**MN DNR FISHERIES
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INTERACTION OF LAKE TROUT AND RAINBOW SMELT IN TWO NORTHEASTERN MINNESOTA LAKES[1]

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ABSTRACT

Lake trout (Salvelinus namaycush) may become isolated from forage fish when thermal stratification occurs. Preferred temperature data suggest that rainbow smelt (Osmerus mordax) may be a suitable source of year-round food for lake trout in these lakes. Sympatric associations were studied in two northestern Minnesota lakes to evaluate the benefits and detriments of their association and to establish management recommendations.

Lake trout were found proximate to the full range of prey species during unstratified periods. During summer stratification, smelt was the only forage fish species readily available to lake trout in the hypolimnion and was a primary food item. Total length at maturity of lake trout increased after smelt introduction. Smelt primarily consumed invertebrates and other smelt but lake trout were eaten. Smelt readily consumed fish up to 15% of their own total length and ate fish up to 48% of their own total length. Abundance of both species declined in both lakes during the study period. The survival rate of smelt fluctuated and could not be correlated with other variables.

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It was concluded that a risk of detrimental impact on lake trout populations from smelt introductions exists and smelt should not be stocked on a routine basis. Additional quantitative, community-wide studies are needed before benefits or detriments of the association can be evaluated with certainty.

INTRODUCTION

Quality lake trout (Salvelinus namaycush) habitat is present in oligotrophic lakes which provide ample cold water during summer. Lake trout prefer 10 C water temperature (Scott and Crossman 1973) and frequent the cooler hypolimnion of lakes which undergo seasonal stratification (Martin 1951). Oligotrophic lakes usually have limited faunal diversity and limited forage diversity for lake trout. Common forage items include a pelagic coldwater fish species (Coregonus spp.) and pelagic invertebrates. If forage fish are not available, invertebrates make up the bulk of the lake trout diet and growth rate is reduced.

Minnesota lakes that contain lake trout usually stratify thermally and pelagic fish are often lacking. Northern pike (Esox lucius), smallmouth bass (Micropterus dolomieui), walleye (Stizostedion vitreum vitreum), minnows (Notropis spp.), darters (Etheostoma spp.) and white sucker (Catostomus commersoni) are common associates. These species prefer warmer epilimnetic or metalimnetic waters under thermally stratified conditions (Scott and Crossman 1973). At this time, lake trout must either venture into the upper strata to feed on fish or rely on invertebrates for food.

The niche of the rainbow smelt (Osmerus mordax) makes them a potential source of lake trout food. They prefer cooler water than most cool and warmwater species. Hart and Ferguson (1966) found that they occupied water at 7.2 C in Lake Erie. Scott and Crossman (1973) reported that smelt were pelagic and occupied hypolimnetic waters in stratified lakes.

The diet of smelt makes them a potential competitor with all sizes of lake trout and a potential predator on juvenile lake trout. Hale (1960) reported that smelt primarily ate invertebrates but did consume fish including lake trout. Selgeby et al. (1975) reported that substantial predation of herring larvae (3.3-11%) by smelt occurred in Black Bay of Lake Superior.

This study was initiated to determine the efficacy of rainbow smelt as forage for lake trout in Minnesota's waters with respect to their role as: (1) a food source for lake trout; (2) a competitor with lake trout and; (3) a predator on lake trout. Data relative to bathymetric distribution, diet, growth, abundance, survival and maturity were collected for each species to assess benefits and detriments of their association.

STUDY AREA

West Bearskin Lake in Cook County, Minnesota, is typical of northeastern lake trout waters. It has a surface area of 200 hectares and maximum depth of 21.3 m. The total alkalinity is 14.5 mg/l. The littoral zone (less than 4.6 m deep) comprises 20% of the surface area. Watershed soils are glacial till vegetated by mixed hardwoods and conifers. Bedrock outcrops are a common feature of the terrain. Forty-two cabins are located along the eastern one-third of shoreline. A well developed public access is located on the east end and a primitive canoe access is located on the southwest bay. The water color is brown due to dissolved and colloidal allochthonous organic material resulting in 7.0 m transparency. Stratification occurs in summer and the hypolimnion remains well oxygenated. West Bearskin Lake has a history of stocked lake trout, rainbow trout (*Salmo gairdneri*), brown trout (*Salmo trutta*) and smallmouth bass (Table 1). Smelt were introduced sometime before 1963 by an unknown, unauthorized mechanism. Other species currently found in the lake include white sucker, northern pike, lake trout, yellow perch (*Perca flavescens*),

Table 1. Stocking record of West Bearskin Lake, 1928-1970.

Date	Species	Number
1928	Lake Trout Fry	92,500
	Lake Trout Fgl.	279,200
	Smallmouth Bass Fgl.	750
	Brown Trout Fgl.	15,000
	Rainbow Trout Fgl.	86,150
1946	Lake Trout Fry	15,000
	Rainbow Trout Fgl.	7,136
1947	Rainbow Trout Fgl.	3,000
	Lake Trout Fry	15,000
	Lake Trout Fgl.	10,800
1948	Lake Trout Fry	15,000
	Rainbow Trout Fgl.	5,000
1949	Lake Trout Fry	10,000
	Rainbow Trout Yrl.	360
	Rainbow Trout Fgl.	15,000
1950	Rainbow Trout Fgl.	9,537
	Lake Trout Fry	25,000
1951	Lake Trout Fgl.	28,000
1954	Lake Trout Fgl.	25,024
1965	Lake Trout Fry	40,000
1966	Lake Trout Fgl.	24,620
1967	Lake Trout Fry	20,000
	Rainbow Trout Fgl.	9,010
1970	Lake Trout Yrl.	5,000[a]

[a] Adipose fin removed

pumpkinseed (Lepomis gibbosus), green sunfish (Lepomis cyanellus), sculpin (Cottus spp.) and various minnows.

Devilfish Lake, Cook County, Minnesota, is a relatively shallow lake with marginal lake trout habitat and a limited fish species diversity. It has a surface area of 161 hectares, a maximum depth of 12.2 m and a mean depth of 4 m. The littoral zone comprises 57% of the surface area and only 6% of the surface area exceeds 6 m depth. Bedrock outcrops interrupt the glacial till watershed soils which are vegetated by mixed hardwoods and conifers. The shoreline is virtually undeveloped except for two active cabins. Boating access is via a primitive trail which limits access to canoes and small boats. The water color is brown due to dissolved and colloidal allochthomous organic matter with a secchi disk transparency of 3.7 m. Hypolimnetic anoxia occurs during the summer months (Fig. 1). Devilfish Lake was treated with toxaphene in 1959 to eradicate existing fish species and was restocked with lake trout in 1961 (Table 2). Smelt were introduced by transplants of eggs in 1970 and adults in 1971. Other fish species found in the lake include brook trout (Salvelinus fontinalis), white sucker, minnows, darters and stickleback. The latter four species were probably introduced by anglers releasing unused live bait.

METHODS

Data relative to vertical distribution, survival rate and relative abundance (CPUE) were collected by bottom set gill nets. Nets were fished at index stations during the last two weeks in August in West Bearskin Lake and during the first two weeks in September in Devilfish Lake. Lake trout were sampled with 76 m by 1.8 m experimental gill nets with five 15 m sections of 19 mm, 25 mm, 32 mm, 38 mm and 51 mm bar measure mesh.

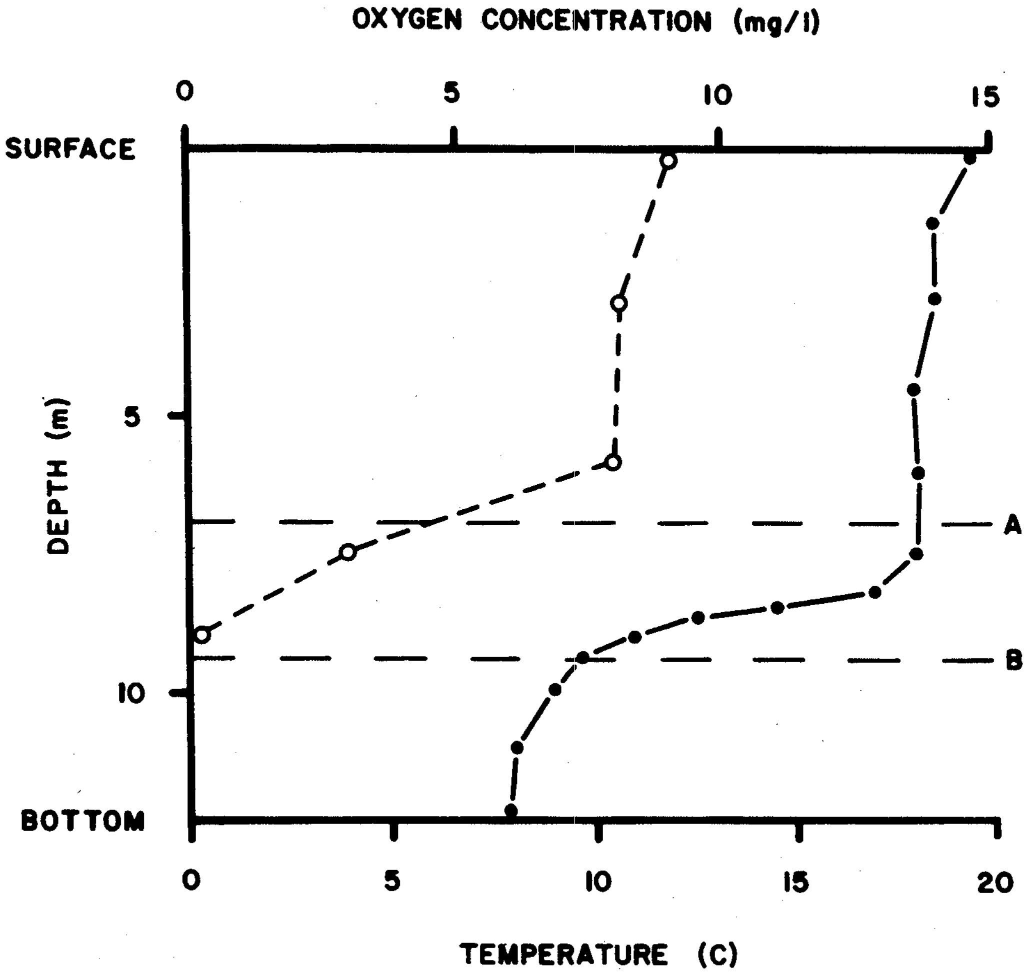

Figure 1. Water temperature (C) and dissolved oxygen (mg/l) profile of Devilfish lake on 27 August, 1980. Open circles are oxygen and solid circles are temperature. "A" is the minimum dissolved oxygen concentration limit of lake trout. "B" is the optimum temperature for lake trout.

Table 2. Lake trout stocking record of Devilfish Lake, 1961-1980.

Year	Size	Number
1961	Fingerling	6,743
	Yearling	5,541
1962	Fingerling	35,100
1963	Fry	40,000
1964	Fry	30,000
1965	Fingerling	13,020
	Fry	50,000
1966	Fingerling	4,620
	Fry	30,000
1967	Fry	35,000
1968	Fingerling	20,026
1970	Fingerling	20,097
1971	Fingerling	19,992
1972	Fingerling	20,097
1973	Fingerling	18,939
1975	Fingerling	20,040
1977	Yearling	8,284
1980	Yearling	8,379

Smelt were captured in 30.5 m by 3.0 m gill nets of 10 mm or 13 mm bar measure mesh. Additional netting during unstratified and other stratified periods to determine vertical distribution and to collect fish for diet studies was completed in West Bearskin Lake May-July and November 1969-73 (Table 3).

Data relative to diet, growth and maturity were collected from specimens captured in the gill nets. Stomachs were removed from lake trout and fixed in 10% formalin for later examination. Smelt stomachs were removed in the laboratory from whole fish preserved in 10% formalin. Large samples of smelt were subsampled. Food items were generally separated to family and quantified by water displacement as percentage of total food volume. All lake trout and smelt in diet studies were measured to the nearest 0.1 inch total length. Lake trout were weighed to the nearest 0.1 pound. English system measurements from both species were subsequently converted to metric. Scale samples were taken from lake trout and smelt for aging purposes and back calculations of length utilized the Lee method (Lagler 1956; Carlander 1981). Survival rates were determined by comparing CPUE of individual year-classes in successive years (Ricker 1975). All lake trout captured after 1968 were examined for sexual maturity.

Growth rates were estimated for juvenile ($\leq$ age 4) and adult (> age 4) lake trout. The differences in average estimated lengths at annulus formation between juvenile year-classes allowed comparisons of growth rates. Growth rates of adults were compared utilizing Walford growth parameters (Ricker 1975). Differences were tested for significance using Student's t-test (Steel and Torrie 1960).

Table 3. Description of single mesh (30.5 mm, 10 mm or 13 mm bar measure) and experimental mesh (exp.) gill net sets in West Bearskin Lake, during stratified and unstratified periods May-July and November 1969-1973.

Date	Limits of metalimnion (m)	Number of sets	Bottom depths sampled (m)	Net length (m)	Net mesh (mm)
10 June 1969	None	3	3.0- 7.6	30.5	25.4
			9.1-10.7	45.7	25.4
			8.5	45.7	25.4
11 June 1969	None	4	15.2-18.3	30.5	25.4
			12.2-13.7	45.7	25.4
			12.2-13.7	45.7	25.4
			12.2-15.2	76.2	exp.
14 July 1969[a]	6.7-9.1	4	12.2-15.2	30.5	25.4
			15.2-18.3	30.5	25.4
			18.9-20.4	76.2	exp.
			6.1-22.9	76.2	exp.
24 June 1970[a]	5.5-6.7	2	6.1-21.3	76.2	exp.
			19.8	15.2	10.0
14 July 1971[a]	7.9-9.1	3	10.7-19.8	76.2	exp.
			9.1-15.2	76.2	exp.
			10.7-13.7	30.5	13.0
17 May 1972	None	2	3.0- 7.9	30.5	10.0
			3.0	30.5	13.0
4 May 1973	None	1	7.6	30.5	13.0
5 November 1973	None	1	3.0- 6.0	76.2	exp.
6 November 1973	None	1	3.0- 6.0	76.2	exp.

[a] Lake was stratified.

RESULTS

Bathymetric Distribution

Spatial segregation of smelt and lake trout from other fish in the West Bearskin association was evident during summer stratification. Smelt was the only fish species occurring readily with lake trout in the hypolimnion (Table 4, Fig. 2).

Lake trout and smelt were found in association with other fish species during unstratified periods in West Bearskin Lake. Yellow perch, sculpin and green sunfish were captured with lake trout and smelt during May netting at bottom depths ranging from 3-8 m (Table 4).

Spatial segregation did not occur in Devilfish Lake. White sucker were caught with lake trout and smelt in 4-12 m depths during September stratification (Fig. 3).

Diet

Fish was the largest component in the lake trout stomach samples from both lakes and smelt comprised the largest percentage of the fish component for lake trout larger than 300 mm (Figs. 4 and 5). After 1974, smelt replaced other fish species as the major food item for lake trout in Devilfish Lake.

Smelt fed on invertebrates and other smelt. Cladocerans, Chironomids and mayfly larvae (Hexagenia spp.) dominated the diet volume of smelt aged 3 or younger (Figs. 6 and 7). Larger food items were more important as the fish grew older. Smelt and unidentified fish made up roughly one-half of the volume of food of smelt ≥ age 4.

Lake trout were found in 2 of the 2,991 smelt stomachs examined from West Bearskin Lake. Each stomach contained one larval lake trout. No lake trout were found in the 1,248 stomachs examined from Devilfish Lake.

Table 4. Net catches during stratified and unstratified periods May-July and November at various depths in West Bearskin Lake, 1969-1973.

Date	Bottom depths sampled (m)	Catch
10 June 1969	3.0- 7.6	0
	8.5	2 smelt
	9.1-10.7	2 smelt
11 June 1969	12.2-13.7	1 smelt
	12.2-13.7	0
	12.2-15.2	2 lake trout
	15.2-18.3	0
14 July 1969[a]	6.1-22.9	2 smelt, 1 lake trout
	12.2-15.2	2 smelt
	15.2-18.3	60 smelt
	18.9-20.4	7 smelt, 1 lake trout
24 June 1970[a]	6.1-21.3	3 lake trout
	19.8	60 smelt, 1 lake trout
14 July 1971[a]	10.7-13.7	0
	9.1-15.2	2 lake trout
	10.7-19.8	3 smelt, 4 lake trout
17 May 1972	3.0- 7.9	87 smelt, 1 green sunfish, 1 yellow perch, 2 sculpins
	3.0	168 smelt, 2 lake trout, 3 yellow perch, 1 green sunfish
4 May 1973	7.6	72 smelt, 1 lake trout
5 November 1973	3.0- 6.0	2 lake trout
6 November 1973	3.0- 6.0	1 lake trout

[a] Lake was stratified

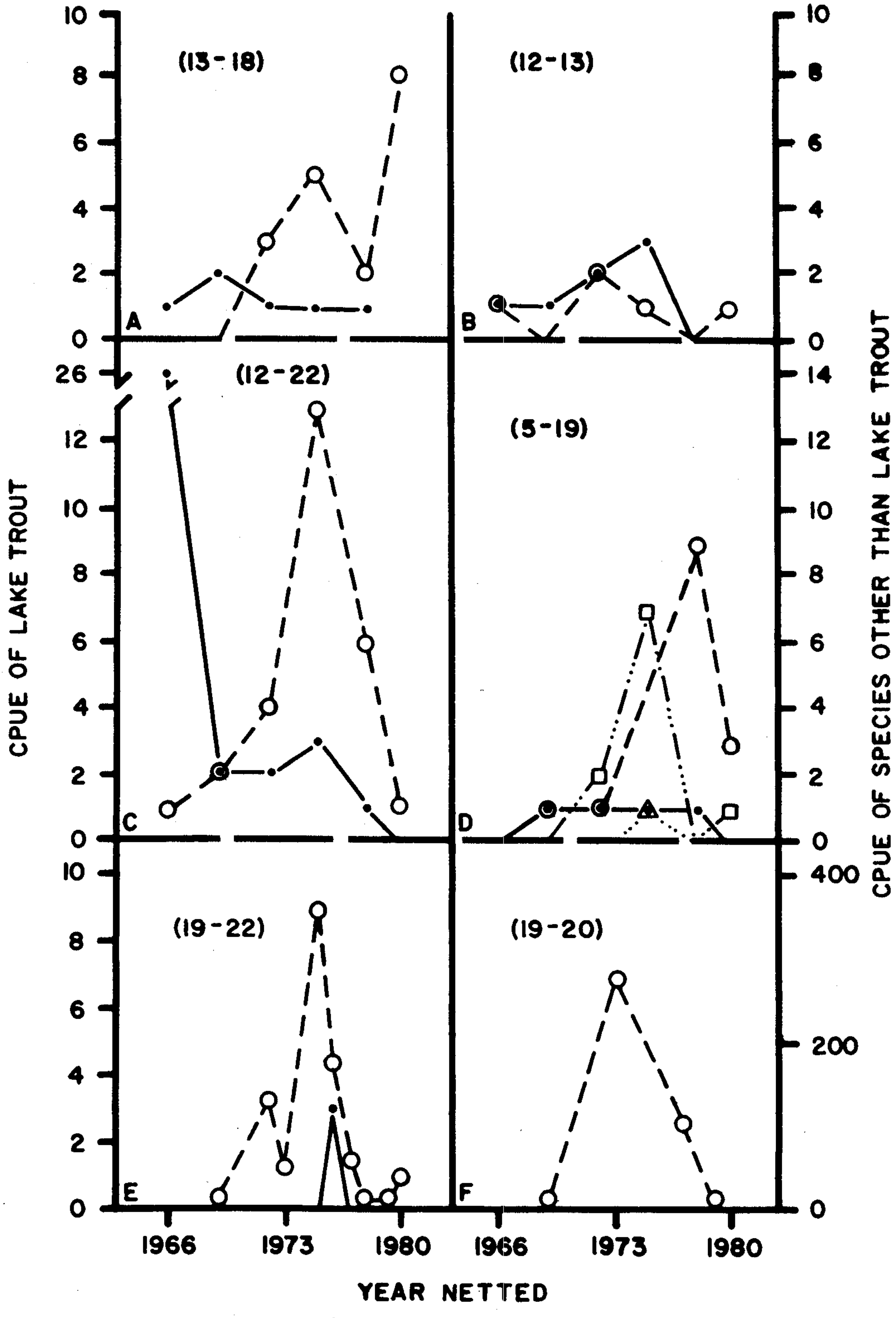

Figure 2. August catches (CPUE) in representative gill nets set in West Bearskin Lake, 1966-1980. Bottom depths sampled (m) are in parentheses. Dots represent lake trout, open circles are smelt, triangles are white sucker and squares are smallmouth bass. Sets A-D are experimental mesh. Sets E and F are smelt mesh.

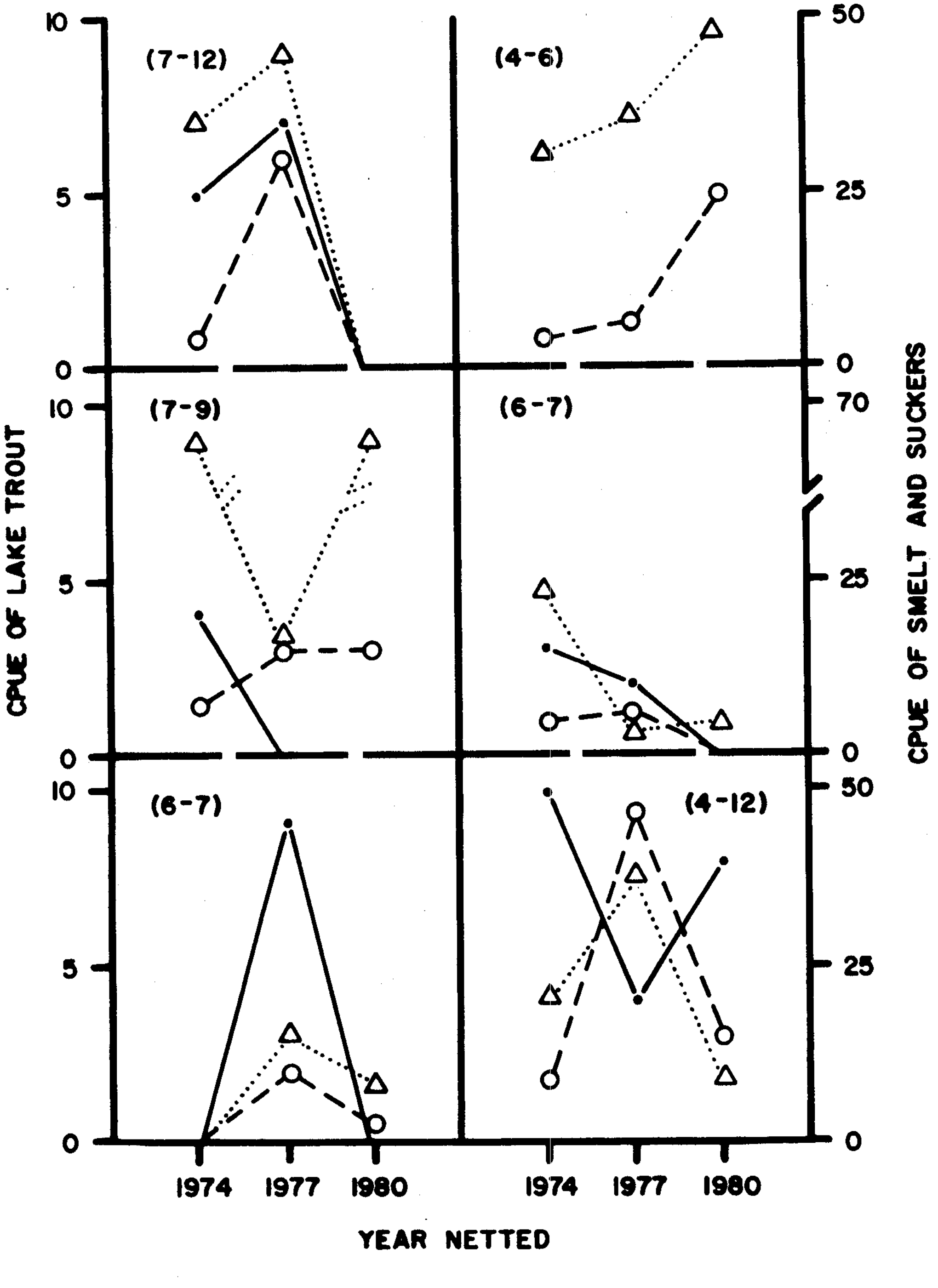

Figure 3. Catches (CPUE) in representative experimental mesh gill nets at six locations and depths (m) in Devilfish Lake, September 1974-1980. Bottom depths sampled are in parentheses. Dots represent lake trout, circles represent smelt and triangles represent white sucker.

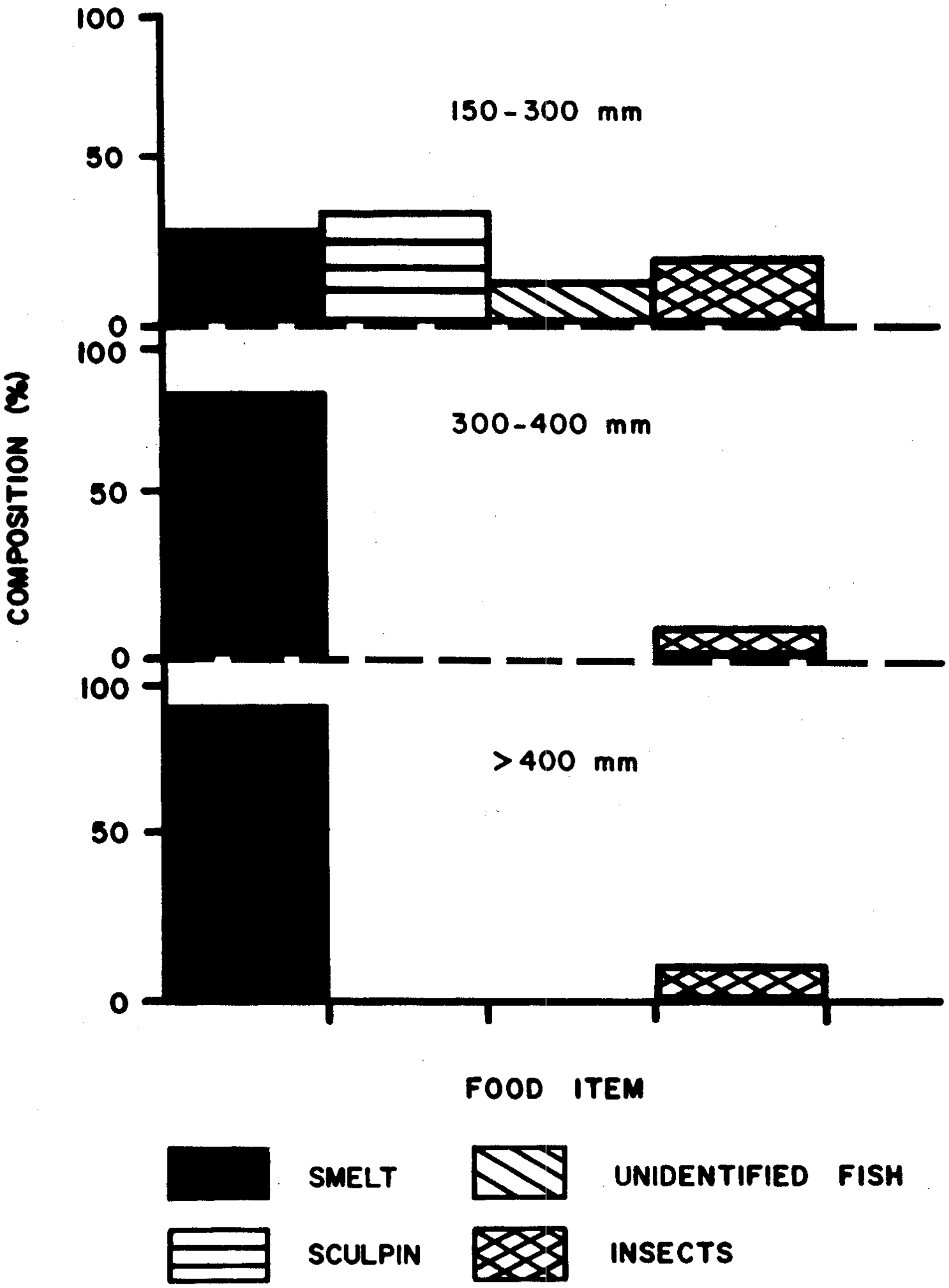

Figure 4. The percent composition by volume of the diet of lake trout 150-300 mm total length, 300-400 mm and larger than 400 mm from West Bearskin Lake, 1966-1980.

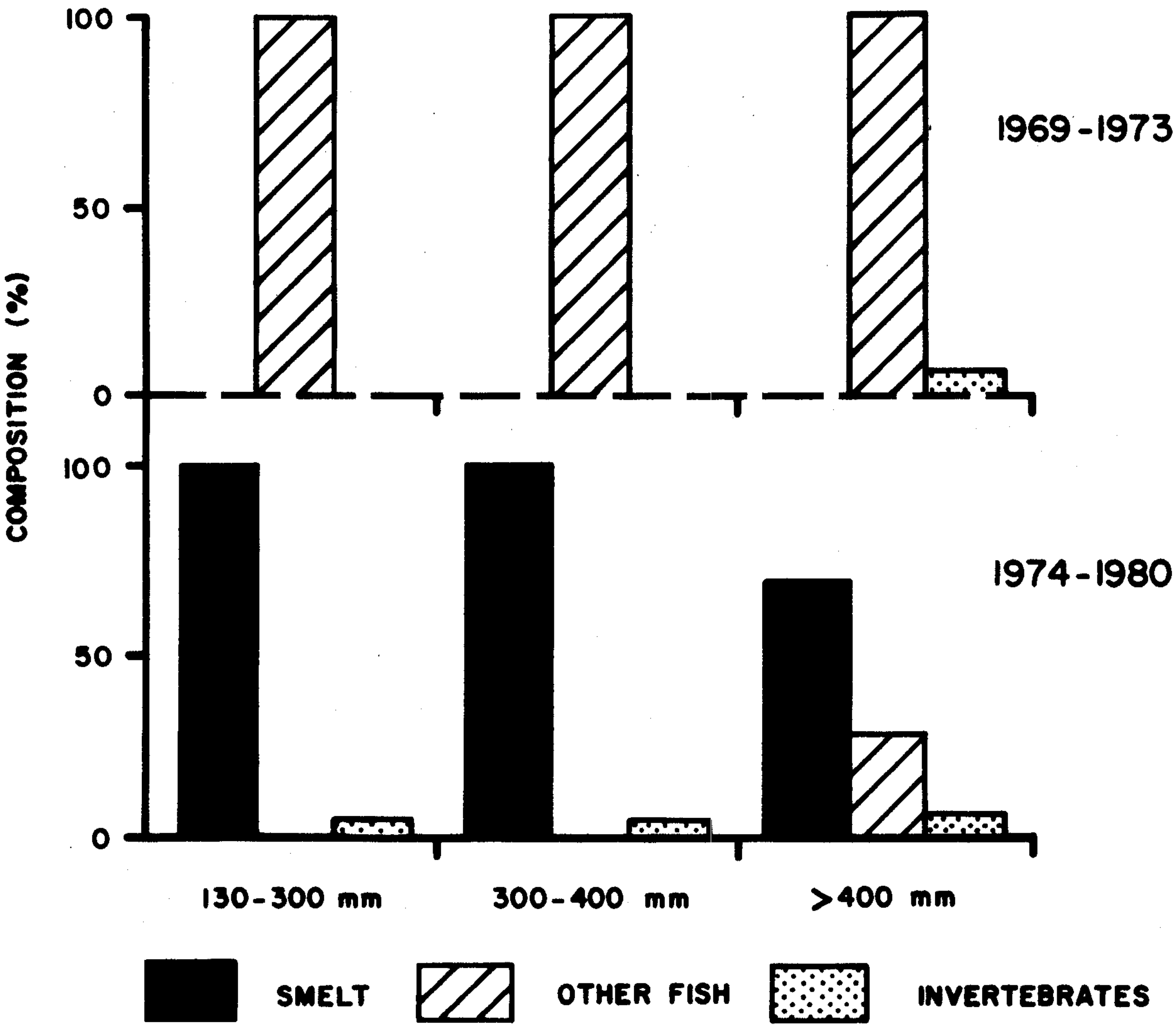

Figure 5. The percent composition by volume of the diet of lake trout 130-300 mm, 300-400 mm and >400 mm total length from Devilfish Lake, 1969-1973 and 1974-1980.

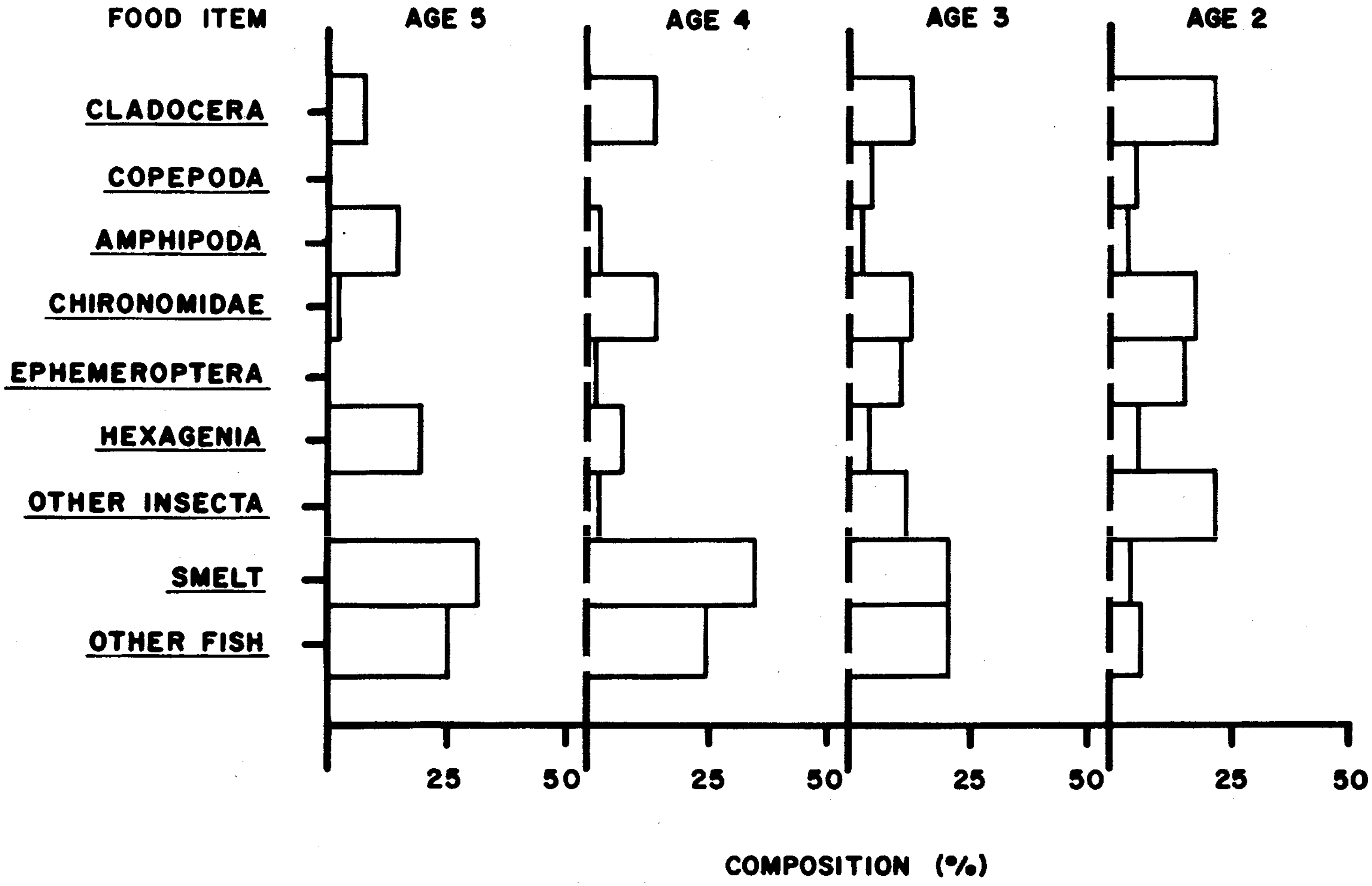

Figure 6. Percent composition by volume of the diet of smelt (age classes 2-5) from West Bearskin Lake. Food items are listed in order of increasing size from top to bottom.

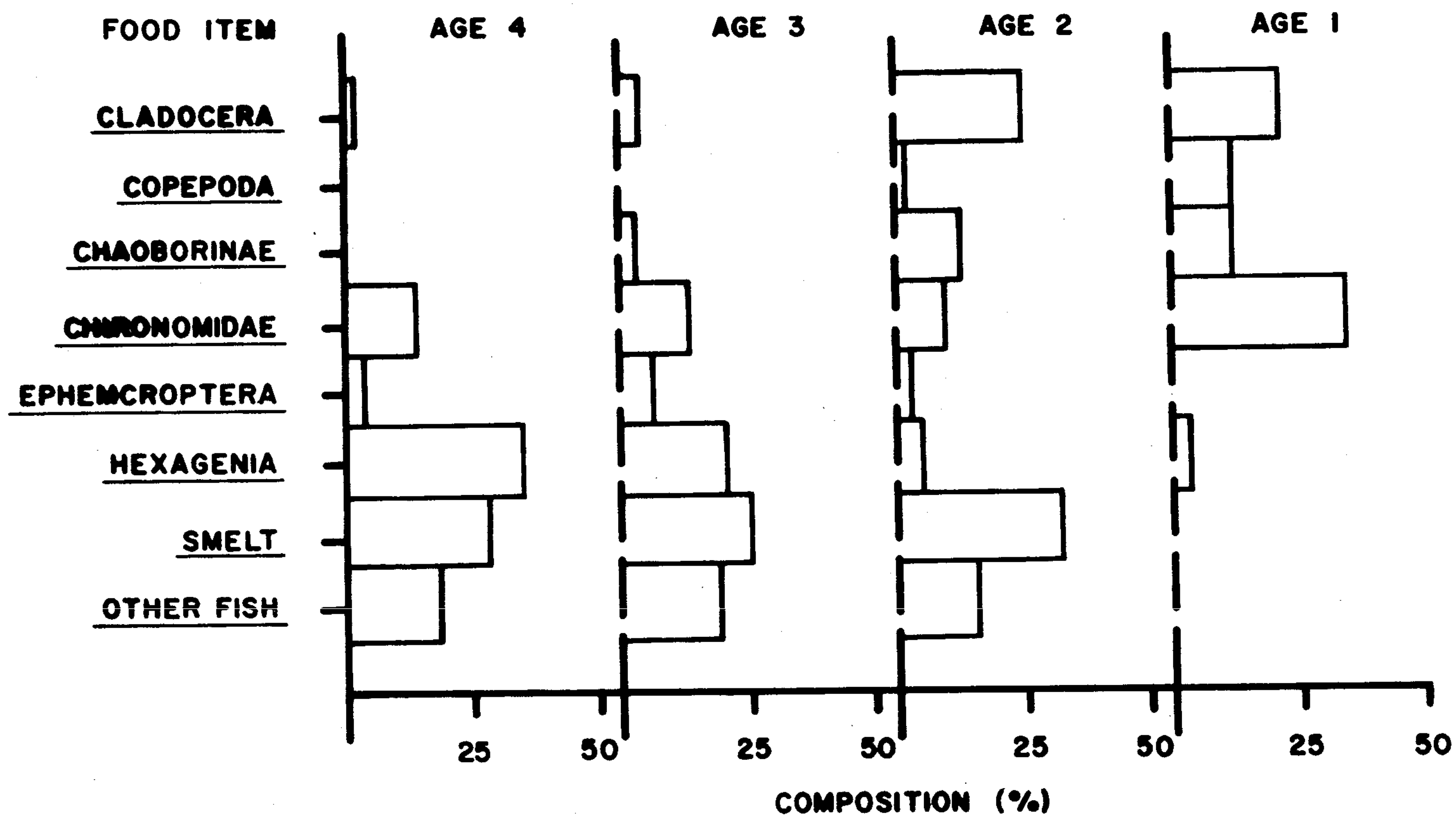

Figure 7. Percent composition by volume of the diet of smelt (age classes 1-4) from Devilfish Lake. Food items are listed in order of increasing size from top to bottom.

Smelt food items increased in size from spring to summer in West Bearskin Lake (Fig. 8). Smelt fed heavily on crustaceans in April and insects in May. Relatively equal portions of each were present in June and July. Fish constituted about 50% of the dietary volume in August with over one-half being other smelt.

Insects comprised the greatest percentage of the diet volume of smelt in Devilfish Lake in all sample months (Fig. 9). Fish comprised slightly over 20% of the volume of smelt food in Devilfish Lake in July, approximately 17% in August and 33% in September. Smelt made up roughly 80% of the volume of the September fish component.

Some aspects of the smelt diet differed between the study lakes. The percentage of smelt stomachs that contained food in West Bearskin Lake decreased with age but the average food volume per stomach of each age-class remained similar (Fig. 10). In Devilfish Lake, the percentage of smelt stomachs that contained food was about the same for ages one through four but the average food volume/stomach increased about twofold with each successive age-class (Fig. 11). Total length of fish prey found in West Bearskin smelt stomachs was usually between 5% and 15% of the total length of the smelt that ate them (Fig. 12). Ratios of prey length:predator length were usually larger in Devilfish Lake (Table 5). One smelt stomach contained a smelt slightly over 48% of the total length of the fish that ate it.

Growth

The growth rate of juvenile lake trout was reduced in West Bearskin Lake after smelt introductions. The average length at annulus formation was significantly lower ($P < 0.05$) for all ages except age one (Fig. 13). Growth data was inadequate from juvenile lake trout to determine if

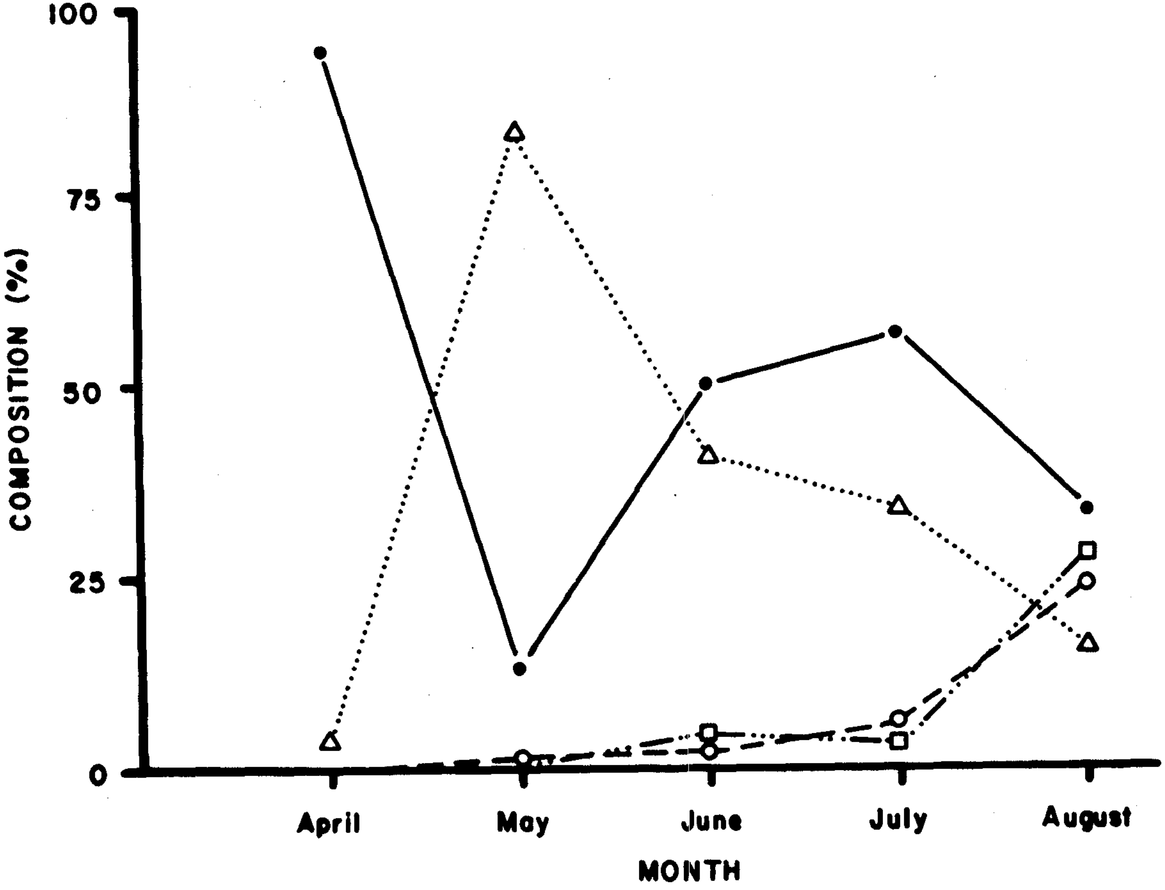

Figure 8. Percent composition by volume of the monthly diet of smelt from West Bearskin Lake. Crustaceans are represented by dots, insects by triangles, smelt by squares and other fish by open circles.

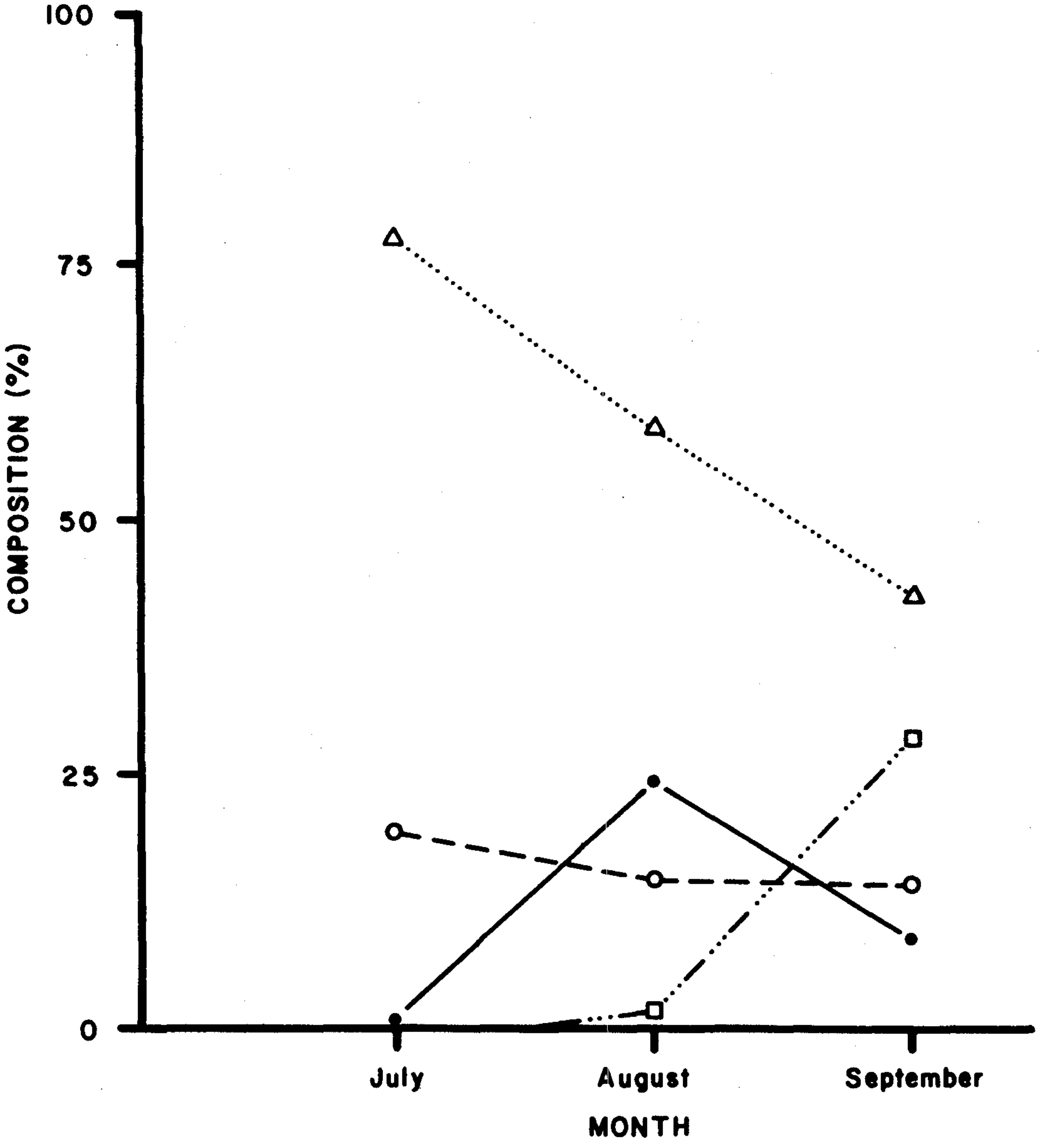

Figure 9. Percent composition by volume of the monthly diet of smelt from West Bearskin Lake. Crustaceans are represented by dots, insects by triangles, smelt by squares and other fish by open circles.

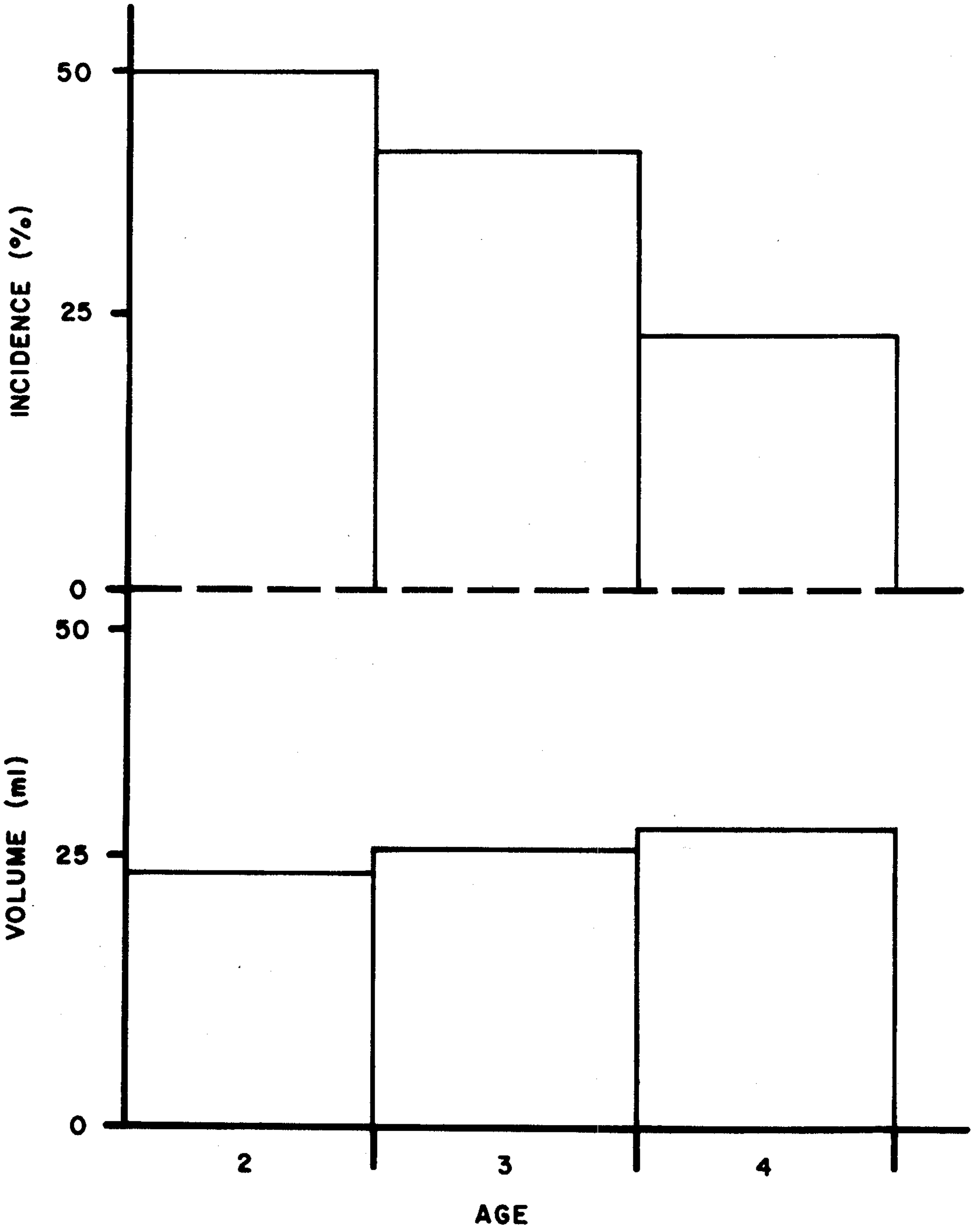

Figure 10. Percent incidence of food and average food volume in stomachs of smelt ages 2-4 from West Bearskin Lake.

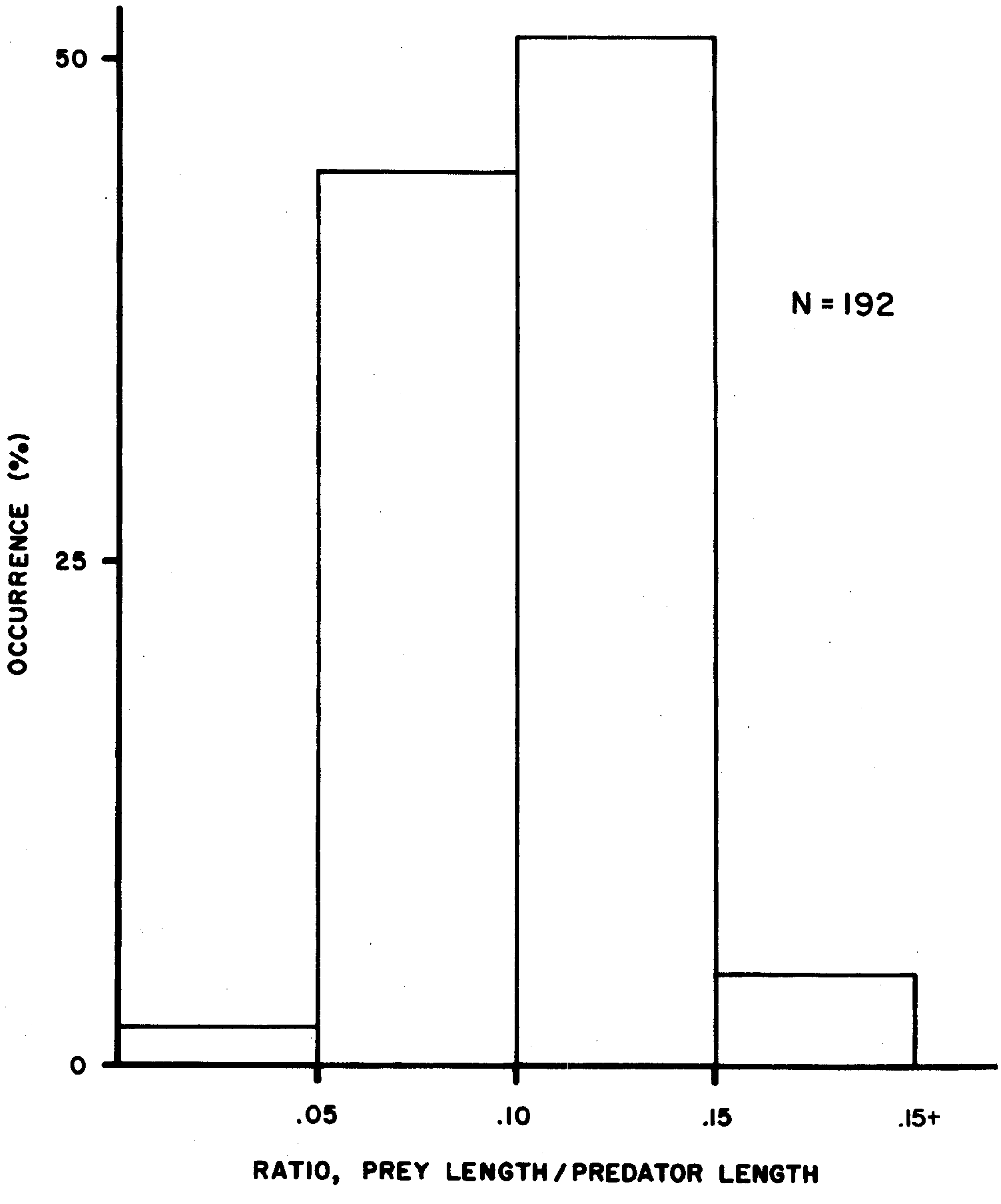

Figure 11. The percent occurrence of prey fish of various total lengths (expressed as a ratio of predator length) in stomachs of smelt from West Bearskin Lake.

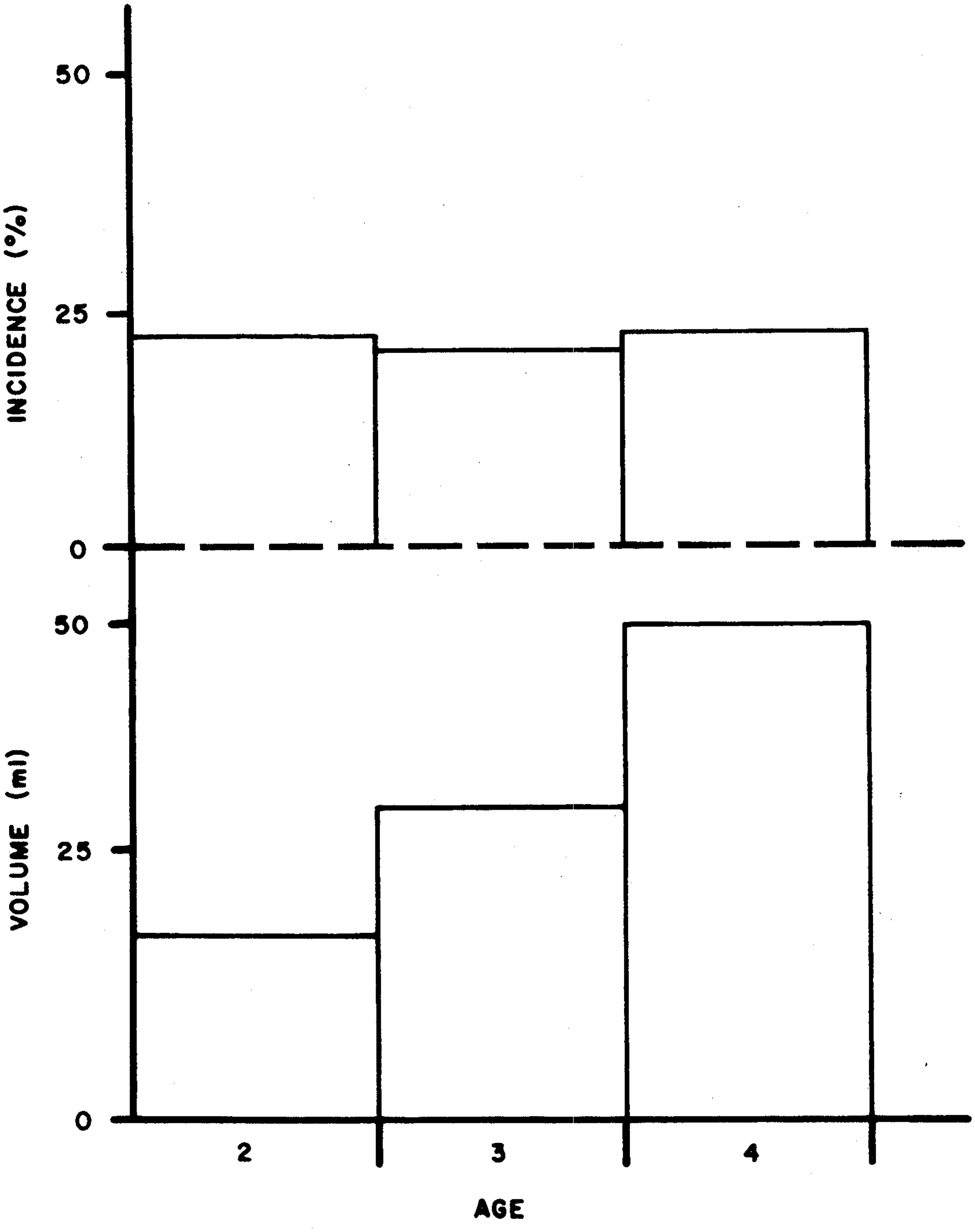

Figure 12. Percent incidence of food and average food volume in stomachs of smelt ages 2-4 from Devilfish Lake.

Table 5. Size of fish prey consumed by Devilfish Lake smelt.

Predator		Prey		Ratio of prey length/ pred. length
Total length (mm)	Age	Species	Total[a] length (mm)	
129	1	Darter	25	0.19
		Darter	20 (2)	0.16
		Darter	15 (2)	0.12
132	2	Darter	34	0.26
142	2	Stickleback	33	0.22
160	2	Smelt	62	0.39
147	3	Darter	20	0.14
145	3	Stickleback	55	0.38
203	3	Smelt	86	0.42

[a] Frequency in parentheses

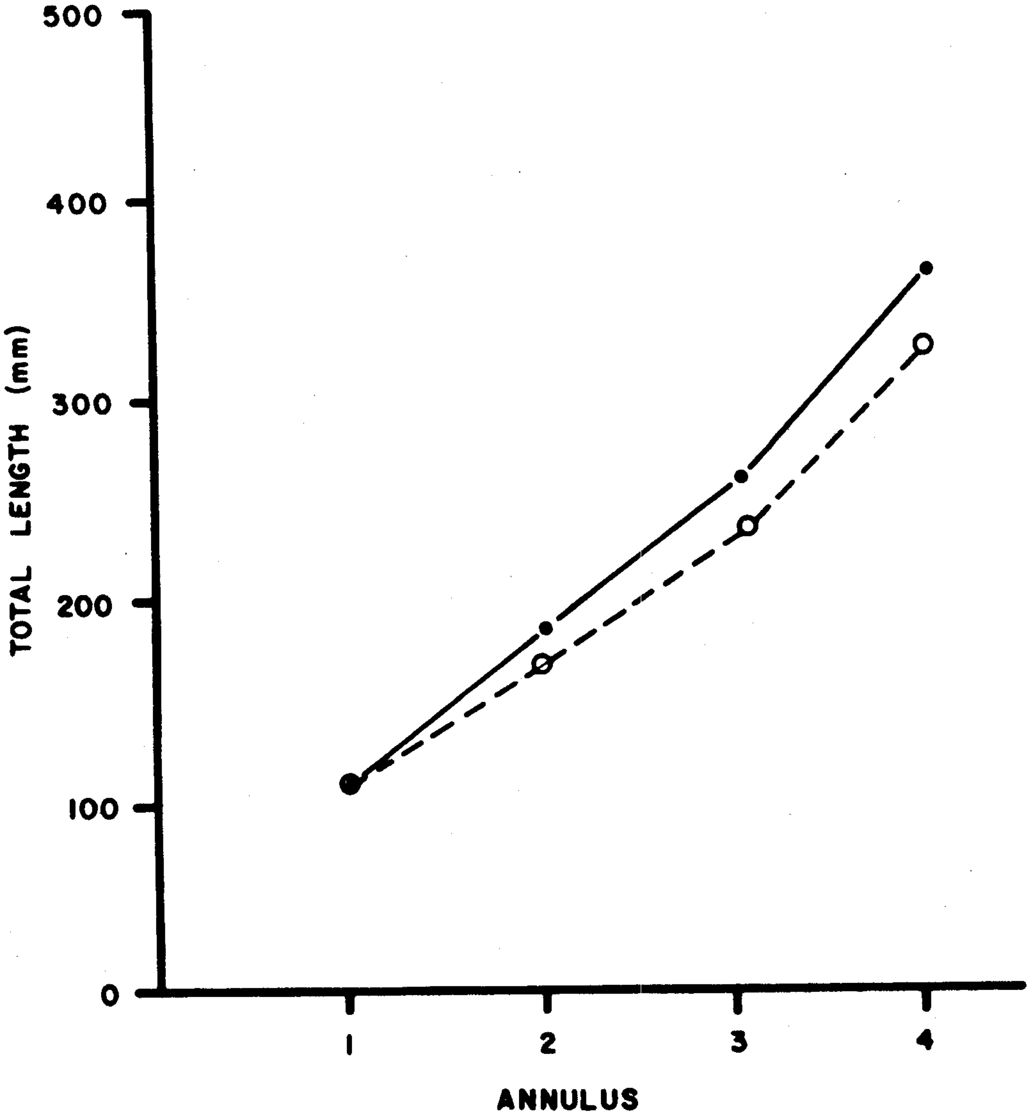

Figure 13. Estimated total length of annulus formation of juvenile lake trout from West Bearskin Lake for growth years before (dots) and after (open circles) smelt introduction.

changes occurred after smelt introduction in Devilfish Lake.

The lake trout growth rate increased annually until fish reached _ 300 mm TL (Fig. 14). The growth rate then changed from an increasing rate to a decreasing rate as fish grew from _ 300 mm to _ 400 mm. Growth rates declined annually thereafter.

Growth data was inadequate from lake trout (> age 5) to determine if changes occurred after smelt introduction in West Bearskin Lake. Post-smelt Walford growth parameters were: $K = 0.887$, $L_{oo} = 1,043$ mm.

Walford growth parameters did not change for adult lake trout in Devilfish Lake after smelt introduction. Estimated growth parameters were (r = coefficient of correlation):

	(K)	$L(_{oo})$	(r)
BEFORE SMELT	0.881	769 mm	0.996
AFTER SMELT	0.888	829 mm	0.997

Growth coefficients were not significantly different ($P \leq 0.05$).

Smelt growth characteristics differed between the study lakes. Smelt growth was faster during the first year in West Bearskin Lake than in Devilfish Lake where growth was more evenly distributed over the fish's life span (Tables 6 and 7). Walford growth parameters were:

	(K)	(L_{oo})	(r)
WEST BEARSKIN LAKE	0.788	238 mm	0.981
DEVILFISH LAKE	0.799	220 mm	0.840

Growth coefficients were significantly different ($P \leq 0.05$)

Length - Weight

Smelt influenced lake trout condition differently in each lake. Equations for length-weight relationships where W = weight in g and L = total length in cm (logarithms to base e) were:

WEST BEARSKIN LAKE:
  BEFORE SMELT $\log W = -7.839 + 3.844 \log L$
  AFTER SMELT $\log W = -5.304 + 3.186 \log L$

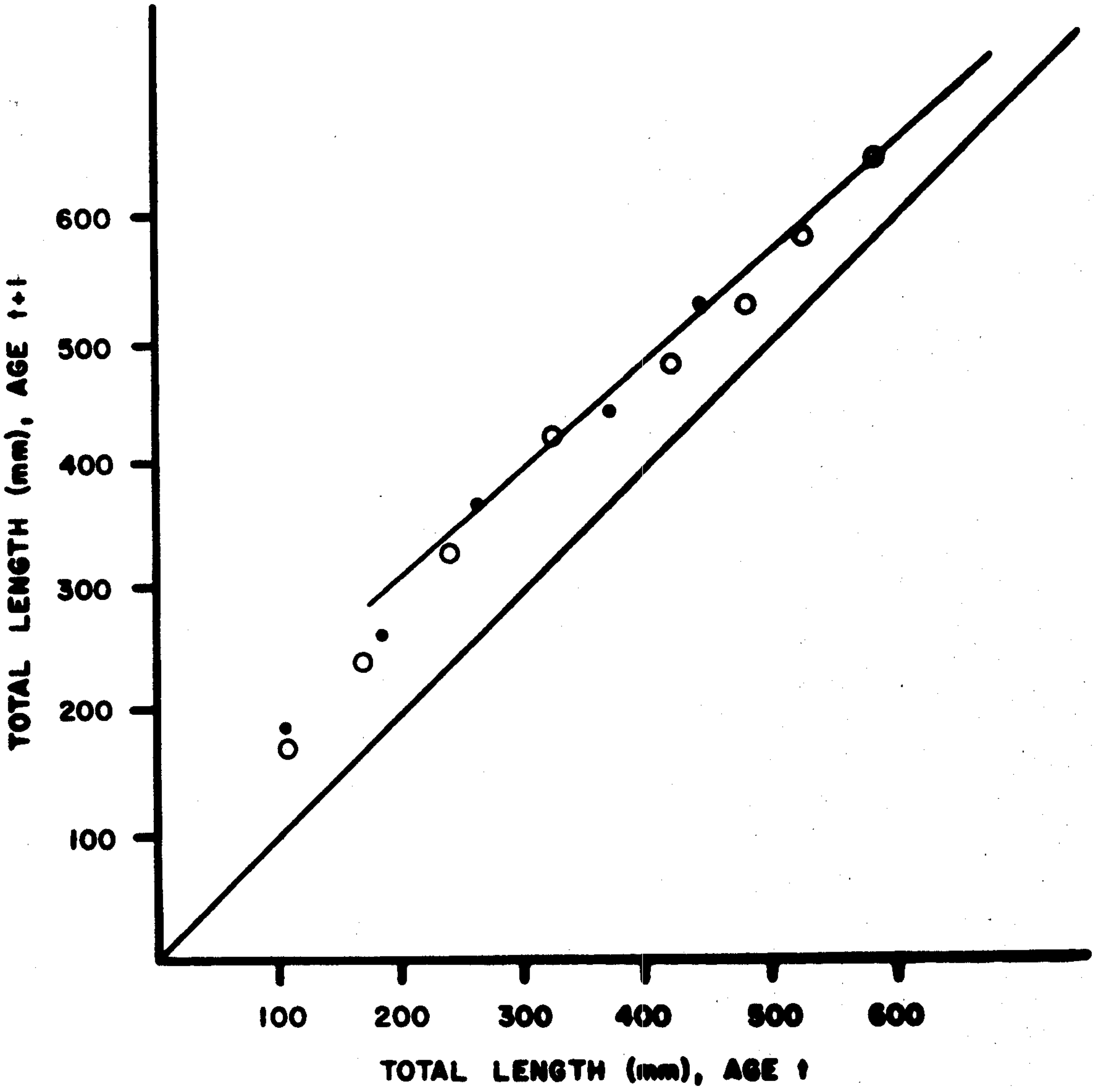

Figure 14. Walford graph of total length (mm) at age t+1 against total length (mm) at age t of lake trout of West Bearskin Lake before smelt introduction (dots) and after smelt introduction (circles).

Table 6. Average total length (mm) at age of West Bearskin smelt.

Year-class	AGE 1	2	3	4	5	6
1963		89	272			
1964		127				
1966		122	180	152		
1967		135	140	102		
1968		135	145	157	168	216
1969		135	152	168	183	188
1970		152	170	102	193	
1971	122	145	173	188	221	
1972	119	122	175	191	183	234
1973		152	157	188	201	
1974		147	163	201		
1975	119	163	193	152		
1976	112	142	150	201		
1977	157	147	183			
1978		175				
1979	165					
1980						
Unweighted mean	118	139	165	183	191	209

Table 7. Average total length (mm) at age of Devilfish Lake smelt.

Year-class	AGE 1	2	3	4	5	7
1970	152	142	157	170	213	
1971	122	150	163	183		
1972	114	109	157	246		170
1973		114	165	355	152	
1974		117	135	140	180	
1975	107	117	137	165		
1976		135	140			
1977	130	130	150			
1978	124	132				
1979	127					
Unweighted mean	121	127	150	183	182	170

DEVILFISH LAKE:
BEFORE SMELT $\log W = -4.603 + 2.960 \log L$
AFTER SMELT $\log W = -4.463 + 2.945 \log L$

Functional slopes of before smelt and after smelt plots were significantly different in both cases ($P < 0.05$). By substitution, both samples (before and after smelt) of lake trout from West Bearskin Lake averaged 1,054 g at 470 mm TL Fish smaller than 470 mm were heavier for their length after smelt while fish larger than 470 mm were heavier for their length before smelt. Average weight for length of Devilfish lake trout was always heavier after smelt than before smelt.

Abundance, Survival and Maturity

Abundance of both species declined in both lakes during the study period (Figs. 15 and 16). Lake trout abundance in West Bearskin was highest in 1966 (CPUE = 8.0) and lowest in 1980 (CPUE = 0.4). Smelt abundance was highest in 1971 (CPUE = 798.0) and lowest in 1979 (CPUE = 7.1). Lake trout abundance in Devilfish Lake was highest in 1969 (CPUE = 5.9) and lowest in 1980 (CPUE = 1.0). Smelt abundance was highest in 1973 (CPUE = 512.0) and lowest in 1979 (CPUE = 73.0).

Smelt survival in both lakes was variable but survival rates tended to decrease with age (Tables 8 and 9). No correlation was found between smelt survival and any of the variables measured in the study.

Total length at maturity of lake trout shifted upwards after smelt introduction in both lakes (Fig. 17). Lake trout collected in West Bearskin Lake between 1969 and 1973 (before smelt) were all mature at 455 mm while fish in a 1977 sample (after smelt) were not 100% mature until 580 mm. Maturity of lake trout in an aggregate sample collected in Devilfish Lake in 1969 and 1970 (before smelt) were 100% mature at 460 mm. A later 1977 sample (after smelt) contained fish as large as 580

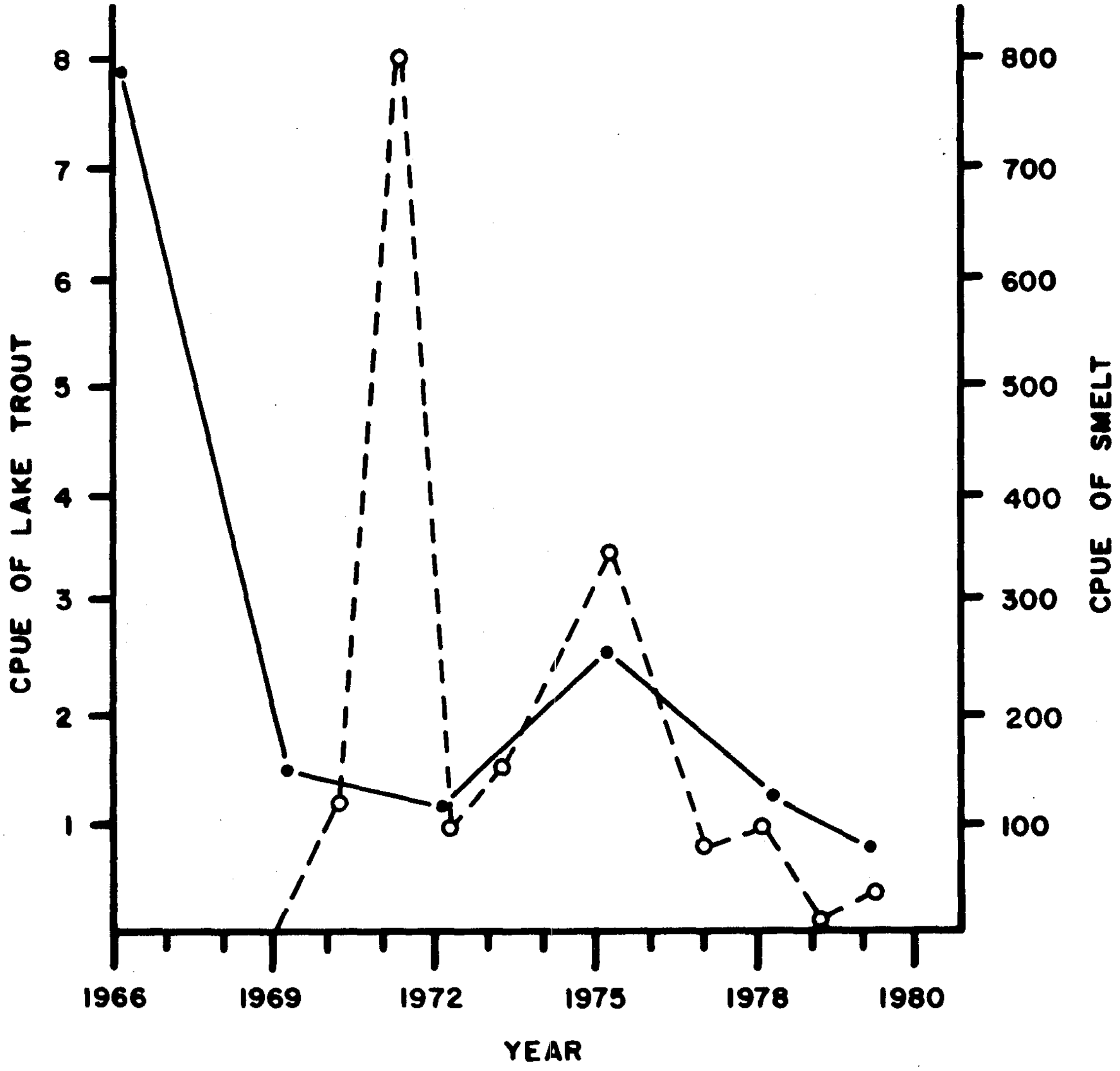

Figure 15. Catches (CPUE) of lake trout (dots) and smelt (open circles) in West Bearskin Lake, 1966-1980.

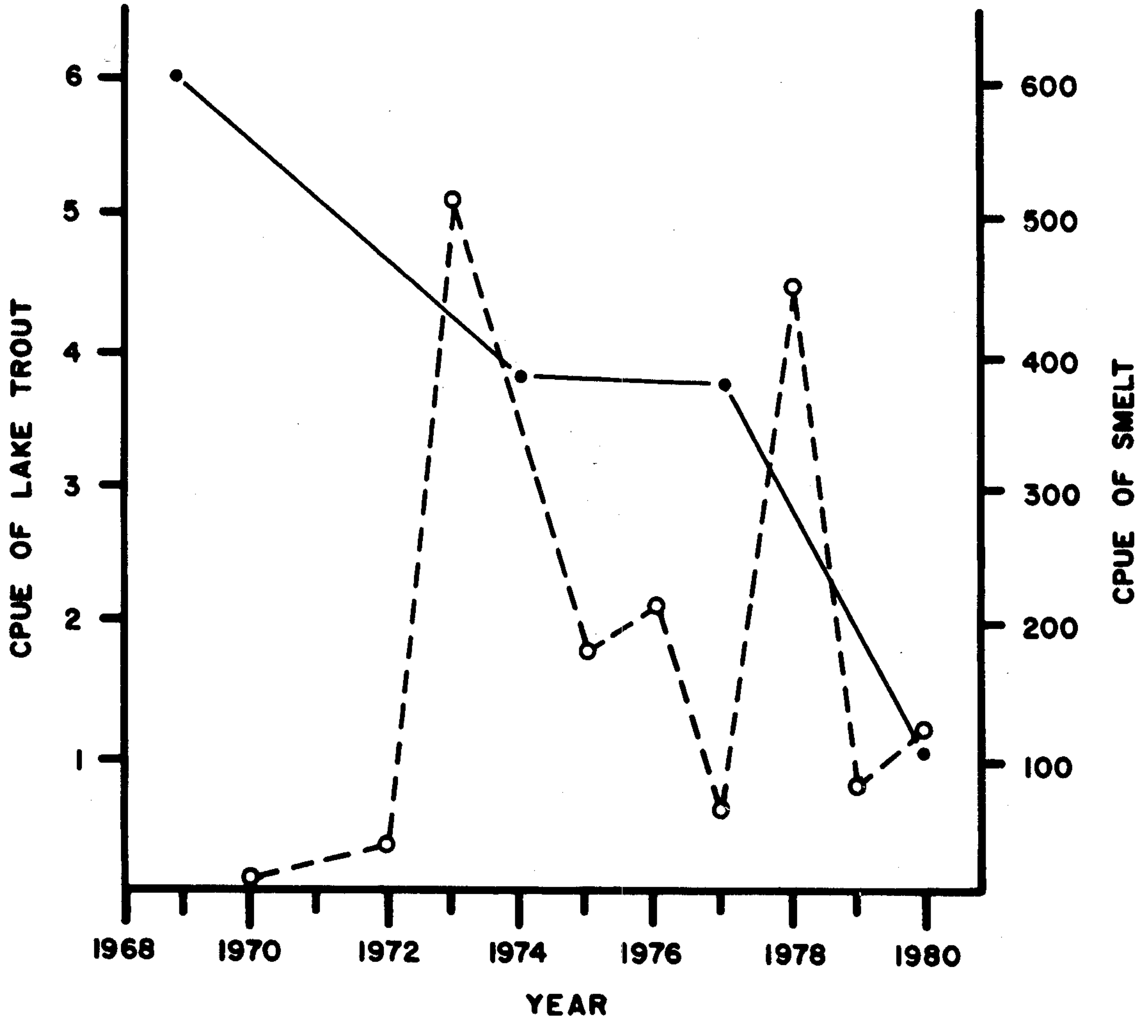

Figure 16. Catches (CPUE) of lake trout (dots) and smelt (open circles) in Devilfish Lake, 1969-1980.

Table 8. Average annual survival rate of West Bearskin smelt year-classes, 1966-1978.

	AGE					
Year-class	1 - 2	2 - 3	3 - 4	4 - 5	5 - 6	6 - 7
1966				0		
1967			0.548	0		
1968		-	0.065	0.254	0.152	0
1969		0.107	0.457	0.452	0	
1970	-	-	0.783	0.155	0	
1971	-	-	0.840	0.005	0	
1972	-	-	0.020	0.267	0	
1973	-	-	0.165	0.068	0	
1974	-	-	0.588	0		
1975	-	-	0.056	0		
1976		0.205	0.051			
1977	0.086	-				
1978	-					

Dashes indicate that the fish were not fully susceptible to the sampling gear.

Table 9. Average annual survival rate of Devilfish Lake smelt year-classes, 1970-1978.

	AGE				
Year-class	1 - 2	2 - 3	3 - 4	4 - 5	5 - 6
1970			0.144	0.117	0
1971		0.874	0.171	0	
1972	-	-	0.004	-	-
1973	-	0.857	0.556	-	0
1974	-	0.083	-	.006	0
1975	-	-	.006	0	
1976	-	.019	0		
1977	.395	.034			
1978	-				

Dashes indicate that the fish were not fully susceptible to the sampling gear

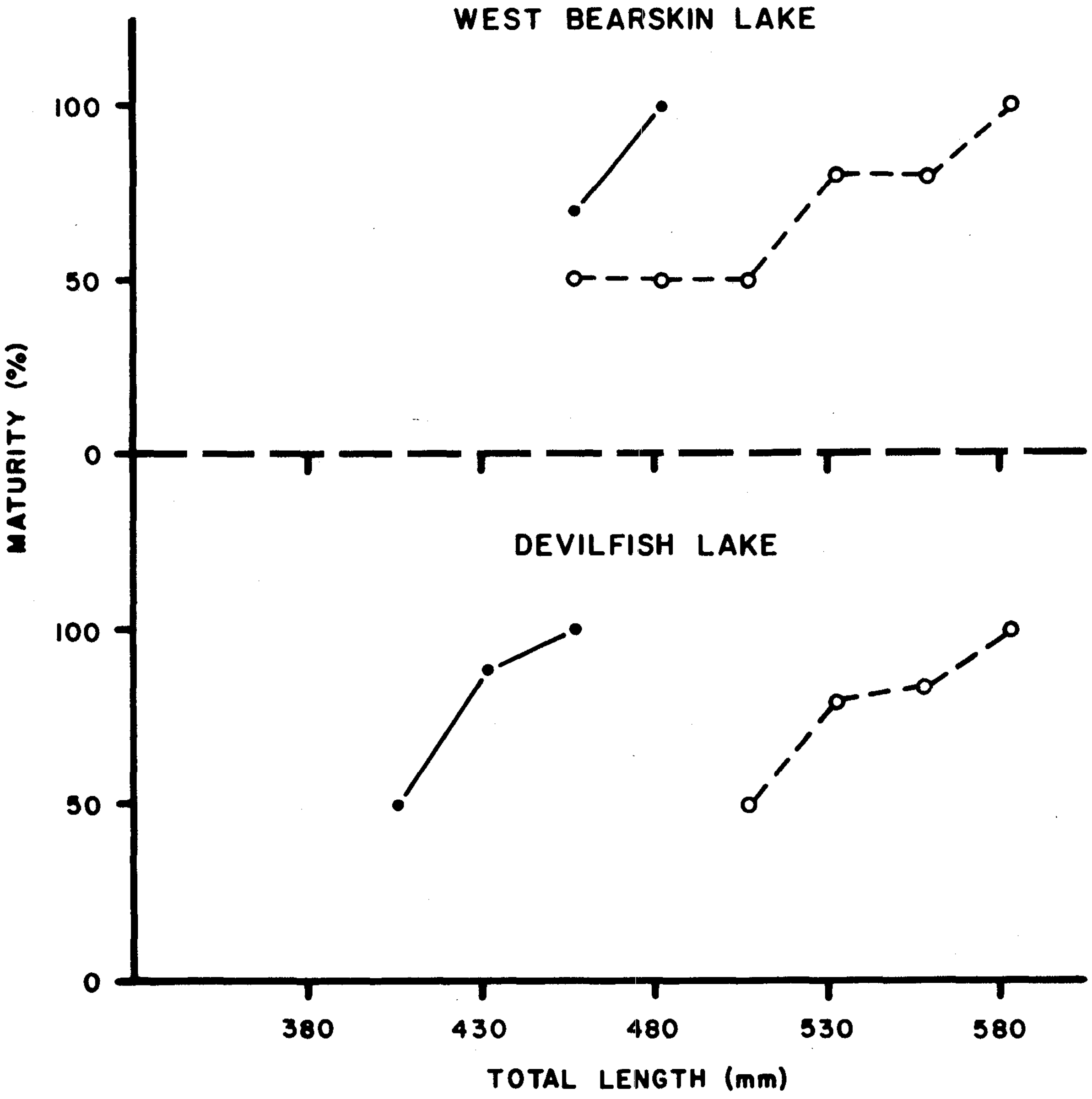

Figure 17. Percent maturity of lake trout at various total lengths (mm) in West Bearskin and Devilfish lakes, before smelt introduction (dots) and after smelt introduction (open circles).

mm that were not sexually mature.

DISCUSSION

Distributional data gathered in this study suggest that rainbow smelt are readily available to lake trout as forage in stratified lakes and are the only forage species in proximity to the lake trout in the hypolimnion. It is unknown if either species frequented the upper strata. Hypolimnetic anoxia apparently prevented spatial segregation of smelt and lake trout from other fish in Devilfish Lake. In this instance, any benefits derived by lake trout from the presence of smelt were not related to spatial factors.

Smelt was dominant in the diet of all size groups of lake trout in West Bearskin Lake except those between 150 mm and 300 mm TL. Whether this dominance was a result of spatial segregation, prey selectivity or the relative abundance of smelt compared to other prey is uncertain.

A greater weight for length of small lake trout (< 470 mm TL) in West Bearskin Lake and for all sizes in Devilfish Lake was observed. However, the sample size of fish < 400 mm was small (10 fish) and the slope of the length-weight function may have been biased by the benefits of smelt to larger individuals (83 fish).

Juvenile lake trout and smelt utilized the same food items. Eschmeyer (1956) and DeRoche (1969) reported that juvenile lake trout ate food items similar to the components of the smelt diet reported here. Werner (1979) discussed the value of body size in competing for food. He stated that young fish have a limited range of food particle sizes available to them. Their minimum food particle size stays the same as they grow but their maximum particle size increases, thus increasing the range of usable food. As food becomes rarer, food particle sizes both larger and smaller than optimum are added to the diet. The relative frequency of smelt stomachs containing food in West Bearskin Lake (Fig. 10) was roughly twice that found in Devilfish Lake (Fig. 12) indicating that food was more abundant in West Bearskin Lake. The average food volume stayed about the same as size (age) increased in West Bearskin Lake (Fig. 10) but average food volume in Devilfish Lake smelt stomachs increased twofold with each year of growth (Fig. 12). Older fish probably used the competitive advantage offered by their larger body size and added food particles that were smaller and larger than optimum to their diet. The advantage offered by larger body size can be utilized by managers by stocking the largest lake trout available when smelt are present.

Predation of juvenile lake trout by smelt is possible where lake trout populations are maintained by natural reproduction. Our data indicated that smelt readily consumed fish 5% to 15% of their own TL. These data probably reflect availability rather than maximum prey size. Devilfish Lake smelt preyed on fish as large as 48% of their own TL. Data from Lake Superior indicated that smelt consumed fish up to 20% of their own body size (W.A. Swenson, Univ. Wisc. Superior, personal communication 1982). Lake trout fry average 23 mm TL at swim-up (Fish 1932). Assuming a 20% ratio of body sizes, swim-up fry could be readily consumed by all smelt larger than 115 mm, virtually all smelt older than age one in both lakes (Tables 8 and 9). Rupp and DeRoche (1960) found that juvenile lake trout prefer hypolimnetic waters and are not immune to predation because of distributional differences. Lake trout in West Bearskin Lake averaged 106 mm at the end of their first growing season (Fig. 13). Assuming a 4 month growing season, equal growth rates during the 4 months and a 20% body size ratio, juvenile lake trout could be preyed upon with decreasing frequency for about 2 months. An average 5 or 6 year old smelt in West Bearskin Lake (200 mm TL) could prey on juvenile trout in West Bearskin Lake for one full year.

Declines of post-smelt juvenile lake trout growth in West Bearskin Lake are a potentially important detrimental factor. Werner (1979) pointed out that faster growth and increased survivorship, improved fitness. Conversely, declines in growth rate in West Bearskin likely decreased fitness thus reducing survivorship. Werner (1979) also described what he called a "bottleneck" phenomenon whereby competition from a morphologically better adapted species limits recruitment to a piscivor population by prolonging the time spent at small, highly vulnerable sizes. The decline in juvenile growth rate observed in West Bearskin Lake may be an empirical example of the "bottleneck" phenomenon. Mortality from decreased fitness and extended vulnerability to predation may have contributed to reduced recruitment in West Bearskin Lake and the observed decline in abundance.

Maturity shifts of lake trout in both lakes would have produced greater fecundities and increased the potential number of recruits per female. Greater potential for recruitment could be a mechanism of compensation by lake trout to offset higher mortality as a result of high numbers of smelt and increased mortality on young, prey size lake trout. Declines in lake trout abundance could have been related to smelt predation. On the other hand, lake trout population declines could just as well have been unrelated to interspecific factors since abundance of both lake trout and smelt declined during the study.

Stock depletion prior to 1966 in West Bearskin Lake provided an open niche for smelt and an essentially open niche for lake trout. Chemical rehabilitation of Devilfish Lake also provided an open niche for both species. Population levels following introduction into a new environment traditionally climb to a peak and then decline and equilibrate at a "normal" lower level. The population declines observed may have been a result of this equilibration. Other factors including fishing (lake trout) and spawning mortality (smelt) could also have been important factors contributing to the population declines.

MANAGEMENT IMPLICATIONS

In light of the risk involved, particularly for lake trout populations maintained by natural recruitment, rainbow smelt should not be stocked in Minnesota's lake trout waters. Although smelt were a suitable forage species based on their spatial distribution and improvements in condition of some life stages of lake trout, several aspects of the smelt-lake trout association could pose considerable risk. Smelt and lake trout utilized the same food items and negative impacts from competition could occur in some situations. The observed declines in juvenile growth rate observed may have been a direct result of the smelt introduction and a probable consequence is increased mortality due to decreased fitness and a longer period of susceptibility to smelt predation.

Lake trout stocked into smelt waters should be in good physical condition and large size to withstand smelt predation and food competition. Further study is needed to ascertain the relationship of smelt predation and food competition to juvenile lake trout and clearly define the need and criteria for lake trout stocking in smelt inhabited lakes.

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