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WAYNE A. WURTSBAUGH, ROBERT W. BROCKSEN, AND CHARLES R. GOLDMAN

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WAYNE A. WURTSBAUGH[1] AND ROBERT W. BROCKSEN
Department of Animal Physiology
and
Institute of Ecology

CHARLES R. GOLDMAN
Institute of Ecology
and
Division of Environmental Studies
University of California, Davis, California 95616

ABSTRACT

A difference was found in the summer distribution of underyearling brook trout, *Salvelinus fontinalis* (Mitchill), and planted rainbow trout, *Salmo gairdneri* Richardson, in Castle Lake, California. Brook trout underyearlings oriented to the bottom and were found primarily in shallow water on the eastern shore of the lake near springs. The rainbow trout underyearlings were more pelagic and were found in the littoral areas along the entire shoreline.

Gravimetrically, the food eaten during the summer by brook trout underyearlings was 13% terrestrial, 11% limnetic, and 76% benthic. Rainbow trout ate 15% terrestrial, 15% limnetic, and 70% benthic food.

In summer, rainbow trout adults are located in the epilimnion in Castle Lake, whereas adult brook trout are found near the bottom of the lake beyond the littoral zone. Due to this spatial isolation, their diets differ considerably. An earlier study showed that during the summer, adult brook trout ate 20% terrestrial, 31% limnetic, and 49% benthic food (by volume). Adult rainbow trout ate 49% terrestrial, 33% limnetic, and 18% benthic food.

Although the diets and distribution of adults of many trout species have been studied, little is known about juvenile trout that inhabit lakes. Many juvenile fish feed extensively on zooplankton, and it is sometimes presumed that fry and fingerling trout also exploit this food resource.[2] However, limnetic crustacea represented only 8% (by weight) of the diet of juvenile steelhead trout, *Salmo gairdneri*, inhabiting a mesotrophic Oregon pond (Coche 1964). Macrobenthos was their primary food. Underyearling brook trout inhabiting streams ate primarily chironomid larvae and pupae (Clemens 1928; White 1930; Ricker 1930; Leonard 1938). Crustacea were of limited importance to their diets. Large cladocerans formed a significant proportion of the diets of adult brook and rainbow trout inhabiting Castle Lake, but smaller zooplankton were not eaten (Wales 1946; Swift 1970).

Our study was undertaken to: (1) determine the relative contribution during the summer of benthic, limnetic, and terrestrial food production zones of Castle Lake to the diets of underyearling brook trout, *Salvelinus fontinalis* (Mitchill) and rainbow trout, *Salmo gairdneri* Richardson; (2) determine diet differences between underyearling and adult fish; and (3) determine the distribution of the underyearling trout.

STUDY AREA

Castle Lake is located in a steep valley in northern California (Siskiyou County) at an elevation of 1,900 m. The lake covers 20.1 hectares and has a maximum depth of 35 m at the south end. The northern half of the lake averages 4 m (Fig. 1). The bottom is almost entirely flocculent mud, except where emerging springs expose gravel. The outlet is located at the north end of the lake, and an intermittent stream enters the lake at the southeast end. The lake is fed primarily by snow melt and spring flow. In summer, the thermocline forms at about 8 m, and surface temperatures may reach 23 C. The lake is oligotrophic,

[1] Present address: Clear Lake Algal Research Unit 1825 South Main Street, Lakeport, California 95453.

[2] Fish were considered underyearlings if they were less than 80 mm. Fish between 30 and 80 mm were designated as fingerlings and fish less than 30 mm were considered fry.

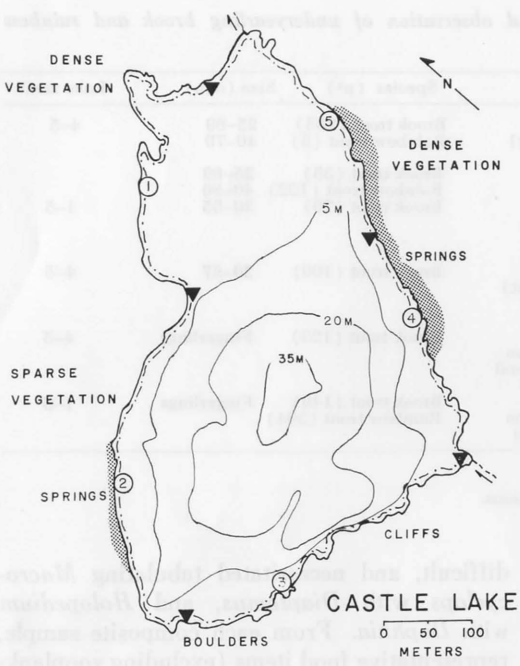

FIGURE 1.—Morphometry and shore character of Castle Lake, California. The five shoreline areas used to study the distribution of the underyearling trout fish are indicated by: ▼—.—○—.—▼. Surface spring areas are shown in stipple.

with total dissolved solids between 20 and 30 mg/l and an average summer secchi depth of 12 m (Goldman 1961). Daily summer air temperatures typically reach 22 to 25 C and drop to 8 C nightly. Ice and snow up to 2.5 m thick normally cover the lake from December until May.

To aid in determining the distribution of the underyearling trout around the lake, the shoreline was divided into five sections, each representing a different type of habitat and/or morphometrically distinct part of the lake (Fig. 1). Section 1 is bordered by moderately dense stands of conifer and deciduous trees. The bottom slopes slowly to a maximum depth of 4 m. Section 2 is bordered by chaparral and boulders. Some subsurface and surface springs are present in this section. Section 3 is bordered by vertical cliffs and large boulders. The shore of Section 4 is wooded with dense stands of alder and conifer trees. This section has many subsurface and surface springs and the bottom has a rapid slope. Section 5 is much like Section 4, except that the slope of the bottom is less steep.

The macrobenthos in the lake is dominated by chironomid larvae (Beatty 1968). The dominant zooplankton are *Diaptomus novamexicanis*, *Macrocyclops albidus*, *Daphnia rosea*, *Holopedium gibberum*, and *Polyphemus pediculus*. Of these, *Daphnia* and *Diaptomus* predominate (Carlson 1968). Two fish species inhabit the lake. Brook trout spawn in the subsurface springs and rainbow trout are maintained by an annual plant of 10,000 highly domesticated fingerlings of the Shasta strain. The rainbow trout are planted each August at the north end of the lake (Cordone and Nicola 1970).

METHODS AND MATERIALS

General behavioral observations were made during the same periods that fish were collected by a swimmer. The swimmer, equipped with snorkel and mask, swam slowly along the shoreline of the lake, first observing the fish from a distance and then capturing them with a hand net. From these general observations, it appeared that fingerling trout stayed in shallow water. To test this, we swam transects parallel to the eastern shore at specified depths, and recorded the number of fingerlings seen at each depth. The distance of effective observation was approximately 3 m.

To determine the distribution of the underyearling trout around the lake, the entire shoreline of the lake was electrofished in 1969 with an AC electric shocker and the number of underyearling brook trout captured in each of the five designated sections was recorded. In 1970, a swimmer equipped with snorkel and mask swam along the shoreline, recording the number of brook and rainbow trout seen in each section. The dates and times of these distribution studies are shown in Table 1.

Underyearling trout were captured during July, August, and September 1969. The fish were captured by four methods. Brook trout fingerlings were caught daily by a swimmer using a 20 cm-diameter hand net, or by electrofishing with an AC electric shocker from a boat. Because only a few brook trout fry were captured in 1969, an additional

TABLE 1.—*Information summary on the collection and observation of underyearling brook and rainbow trout in Castle Lake*

Date	Time	Use	Method	Species (n[a])	Size (mm)	Lake area[b]
13 July to 13 Sept. 1969	0800–1700 (once daily)	Stomach analysis	Hand net (swimmer)	Brook trout (283) Rainbow trout (5)	25–69 40–70	4–5
			Trap	Brook trout (35) Rainbow trout (132)	25–69 40–80	
30 July 1969	1000–1600	1) Lateral distribution 2) Stomach analysis	Electric shocker	Brook trout (70)	30–55	1–5
16, 17, 31 May 1970	0800–2230 (4 times daily)	Stomach analysis	Hand net (from boat)	Brook trout (100)	20–27	4–5
7, 8 Aug. 1970	1000–1600	Depth distribution	Visual observation (snorkel and SCUBA[c])	Brook trout (123)	Fingerlings	4–5
14 Sept. 1970	1400–1600	Lateral distribution	Visual observation (snorkel[c])	Brook trout (149) Rainbow trout (394)	Fingerlings	1–5

[a] Number of fish in sample.
[b] Refers to lake areas shown in Figure 1.
[c] Equipment used by the swimmers to make the observations.

sample was taken in the spring of 1970. The recently emerged fry were dipped from water less than 20 cm deep with a hand net. Rainbow trout were captured primarily in a plastic trap. The trap, an enlarged version of one designed by Breder (1960), measured 30 cm × 30 cm × 60 cm. The trap was set daily along the shoreline and checked every 2 hours during sampling periods. Most fish used for stomach analysis were captured in Sections 4 and 5 in water less than 1 m deep. The majority of the fish were captured in the northern end of the lake (Section 5) where the maximum depth is 4 m. This sampling procedure probably had little effect on the analysis of the diet of the brook trout, since most of them were located in shallow water in Sections 4 and 5 (see results). The effect of this sampling procedure on the analysis of the rainbow trout's diet is unknown. Diurnal samples were not taken, but the samples taken in the early morning should have included some food eaten during the night. The dates and times fish were captured are given in Table 1.

The entire contents of each stomach were individually examined. Food organisms were counted and preserved with 10% formalin in 2-wk composite samples. Immature aquatic insects were considered benthos, although some were probably eaten in the limnetic zone when they emerged. Small size and rapid digestion made identification of zooplankton difficult, and necessitated tabulating *Macrocyclops* with *Diaptomus*, and *Holopedium* with *Daphnia*. From each composite sample, representative food items (excluding zooplankton) which appeared undigested were dried for 24 h at 80 C and weighed. Zooplankton dry weights were determined from plankton collected on October 5, 1969 with a plankton net.

RESULTS

Distribution and Behavior

Brook trout fingerlings were unevenly distributed within the lake. The fingerlings were most abundant in Sections 4 and 5 near springs used for spawning (Table 2; Fig. 1). These spawning beds are large, graveled springs in water 2 to 8 m deep and 4 to 15 m offshore. Fingerling brook trout were seldom seen directly over the spawning beds, but were found in shallower, nearshore areas. In May 1970, swim-up fry, some with yolk remaining, were plentiful within 10 to 20 cm from shore. Section 2 had the next highest density of underyearling brook trout. Spawning beds are also present on this shore (J. H. Wales, personal communication). Section 1, which has no springs, and Section 3, which is bordered by cliffs, had very few underyearling brook trout.

Besides the proximity of the spawning beds, additional factors may have favored higher

TABLE 2.—*Distribution of underyearling brook and rainbow trout along the shoreline of Castle Lake. Dates, times and methods for each observation are given in Table 1*

Lake section[a] Length (m) in parentheses	Number of fish observed/100 meters of shoreline		
	Brook trout		Rainbow trout[b]
	July 1969	Sept. 1970	Sept. 1970
1 (500)	0.0	0.2	16.2
2 (460)	1.7	4.4	20.0
3 (500)	0.8	0.6	4.2
4 and 5 (760)	5.0	16.5	26.4

[a] Lake sections shown in Figure 1.
[b] The 1969 observation was made prior to the yearly plant of rainbow trout fingerlings, so no count was possible.

TABLE 3.—*Midday depth distribution of brook trout fingerlings in Castle Lake 7–8 August 1970*

Lake section	Length of transect (m)	Number of fish observed			
		Depth of transect (m)			
		0	2	4	6
5	90	52			
5	45	25	2		
5	45	22	2		
4	90	18	2	0	0

densities or survival of underyearling brook trout in Sections 4 and 5. First, these sections have more terrestrial vegetation than the other shores, and consequently there is more debris in the water which may provide cover for the underyearling fish and increase food production. Secondly, there are many small, cold springs in the nearshore areas of Sections 4 and 5, and brook trout fingerlings were usually found at each spring. The spring water emerged at 5 C and was quickly diluted. During summer, lake surface temperatures reached 23 C, higher than the preferred temperatures of juvenile brook trout (Ferguson 1958; Javaid and Anderson 1967). Cooler water was present at greater depths, but the underyearling brook trout preferred shallow areas (as discussed below). The springs apparently allow at least part of the underyearling brook trout population to remain in water of preferred temperature while also staying in shallow water.

Brook trout fingerlings were seen only in littoral areas at depths less than 2 m during our midday observations (Table 3). The brook trout usually stayed within 4 to 10 cm of the substrate and were rather inactive unless disturbed. This bottom-seeking behavior of the trout may be due at least in part to the influence of the cold spring water noted above. Additionally, it is possible that the

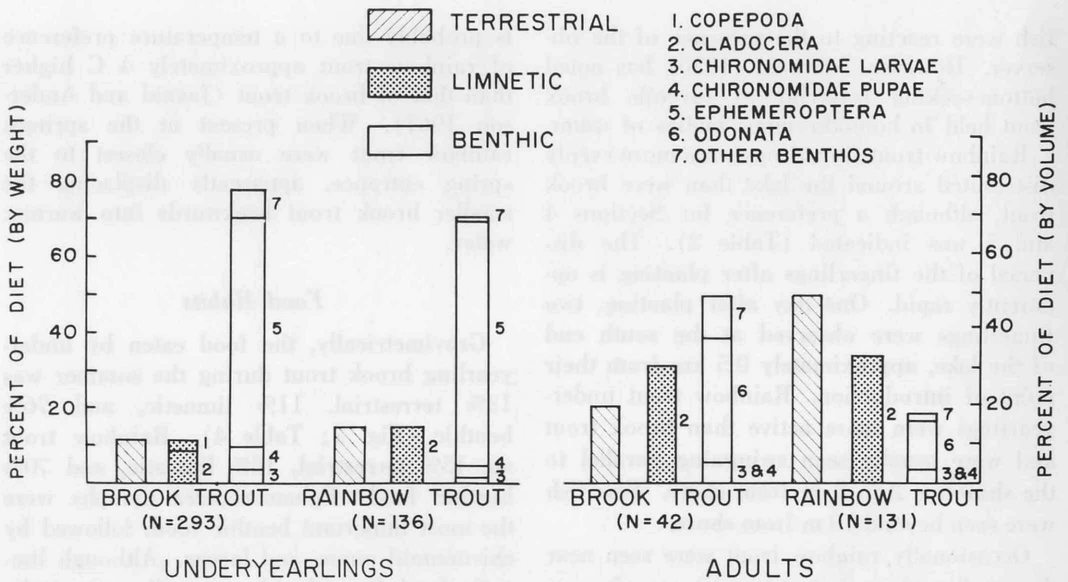

FIGURE 2.—Diets of underyearling and adult trout from July to September in Castle Lake, California. Data for underyearlings are from our 1969 sample. Data for adults are from Swift (1970).

TABLE 4.—*Food of underyearling brook and rainbow trout, Castle Lake, summer 1969*

Food item	Brook trout (n = 293) Number	Mean weight (μg)	Percent (by weight)	Rainbow trout (n = 136) Number	Mean weight (μg)	Percent (by weight)
Terrestrial						
Diptera	104	302	5.8	104	289	7.2
Hymenoptera	40	352	2.6	71	325	5.5
Thysanoptera	139	55	1.4	78	31	0.6
Coleoptera	9	800	1.3	4	800	0.8
Homoptera	67	88	1.1	17	106	0.4
Hemiptera	6	300	0.3	1	200	T
Arachnida	8	162	0.2	8	225	0.4
Subtotal	373		12.7	283		14.9
Limnetic						
Cladocera						
Daphnia and *Holopedium*	4,953	8	7.4	4,652	8	8.9
Polyphemus	2,000	4	1.5	6,465	4	6.2
Chydoris	37	5	T	0		
Copepoda						
Diaptomus and *Cyclops*	3,864	3	2.2	7	3	T
Subtotal	10,854		11.1	11,124		15.0
Benthic						
Ephemeroptera (n)	224	1,430	58.5	182	1,486	64.4
Chironomidae (p)	259	136	6.4	116	116	3.2
Chironomidae (l)	817	23	3.4	106	32	0.8
Cladocera						
Eurycercus	2,399	11	4.7	245	11	0.6
Tricoptera	17	400	1.2	10	400	1.0
Ostracoda	32	144	0.8	1	200	T
Odonata	9	344	0.6	0		
Gastropoda	3	367	0.2	0		
Copepoda						
Harpacticoida	133	3	0.1	0		
Helidae (p)	3	100	0.1	0		
Helidae (l)	8	38	0.1	1	38	T
Coleoptera	1	800	0.1	0		
Arachnida	3	130	T	1	130	T
Subtotal	3,908		76.2	661		70.1
Total	15,135		100.0	12,068		100.0

n = nymph, p = pupae, l = larvae, T ⩽ 0.05%.

fish were reacting to the presence of the observer. However, Newman (1956) has noted bottom-seeking behavior of juvenile brook trout held in homothermous bodies of water.

Rainbow trout fingerlings were more evenly distributed around the lake than were brook trout, although a preference for Sections 4 and 5 was indicated (Table 2). The dispersal of the fingerlings after planting is apparently rapid. One day after planting, two fingerlings were observed at the south end of the lake, approximately 0.5 km from their point of introduction. Rainbow trout underyearlings were more active than brook trout and were usually seen swimming parallel to the shoreline 2 to 5 m from shore. Few fish were seen beyond 10 m from shore.

Occasionally rainbow trout were seen near the small springs, but not nearly as often as were brook trout. This difference in behavior is probably due to a temperature preference of rainbow trout approximately 4 C higher than that of brook trout (Javaid and Anderson 1967). When present at the springs, rainbow trout were usually closest to the spring entrance, apparently displacing the smaller brook trout backwards into warmer water.

Food Habits

Gravimetrically, the food eaten by underyearling brook trout during the summer was 13% terrestrial, 11% limnetic, and 76% benthic (Fig. 2; Table 4). Rainbow trout ate 15% terrestrial, 15% limnetic, and 70% benthic food. Ephemeroptera nymphs were the most important benthic food, followed by chironomid pupae and larvae. Although limnetic food formed only a small part of the diets by weight, it represented 72% and 92%

TABLE 5.—*Food of 100 brook trout fry captured in Castle Lake 16, 17, and 31 May 1970*

Food item	Number	Mean weight (μg)	Percent by weight
Terrestrial			
Homoptera	55	109	31.7
Thysanoptera	49	12	3.2
Diptera	8	75	3.2
Hemiptera	1	100	0.5
Subtotal	113		38.6
Limnetic			
Copepoda	206	8	8.5
Benthos			
Chironomidae larvae	37	132	25.9
Chironomidae pupae	54	78	22.2
Copepoda			
Harpactocoida	68	7	2.6
Ephemeroptera	4	75	1.6
Ostracoda	6	17	0.5
Cladocera			
Eurycercus	2	11	T
Subtotal	271		52.8
Total	590		99.9

T ⩽ 0.05%.

of the number of organisms eaten by juvenile brook and rainbow trout, respectively. Cladocera predominated in the limnetic component of the diets of both species, even though copepods were the most abundant zooplankton throughout the summer (Goldman, unpublished). Rainbow trout fingerlings almost totally ignored copepods as a food item, while brook trout ate large numbers of these organisms. The principal terrestrial organisms eaten by the trout were Diptera and Hymenoptera.

With the progression of summer, as the fish grew and the availability of foods changed, their diets fluctuated. For one week in mid-August, terrestrial food replaced benthic food as the dominant food item of underyearling brook trout. The proportion of limnetic food in the diet changed little throughout the summer. However, as the fish grew, they ate fewer copepods. In mid-August, when rainbow trout were planted, terrestrial food dominated in their diet, but by September their diet was primarily benthic food. The proportion of limnetic food in their diet changed little during the summer.

Benthic food predominated in the diet of the brook trout fry captured in 1970 (Table 5). Chironomid larvae and pupae were the principal benthic organisms eaten, while only a small part of the diet was composed of the larger Ephemeroptera nymphs. The small limnetic component of the diet consisted entirely of copepods, as did zooplankton samples taken that spring. Terrestrial food formed a large portion of the brook trout fry's diet. The diet of the brook trout fry captured in July 1969 differed considerably from that of those captured in May 1970. During 1969, 90% (by numbers) of the organisms eaten by fry were limnetic, 8% benthic, and 2% terrestrial. In 1970, only 35% of the organisms eaten were limnetic, 46% benthic, and 19% terrestrial. The differences between the two years is probably due primarily to differences in food availability. In July 1969, zooplankton densities were approximately 11 organisms per liter (mostly copepods), while in May 1970, only 0.6 organisms per liter were present (Goldman, unpublished). It appears that when copepod densities are high, brook trout fry may feed extensively on them.

DISCUSSION

The unequal distribution of the brook trout in Castle Lake, while probably influenced by the greater amount of cover and the small coldwater springs present in sections of the lake, may be due in part to a lack of dispersal of the juveniles after an initial migration from the spawning beds to the immediate shore areas. White (1930) observed similar behavior in brook trout emerging in running water. After an initial dispersion at emergence, he found little more dispersion until the fish reached 38 to 50 mm. Regardless of the causes of the limited distribution of the brook trout underyearlings, the result is that they use only a small part of Castle Lake for rearing. A much greater area of the lake is used for rearing by the introduced, domesticated strain of rainbow trout. We should caution that the behavior and distribution of the planted rainbow trout in Castle Lake may not be representative of the behavior of wild rainbow trout, as domestication and hatchery conditioning may greatly affect the behavior of salmonids (Vincent 1960; Ritter and MacCrimmon 1973).

The foods eaten by the trout in Castle Lake are affected by food selectivity and availability, and by the distribution of the food organisms in relation to the distribution of the fish. Although the underyearling brook and rainbow trout were distributed differently around the lake and the two species had different microhabitats, both were limited to the littoral zone of the lake; consequently they had similar food resources and their diets were similar. Adult brook and rainbow trout in the lake were more spatially isolated than the underyearlings, and consequently their diets differed more (Swift 1970). In summer, rainbow trout adults were located in the epilimnion, whereas brook trout adults were found near the bottom beyond the littoral zone. From May to October, brook trout ate (excluding detritus) 76% benthos, 14% limnetic food, and 10% terrestrial food (by volume), while rainbow trout ate 22% benthos, 33% limnetic food, and 45% terrestrial organisms (Swift 1970). For comparison with our study, we derived the diets of the adult trout during July, August, and September from Swift's data (Fig. 2). Odonata (dragonfly nymphs) were the primary benthic organism eaten by adult trout, whereas underyearlings ate primarily Ephemeroptera. Dragonfly nymphs may have been too large for the underyearlings to eat, but it is not clear why adults ate so few Ephemeroptera. Chironomid larvae contained 84% of the energy of the benthic macro-invertebrates in Castle Lake, but because they were generally unavailable to the trout, the Chironomidae represented only 5% of the benthic food in the stomach of adult trout (Swift 1970) and only 10% of the benthic food of underyearling trout (Fig. 2). The adult and underyearling trout were selective in their choice of zooplankton. *Daphnia* was the only zooplankter that was significant in the diet of adult fish, while underyearling rainbow and brook trout ate significant quantities of *Daphnia*, *Holopedium*, and *Polyphemus*. Underyearling brook trout also ate copepods. Presumably, all of these zooplankton species were available to the adult fish as well as to the underyearlings. The small size of the copepods may have deterred their consumption by the large trout, but it is unclear why copepods were not eaten by underyearling rainbow trout.

While adult brook and rainbow trout do not eat a variety of zooplankton, Swift (1970) found that this food resource is an important component of their summer diet (Fig. 2). Wales (1946) found that 1- and 2-year-old rainbow trout in Castle Lake ate an average of 23% plankton (by volume). Older fish ate no more than 4% plankton. Similarly, plankton was 35% of the diet of yearling brook trout but only 7% of the diet of older fish. Presumably, zooplankton decreased in the diets of the older trout because they converted to larger prey items. Our data, when combined with Swift's and Wales', indicates that zooplankton is most important for trout approximately 1 year old. The difference in amount of zooplankton eaten by adult and underyearling trout probably results from differences in the distribution of the fish. In summer, underyearling trout in Castle Lake remain in the littoral areas, while adult trout are benthic (brook trout) or limnetic (rainbow trout). In Castle Lake, *Daphnia* densities from August to October are 3 to 10 times greater between 5 and 10 m than in water less than 2 m deep (Carlson 1968). Additionally, zooplankton avoidance of the littoral zone has been noted for species of *Daphnia* and *Diaptomus* (Ruttner 1953). Similar avoidance of the littoral areas by Castle Lake zooplankton may further reduce the zooplankton densities in underyearling trout rearing areas, and consequently the amount of zooplankton eaten by underyearling fish.

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