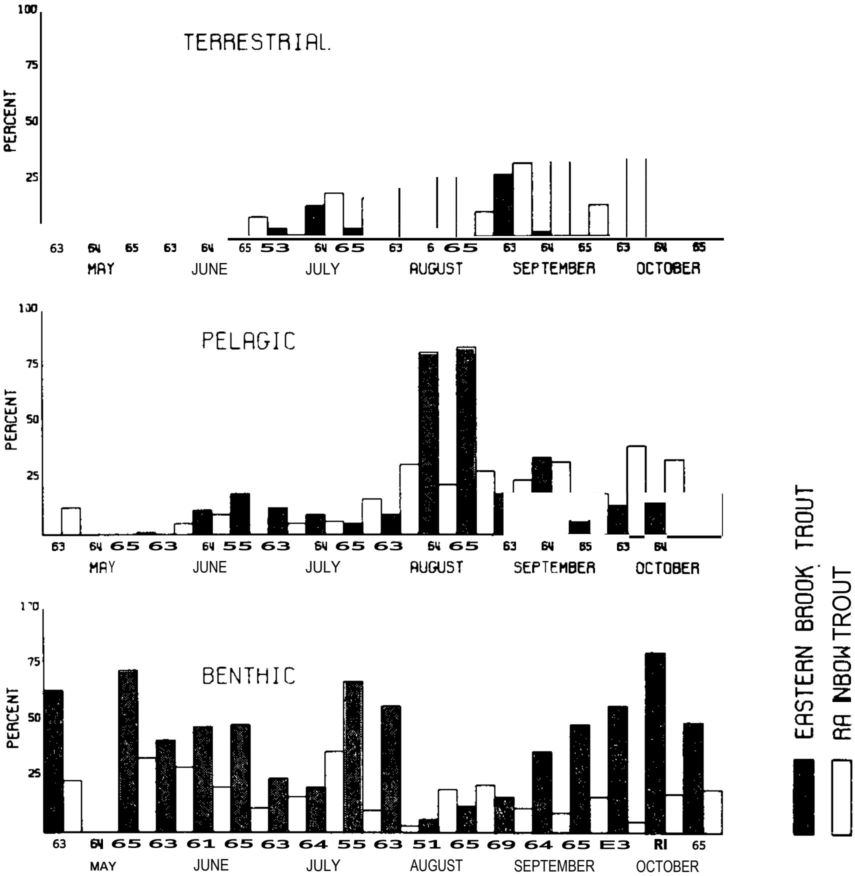

FIGURE 2—Food of eastern brook and rainbow trout in Castle Lake; percentage of the total volume of food items by category and month, 1963, 1964, and 1965.

Sampling during the winter months of 1967-68 showed that after the lake froze, benthos comprised virtually 100% of the food of both eastern brook and rainbow trout. When the lake thawed in May, terrestrial food was again utilized.

The relative value of each food item as an energy source was determined from calorimetric data and is expressed as the number of each food item required to produce 1,000 calories (Table 3). Dragonfly nymphs, *Sialis* larvae, Coleoptera, ants, and damselfly nymphs are clearly the most energy-rich foods. The energy provided to the fish by each food item (Table 4) was estimated using stomach content data for 1963, 1964, and 1965 (Tables 1 and 2) and the energy available per food item (Table 3). Dragonfly nymphs (61.6%), ants (11.3%), Daphnia (10.0%), and chironomid larvae (8.2%) accounted for 91.1% of the total calories eaten by brook trout. Ants (42.8%), Daphnia (25.6%), beetles (11.1%), and dragonfly nymphs (8.1%) made up 87.6% of the total calories eaten by rainbow trout. Grouping these data into the three food categories showed brook trout energy intake to be 75.9% benthic, 14.1% terrestrial, and 10.0% pelagic. For the rainbow trout 55.9% was terrestrial, 25.6% was pelagic, and 18.5% was benthic. For the two trout populations, the benthos provided 36.3% of the total energy consumed, 20.7% was from pelagic food, and 48.2% was from terrestrial food.

TABLE 3

Energy Content of Some Food Items of Trout in Castle Lake

	Calories per gram of ash-free dry weight*	Number • 1000 cal
Dragonfly nymphs	5514 ± 285	15
Sialis larvae	5928 ± 225	17
Coleoptera	5738 ± 596	26
Hymenoptera: ants	5898 ± 319	70
Damselfly nymphs	5374 ± 125	85
Homoptera	5494 ± 303	623
Diptera	4989 ± 789	677
Chironomid larvae and pupae	5542 ± 104	759
Caddisfly larvae	4409 ± 871	1000
Heleidae larvae	5708 ± 271	1481
Heleidae pupae	5508 ± 463	1966
Cladocera (Daphnia)	5272 ± 149	2586
Clams (without shell)		2925
Clams (with shell)	3787 ± 367	367
Hymenoptera	5320 ± 207	207
Hemiptera	5771 ± 100	100
Snails	3484 ± 229	229

Shown with 95% confidence limits.

TABLE 4

Energy and Percentage of the Total Energy in Food Consumed by Trout in Castle Lake, 1963-65 *

	Eastern brook trout			Rainbow trout		
		Cal			Cal	
Dragonfly nymphs	329	22000	61.6	96	6400	8.1
Sialis larvae	6	353	1.0	1	59	0.1
Coleoptera	21	808	2.3	228	8769	11.1
Hymenoptera: ants	823	4043	11.3	2356	33657	42.8
Damselfly nymphs	43	506	1.4	43	506	0.6
Homoptera	71	114	0.3	368	591	0.8
Diptera	48	71	0.2	655	968	1.2
Chironomid larvae	2225	2931	8.2	3092	4074	5.2
Caddisfly larvae	348	348	1.0	247	247	0.3
Heleidae larvae	411	278	0.8	675	456	0.6
Heleidae pupae	1334	679	1.9	5600	2848	3.6
Clams	30	10	Tr	36	12	Tr
Daphnia	9632	3572	10.0	52060	20131	25.6

* N = number eaten, Cal = calories eaten, % = percentage of the total calories eaten, Tr = less than 0.05%.

Utilization of the available benthos by fish was computed using Beatty's (1968) data on benthic standing crop for 45 months from 1963 through 1967, and the 1963-65 stomach content data (Table 5). Chironomid larvae contained most (83.8%) of the benthic energy but only a small fraction of their potential energy was consumed (5.8%). Caddisfly larvae (37.1%), dragonfly nymphs (59.8%), and damselfly nymphs (33.5%) were the benthic food items eaten most by trout in Castle Lake.

TABLE 5

Total Energy in Seven Selected Benthic Food Items and Their Utilization by Trout in Castle Lake

	Percentage of total benthic energy	Percentage utilization by fish
Chironomid larvae	83.8	5.8
Heleidae larvae	6.9	1.8
Heleidae larvae and pupae	7.9	10.1
Clams (without shell)	0.1	3.3
Caddisfly larvae	0.3	37.1
Dragonfly nymphs	8.2	59 8
Damselfly nymphs	0.5	33.5

DISCUSSION

Studies of brook trout diet have shown that aquatic insect larvae are the primary food source throughout the year. Lord (1933) found that by volume aquatic food ranged from 38% in summer to 98% during winter in a Vermont stream. Results reported here show similar percentages (Table 1). Although rainbow trout also fed primarily on insects, most of their food was terrestrial rather than benthic. Wales (1946) showed that benthic food decreased in importance as rainbow trout got older. Rainbow trout fed more regularly and on a wider variety of organisms than brook trout (Tables 1 and 2). This apparently is due to their extensive use of the terrestrial food source.

Although sparse, data on the food of fingerling rainbow trout suggest that zooplankton makes up a large proportion of the food of these fish. Cladocerans are probably most important in the summer, while copepods might be more important in the winter.

Nilsson (1963, 1965, 1966) demonstrated that sympatric fish species are often found in a more restricted habitat than allopatric species and that this interactive segregation is reflected in their food habits. This, I believe, is the case in Castle Lake. The presence of rainbow trout and the tendency of the brook trout to avoid the high summer water temperatures (22 C) caused the brook trout population to be displaced to the lower strata of the lake. This allowed the rainbow trout to exploit the surface waters and terrestrial food. When brook trout existed alone in Castle Lake, an average of 46%, by volume, of their food was terrestrial (Wales and German, 1950). During this study, terrestrial food exceeded 25% of the total volume of brook trout food only during September 1963.

The amount of energy available and eaten is of primary importance to any fish population. It is evident that a few food items are providing the bulk of the energy eaten by each species (Table 4). Four food items account for 91% of the total calories eaten by brook trout and for 88% of the calories eaten by rainbow trout.

There is a large discrepancy between the energy present in the benthos in Castle Lake and the benthic energy actually consumed (Table 5). Since food utilization is directly related to its availability, it is clear that most of the potential energy represented by benthos is unavailable to the fish. Because chironomid larvae live below the flocculent mud-water interface, they are less subject to predation than are the dragonfly and damselfly nymphs and the caddisfly larvae, which live on aquatic vegetation and rocks. Accordingly, they are eaten less by the fish than are the more exposed nymphs and larvae. The high percentage utilization for Heleidae (larvae and pupae) is due to predation on the pupal stage, which is seldom found in the mud (K. Beatty, College of the Siskiyous, pers. comm.).

An apparent solution to the problem of increasing the energy consumption of fish is to manipulate the food supply either by fertilization or by the addition of new food items. Fertilization with micronutrients is currently being investigated in Castle Lake. Manipulation of the food chain, however, might lead to a reduction in available energy rather than in an increase if it is done without a thorough knowledge of the system in question. This method, however, would seem to hold the most promise for increasing fish yield, in spite of its difficulties.

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