Population Characteristics of Lake Trout in Walker Lake, Gates of the Arctic National Park and Preserve, Alaska

by

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POPULATION CHARACTERISTICS OF LAKE TROUT IN WALKER LAKE.
GATES OF THE ARCTIC NATIONAL PARK AND PRESERVE,
ALASKA

A
THESIS

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Francis Jeffrey Adams, B. S.

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For my family.

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GATES OF THE ARCTIC NATIONAL PARK AND PRESERVE,
ALASKA

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Francis Jeffrey Adams

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Date

Abstract

The population of lake trout in Walker Lake, southern Brooks Range, was investigated during summers, 1987 and 1988. Adults were most abundant at stream mouths after ice-out. Juveniles were most abundant in pelagic areas. Fingerlings preferred stream mouths. Ages ranged from 5 to 26 years. Lengths ranged from 203 to 924 mm; weights from 83 to 8,500 g. Both sexes had similar condition and matured at age 12. Fecundity increased with length and age. Females spawn every other year. Comparisons of growth curves and fecundity-at-length curves among populations in various Alaskan lakes suggested that lake trout in Walker Lake have not experienced heavy exploitation. The lake trout population in Walker Lake should be monitored in the future through angler surveys and selected studies of life history.

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Introduction

Walker Lake in Gates of the Arctic National Park and Preserve is a National Natural Landmark, and is located in a designated wilderness area. Fish species present include lake trout (*Salvelinus namaycush*), Arctic char (*Salvelinus alpinus*), Arctic grayling (*Thymallus arcticus*), round whitefish (*Prosopium cylindraceum*), northern pike (*Esox lucius*), burbot (*Lota lota*), least cisco (*Coregonus sardinella*), slimy sculpin (*Cottus cognatus*), and chum salmon (*Oncorhynchus keta*). Sport fishing is a primary activity for visitors to Walker Lake (USDI 1986).

Lake Trout

One of the species most sought by sport fishermen at Walker Lake is the lake trout. This species can attain great size, is notably admired as a trophy, and is well esteemed as a food fish (Martin and Olver 1980; Morrow 1980). The lake trout is confined to the northern temperate and subarctic-arctic freshwater systems of North America, and reach their greatest abundance in oligotrophic lakes (Ryder 1972). Oligotrophic lakes have low productivity (Wohlschlag 1953; Thomasson 1956; Ryder1972; Wong 1973; Schindler et al. 1974; Welch 1974, 1985; Johnson 1975a; Bergmann and Welch 1985; Welch and Bergmann 1985a, 1985b), and are typically large, deep, clear, cold and well oxygenated

(Martin and Olver 1976). Lake trout from these areas exhibit slow growth rates (Kennedy 1954; Healey 1978a), and combined with the fish's late maturity and intermittent spawning, these fish are vulnerable to overexploitation with little chance for short term recovery (Martin and Olver 1980).

Most information about lake trout life history comes from Canada and the Great Lakes region where lake trout populations experience drastically different climatic conditions than Alaskan stocks (Burr 1987a). Few reports are available concerning lake trout in Alaska, and these lack substantial information about the fish's habitat preferences, growth, condition, age structure and maturity. Even fewer reports are available for lake trout populations in northern Alaska with only two reports from waters within Gates of the Arctic National Park and Preserve. Both studies were mainly general surveys, and both were conducted before the area was selected as a national park. Roguski and Spetz (1968) captured 13 lake trout in two net nights of sampling on Walker Lake, and McCart et al. (1972) captured 87 lake trout with periodic sampling during one season at Itkillik Lake. These studies were conducted over 15 years ago when management jurisdictions and mandates were different than they are currently.

Purpose

The Alaska National Interest Lands Conservation Act of 1980 provided the National Park Service with a management directive for Gates of the Arctic National Park and Preserve:

> ... to maintain the wild and undeveloped character of the area, ... and the natural environmental integrity and scenic beauty of the mountains, forelands, rivers, lakes, and other natural features; ...and to protect habitat for and the populations of, fish and wildlife ... (USDI 1986).

With an inevitable increase in sport fishing pressure, and the lake trout's inherent vulnerability to overharvest, accurate and dependable information about lake trout biology in Walker Lake is imperative for the National Park Service to meet its Congressional mandate.

The goal of this study was to provide information concerning lake trout life history in Walker Lake to serve as a baseline for future monitoring, management and conservation. To meet this goal the study objectives were to:

1) estimate relative abundance;
2) determine habitat preferences;
3) document age and growth;
4) calculate the weight-length relation;
5) determine fish condition indices; and
6) provide indices of maturity and fecundity.

The results were compared with other pertinent studies providing a basis for future comparisons and management. Recommendations for monitoring and maintaining the Walker Lake lake trout population were also presented. The study was conducted during summers, 1987 and 1988.

Study area

Walker Lake (67° 08' N 154° 20' W) is located in the southwestern portion of Gates of the Arctic National Park and Preserve in the Brooks Range of northern Alaska (Figure 1). The lake is 206 m above sea level on the south side of the Endicott Mountains, and lies in the subarctic climate zone of the boreal forest (taiga) (USDI 1986). Annual precipitation averages from 30 to 48 cm of rain and 152 to 203 cm of snow. The average maximum and minimum temperatures in January are -24 and -36 C, and in July are 23 and 13 C. It is an oligotrophic lake (Jones et al. 1990) with sparse patches of aquatic macrophytes and scattered areas of *Chara* sp. and *Potamogeton* sp. Ice-out usually occurs during the first week of June; freeze-up in early October. The lake has a surface area of 3,800 ha, and is 21 km long (Figure 2).

The majority of the lake is contained in a narrow glacially-carved valley, oriented northwest-southeast, with steep slopes that climb to 1,400 m (Reanier and Anderson 1986). The steepness of these slopes is reflected in the sides of the two major lake basins. The northern basin, detached from the southern basin by a relatively shallow area containing several islands, is 120 m deep and rather symmetrical. The southern basin is more complex with its deepest

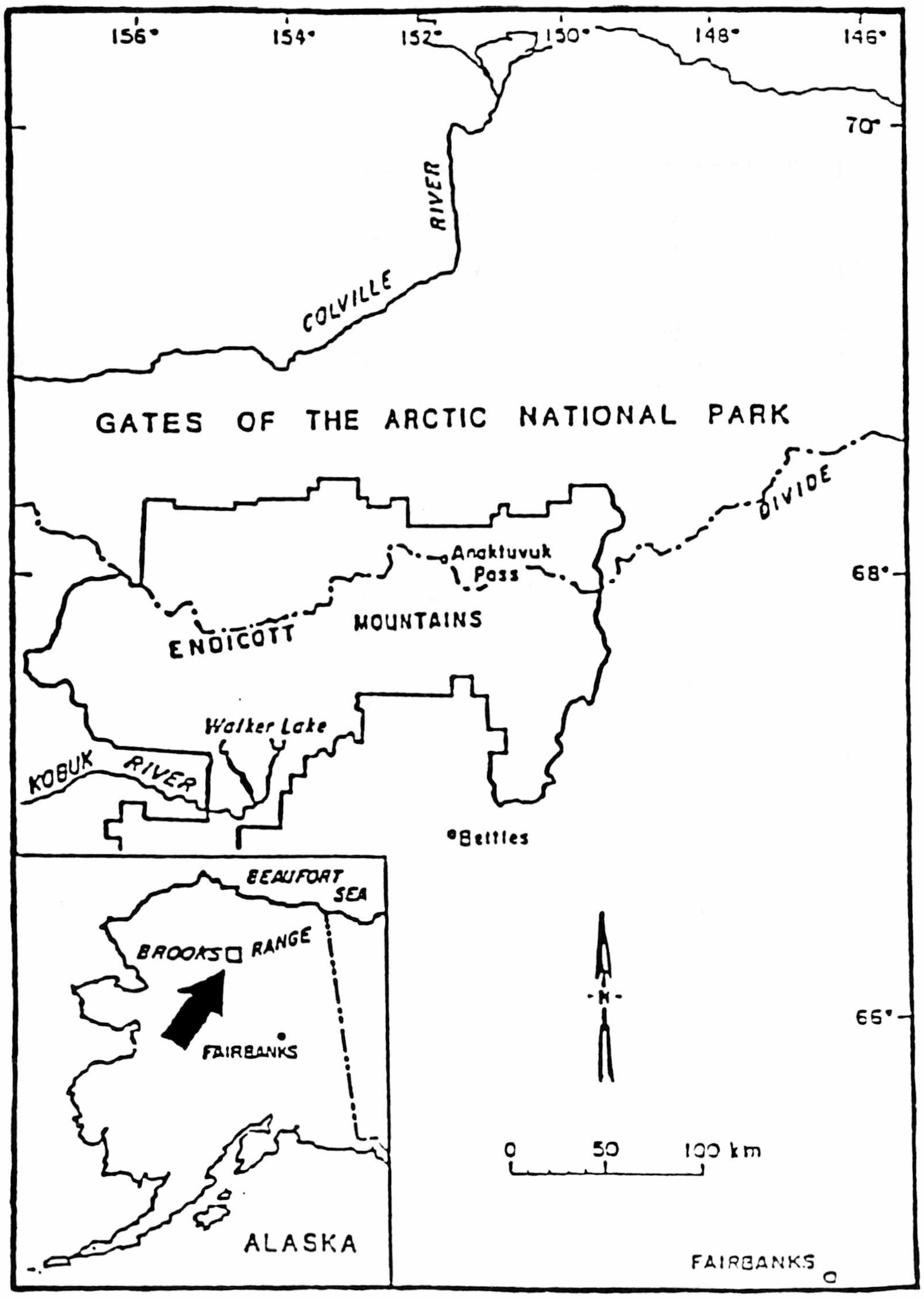


Figure 1.-The location of Walker Lake in Gates of the Arctic National Park and Preserve.

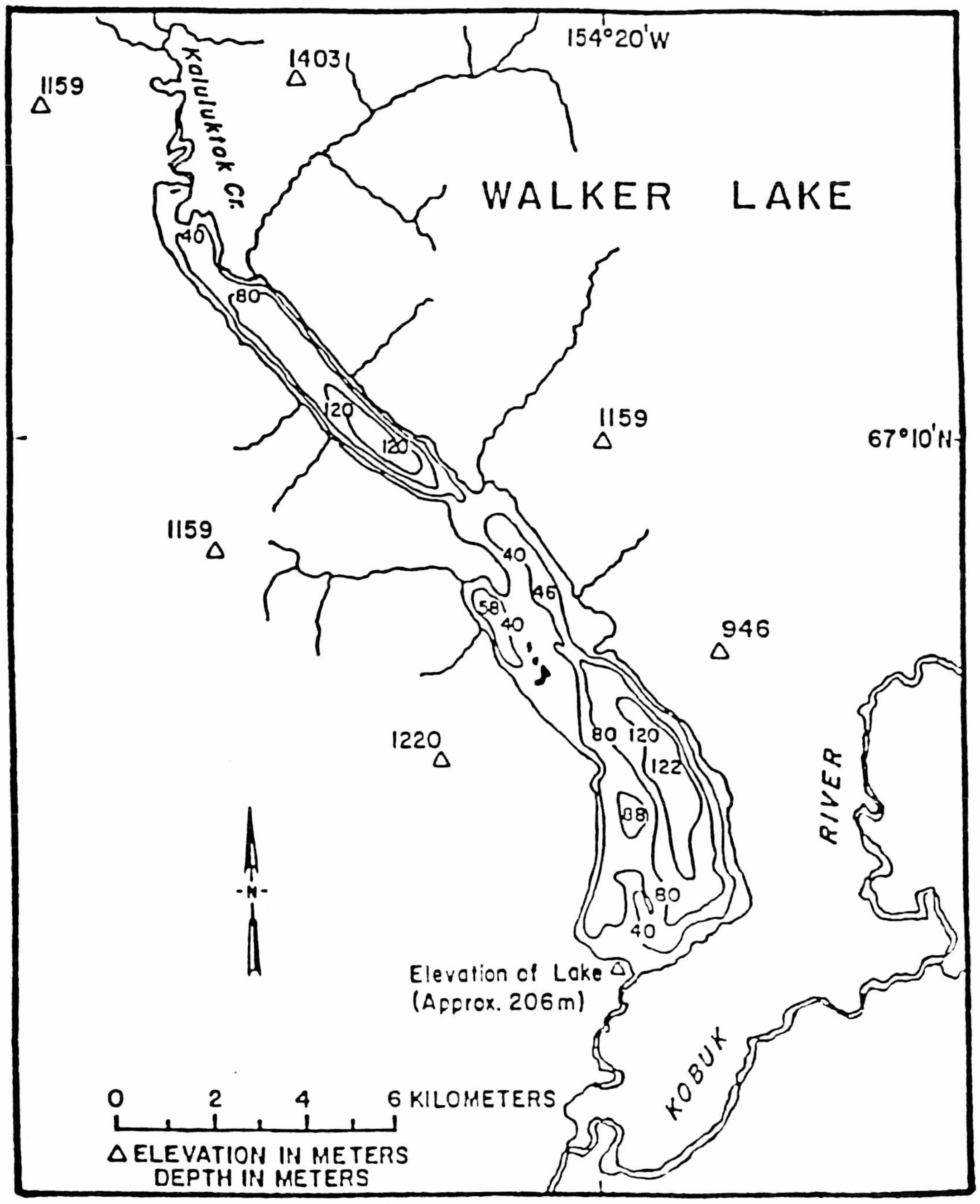


Figure 2.-Some physical features of Walker Lake, its primary tributaries and surrounding terrain.

portion reaching to 122 m in the east and a secondary basin of 88 m in the west. The lake forms its broadest point (4 km) at the south end where a low terminal moraine dams the valley. The major inlet stream, Kaluloktok Creek, enters from the north and several permanent and many intermittent streams are located throughout the lake. The unnamed outlet stream exits the lake at the south end, and extends 4 km before entering the Kobuk River.

Walker Lake is one of the most heavily used areas within Gates of the Arctic National Park and Preserve (USDI 1986). A lodge that advertises primarily for guided fishing is located on the lake. Air-taxi operators bring clients for fishing, and outfitters use the lake as a starting point for float trips on the Kobuk River. Hiking and backpacking also occur in the Walker Lake area (USDI 1986).

Relative Abundance

Relative abundance provides an indication of population density assuming that catch per unit effort (CPUE) is proportional to density (Hubert 1983). Fish behavior can cause great variability in the catch rate; therefore, it is imperative to minimize this variability by standardizing the sampling design, gear, and methods. The 1987 season was used for reconnaissance of the lake trout in Walker Lake, and data for meaningful interpretation of relative abundance were not collected. However, after the 1987 sampling season, it was apparent that fish greater than 400 mm fork length (considered to be adults) were more easily captured in shoreline sets than fish that were less than or equal to 400 mm (considered to be juveniles). Adult catch rates were also higher during the early and late parts of the field season than during the mid-summer period. At a lake in northern Canada, Johnson (1972) captured the greatest number of large lake trout (≥ 400 mm) in shallow water, and the greatest number of small lake trout (< 400 mm) in deep water. For these reasons, sampling in 1988 concentrated on adult lake trout along shorelines during early and late field season, and on juvenile lake trout in pelagic and shallow water areas during the mid-summer period. Relative abundance information is concerned only with 1988 data.

Methods

Adult lake trout

A stratified sampling technique was employed to capture adult lake trout. The lake was divided into three sections (north, middle, and south) along natural breaks in its perimeter (Figure 3). From 7 June to 10 June, each section's shoreline was examined by three independent observers, and described by general substrate types: *sand and gravel* - 50% or more of the substrate < 64 mm in diameter; *cobble and boulder* - 50% or more of the substrate > 64 mm in diameter; or *mixed* - no apparent distinction between sand and gravel or cobble and boulder. A lead ball with a diameter of 64 mm was used as a standard to differentiate the substrate types.

The shoreline was further stratified by its configuration: *straight* - areas with a shoreline that was relatively uniform with no abrupt change in its form (including bays and coves); *peninsulas* - where the shoreline was more involved with distinct points or fingers of land jutting into the lake; *stream mouths* - areas where permanent creeks entered the lake; *islands* - where islands or shoals existed; *inlet zone* - the area near the mouth of Kaluloktok Creek; and *outlet zone* - the area where the unnamed creek drained the lake. The combination of shoreline feature and substrate type defined a habitat type.

The number of sampling sites per section was determined by the proportion of each habitat type in that section. A minimum of two sampling sites per habitat type per section was chosen. After the

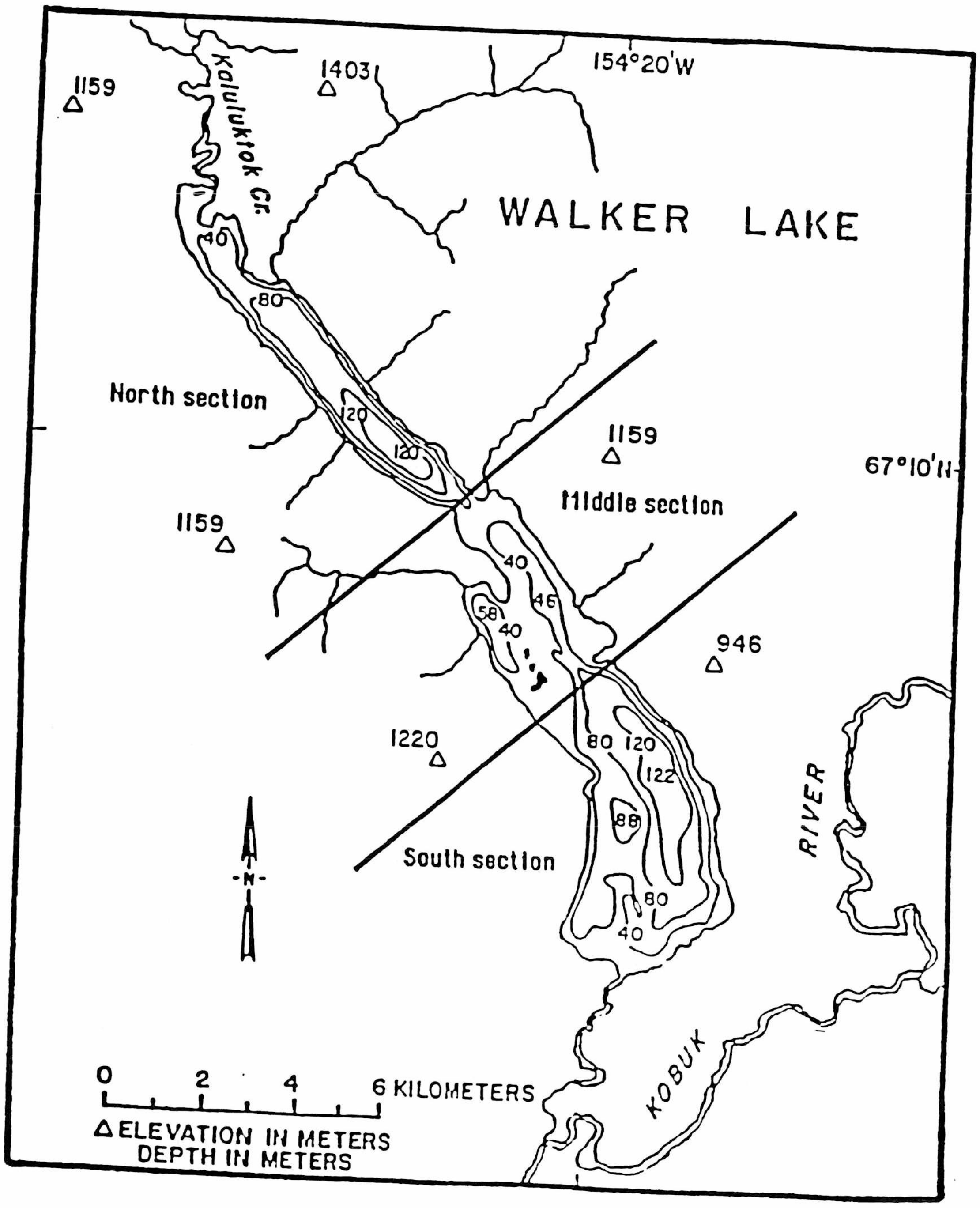


Figure 3.-The north, middle and south sections for the 1988 sampling season at Walker Lake.

number of sampling sites of each habitat type was established, actual sampling sites were randomly chosen from a numbered grid of the lake's shoreline; 13 sites in the north section, 11 in the middle, and 10 in the south for a total of 34 sampling sites (Figure 4).

At each site, the smallest mesh panel of a monofilament gill net (45.7 x 4.9 m with three equal size panels of 1.3, 1.9, and 2.5 cm mesh bar measure) was attached to the shore, and set perpendicular to the contour. A second gill net (45.7 x 4.9 m with 3.8 cm mesh) was attached to the deep end of the first net. These small mesh nets snagged larger fish by the teeth, rather than gilling them, and resulting in reduced mortality (Williams 1966; Burr 1987a).

An early sampling season (13 June to 4 July) and a late season (24 August to 15 September) were completed by two crews of two people each. Four sites were usually sampled each day with an individual site being sampled during the daytime (net set before 1700 hours) and during evening (net set after 1700 hours) in each season. Nets were fished for 4 h and checked at 0.3 h intervals to minimize mortalities.

Because all the sites received equal effort, and were fished with the same gear, each set was standardized into one net of 4 h effort. This amounted to 8 h of effort for each site in each of the two seasons for a total of 16 h of effort per site for the entire field season. Catch per unit effort (catch per hour, CPUE) was analyzed by season, time of day, lake section, substrate type, shoreline type, and interactive effects from a combination of some of these factors.

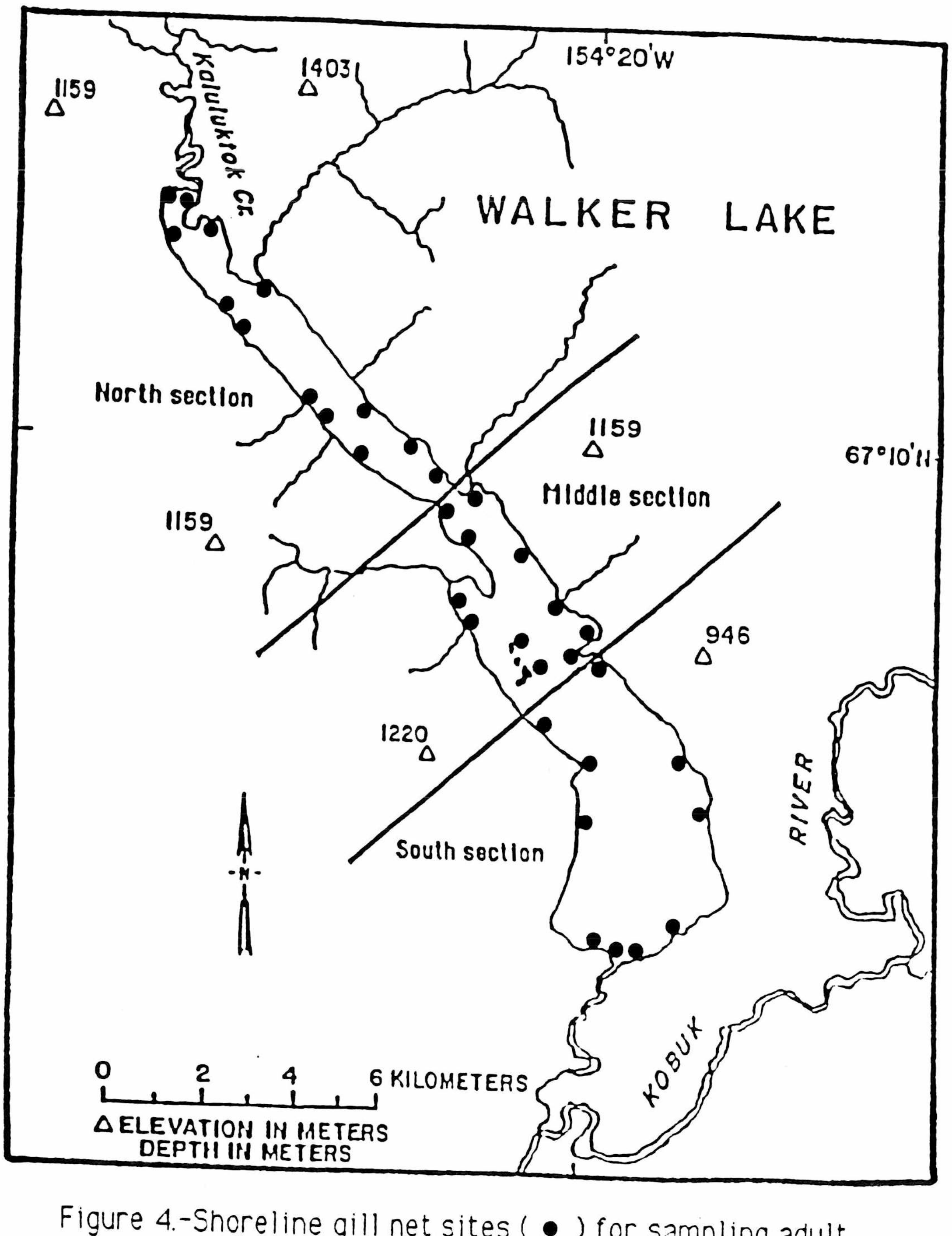


Figure 4.-Shoreline gill net sites (●) for sampling adult lake trout.

Juvenile lake trout

Sampling for juvenile lake trout was performed between 6 July and 26 August. Two monofilament gill nets (45.7 x 4.9 m with three equal size panels of 1.3, 1.9, and 2.5 cm mesh) were used to sample the pelagic areas (> 30 m depth) of Walker Lake. One net was set on the bottom, and the second was concurrently set halfway between the lake's surface and the bottom set. All bottom nets fished at 45 m or deeper, and all mid-water nets fished at 20 to 50 m depth. The number of sampling sites was proportional to the pelagic area of each section. Six sampling sites were established in the north section, 4 in the middle section, and 12 in the south section for a total of 22 pelagic sampling sites (Figure 5). Nets were initially set for 1 h to minimize mortalities. Because only one mortality was encountered during these 1 h sets, each site was fished for an additional 24 h period. Nets were checked only at the end of each period. Catch per unit effort from the pelagic sites was calculated by dividing the catch from each net (bottom or midwater) by 25 h of effort. Catch per unit effort data were classified by section and depth (bottom or mid-water).

While the pelagic gill nets were fishing, a 10 x 1.5 m beach seine with 6 mm mesh was used to capture lake trout fingerlings. Because of the predominance of the lake's steep shoreline, appropriate seining sites were rare, and were limited to a few shallow areas with sand/gravel substrate. Three straight shoreline and three stream mouth sampling sites were established in the north and middle sections. Due

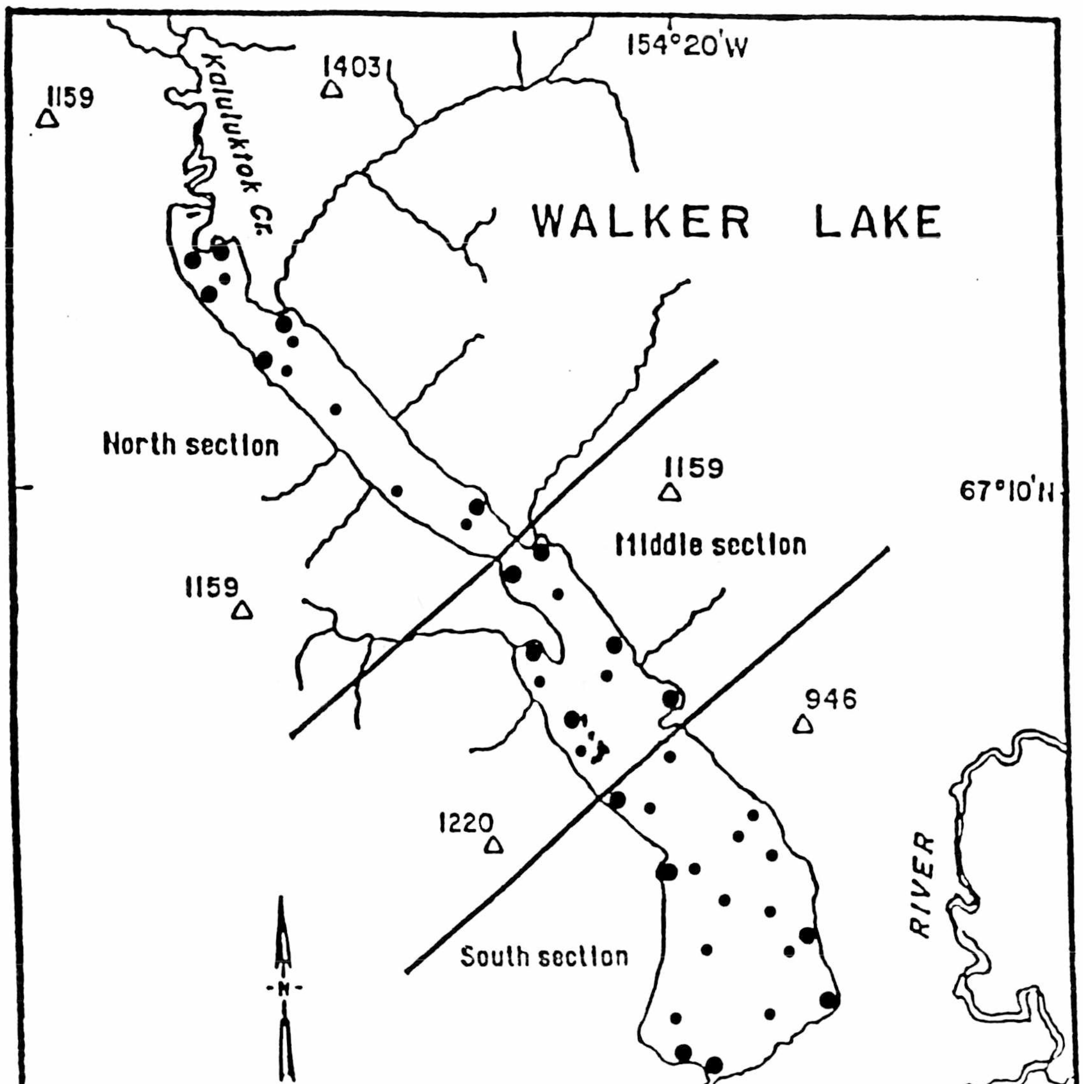


Figure 5.-Pelagic gill net sites (•) and seining sites (●) for sampling juvenile lake trout.

to a lack of streams that enter the lake in the south section, four straight shoreline sites and only two stream mouth sampling sites were used in this section. At stream mouths where it was possible, one of the seine hauls was performed in the stream itself. This amounted to six sites per section for a total of 18 seining sites (Figure 5). Each site was sampled five times with a minimum of five d between samples from the same site. Each sample consisted of two seine hauls, and each haul consisted of pulling the seine parallel to the shore for approximately 10 m. Catch per unit effort was the average catch of the two hauls for each sample. These values were compared by lake section and shoreline type.

The sign test for asymmetrical data (Zar 1984) was used for analyses of adult catch per unit effort that involved paired samples (season and time of day). The Mann-Whitney U test (Hollander and Wolfe 1973; Zar 1984) was used to test for significant differences in juvenile catch per unit effort between mid-water and bottom pelagic sets, and between shoreline features for seining. For the analyses of adult and juvenile catch per unit effort with more than two factors (lake section, substrate type, shoreline feature, and the combinations of factors), the nonparametric Tukey multiple comparison test was used (Zar 1984). All tests were performed at the 0.05 significance level.

Results

Adult lake trout

A total of 136 sets (544 h of effort) were made during the early and late sampling seasons; 318 adult lake trout were captured (Table 1). The number of lake trout captured per set ranged from 0 to 9; 1 lake trout was captured in most sets. The catch per unit effort for the early season (before 4 July) was significantly higher than the catch per unit effort during the late season (after 24 August) ($P < 0.05$). There was no significant difference in catch per unit effort between daytime (before 1700 hours) and evening (after 1700 hours) sets. There was no significant difference among catch per unit effort from the lake sections or the three substrate types. The only significant differences in catch per unit effort were found among certain shoreline features. The catch rates from the straight shore type were significantly higher than the catch rates from the outlet ($P < 0.05$), and the stream mouth catch rates were also significantly higher than the outlet ($P < 0.002$). The analysis of catch per unit effort for combined factors included: sampling season and time of day; sampling season and lake section; and sampling season and substrate type (Table 2). No significant differences were noted for combined factors.

Juvenile lake trout

Pelagic gill nets were fished at 22 sites for a total of 550 h of effort. Twelve lake trout with fork lengths that ranged from 203 to 667 mm were captured from the bottom sets and one lake trout

Table 1.-Relative abundance estimates by factor for adult lake trout sampling (shoreline sets) at Walker Lake, 1988.

Factor	Number of sets	Number captured	Effort (h)	CPUE Mean	CPUE Range
Season					
Early	68	178	272	0.65	0-2.25
Late	68	140	272	0.52	0-2.00
Time of day					
Early	68	170	268	0.63	0-2.00
Late	68	148	276	0.54	0-2.25
Lake section					
North	52	128	208	0.62	0-2.25
Middle	44	118	176	0.67	0-2.00
South	40	72	160	0.45	0-2.00
Substrate					
Sand-gravel	88	208	352	0.59	0-2.00
Cobble-boulder	20	41	80	0.51	0-2.25
Mixed	28	69	112	0.62	0-2.00
Shoreline					
Straight	48	123	192	0.64	0-2.25
Peninsula	40	82	160	0.51	0-1.75
Island	8	17	32	0.53	0-1.75
Stream mouth	24	77	96	0.80	0-2.00
Inlet	8	15	32	0.47	0-1.50
Outlet	8	4	32	0.13	0-0.25
Total per factor	136	318	544	0.58	0-2.25

Table 2.-Relative abundance estimates by combined factors for adult lake trout sampling (shoreline sets) at Walker Lake, 1988 (s-g = sand and gravel; c-b = cobble and boulder).

Factor	Number of sets	Number captured	Effort (h)	CPUE Mean	CPUE Range
Season x time of day					
Early x early	33	97	132	0.73	0-1.75
Early x late	34	73	136	0.54	0-2.00
Late x early	35	81	140	0.58	0-2.25
Late x late	34	67	136	0.49	0-2.00
Season x lake section					
Early x north	26	77	104	0.74	0-2.25
Early x middle	22	57	88	0.65	0-1.75
Early x south	20	44	80	0.55	0-2.00
Late x north	26	51	104	0.49	0-1.25
Late x middle	22	61	88	0.69	0-2.00
Late x south	20	28	80	0.35	0-2.00
Season x substrate					
Early x s-g	44	120	176	0.68	0-1.75
Early x c-b	10	25	40	0.63	0-2.25
Early x mixed	14	33	56	0.59	0-2.00
Late x s-g	44	88	176	0.50	0-2.00
Late x c-b	10	16	40	0.40	0-1.25
Late x mixed	14	36	56	0.64	0-2.00
Total per factor	136	318	544	0.58	0-2.25

(309 mm) was captured from the mid-water sets (Table 3). Eleven (85%) of these fish were juveniles and were smaller than 400 mm. Although the depth of the mid-water nets ranged from 20 to 50 m and the deep water sets ranged from 40 to 115 m, only one fish was captured at a depth greater than 50 m. There were no significant differences in catch per unit effort among the lake sections for bottom or mid-water sets. When catch per unit effort for bottom and midwater sets were combined and compared by section, no significant differences were noted.

Because Arctic char also occur in Walker Lake, the fingerlings that were captured in seines could not be positively identified as lake trout or Arctic char. The characters of identification for both overlap, and can only be identified to genus (D. E. Snyder, Larval Fish Laboratory, Colorado State University, personal communication). For this study, all fingerlings were considered to be lake trout.

Note: Subsequent to the analysis reported in this thesis, further investigation revealed that pyloric caeca counts may distinguish lake trout from Arctic char. Lake trout have 93-208 pyloric caeca (Behnke 1980; Morrow 1980; Scott and Crossman 1985). Pyloric caeca counts for Arctic char range from 40-50 (Behnke 1980), 35-75 (Morrow 1980), and 20-74 (Scott and Crossman 1985).

In response to this additional information, the pyloric caeca counts of three fingerling specimens from Walker Lake were compared to the pyloric caeca counts of two fingerling lake trout from the reference collection of the Larval Fish Laboratory at Colorado State

Table 3.-Relative abundance estimates by set and lake section for juvenile lake trout sampling (pelagic sets) at Walker Lake, 1988.

Factor	Number of sets	Number captured	Effort (h)	CPUE Mean	CPUE Range
Bottom set					
North	6	5	150	0.03	0-0.16
Middle	4	7	100	0.07	0-0.12
South	12	0	300	0.00	-
Midwater set					
North	6	0	150	0.00	-
Middle	4	0	100	0.00	-
South	12	1	300	0.003	0-0.04
Total	44	13	1100	0.01	0-0.16

University. The total lengths for the Walker Lake specimens were 33, 38 and 42 mm, and these fish had approximate pyloric caeca counts of 30-45 (D. E. Snyder, Larval Fish Laboratory, Colorado State University, personal communication). The lake trout specimens from the reference collection were hatchery reared fish from Colorado stock. The total lengths of these lake trout were 29 and 40 mm with 50 or more and 70 or more pyloric caeca, respectively. Although these counts were approximate, the differences in density and distribution of pyloric caeca between the two collections were obvious.

Several factors may influence the interpretation of pyloric caeca counts for these small fish. The criteria for positive identification of early juveniles of these species have not been sufficiently documented (D. E. Snyder, Larval Fish Laboratory, Colorado State University, personal communication). Also, small fish, especially in lake trout, usually have an incomplete complement of pyloric caeca with the full complement not achieved until the fish is an adult (Morrow 1980; Scott and Crossman 1985; D. E. Snyder, Larval Fish Laboratory, Colorado State University, personal communication). Therefore, the Walker Lake specimens may have been lake trout that had not attained their full complement of pyloric caeca. However, the higher number and greater density of pyloric caeca in the lake trout reference specimens indicate with reasonable confidence that the three specimens from Walker Lake were Arctic char. This suggests that some, or perhaps all, of the fingerlings captured in Walker Lake were Arctic char.

The 18 seining sites yielded a total of 96 fingerlings in 180 hauls of the seine (Table 4). The number of fish captured in 1 haul ranged from 0 to 19, and fork length ranged from 37 to 60 mm. Mean catch per unit effort for each site on each sampling day was used to compare the abundance of fingerling lake trout in each lake section, and each section received the same amount of effort. No significant differences were noted among catch rates for the lake sections. Between 0 and 9 fingerlings were captured per haul at straight shoreline sites, while stream mouth areas yielded from 0 to 19 fish. Significantly more fingerlings were caught at stream mouth areas than at straight shoreline sites ($P < 0.01$).

Discussion

Adult lake trout

In subarctic-arctic areas lake trout concentrate on their spawning beds along shorelines and shoals any time from mid-August through October (Rawson 1947; Miller and Kennedy 1948; Johnson 1972; Van Whye and Peck 1968; McCart et al. 1972; Martin and Olver 1980). The fish begin arriving at dusk with spawning beginning soon after and continuing into darkness (DeRoche 1969; Martin and Olver 1980). For these reasons it was expected that the sets made in the late season and after 1700 hours would capture significantly more lake trout than nets that were set at any other time.

However, the only temporal factor that exhibited a significant difference was sampling season. More lake trout were captured during

Table 4.-Relative abundance estimates by lake section and shoreline type for juvenile lake trout sampling (seining) at Walker Lake, 1988.

Factor	Number of sites	Number captured	Number of seine hauls	CPUE Mean	CPUE Range
Lake section					
North	6	30	60	0.50	0-8.50
Middle	6	34	60	0.57	0-9.50
South	6	32	60	0.53	0-4.50
Shoreline type					
Straight	10	17	100	0.17	0-4.50
Stream mouth	8	79	80	0.99	0-9.50
Total per factor	18	96	180	0.53	0-9.50

the early sampling season than were captured during the late season. This indicates that lake trout are more active soon after ice-out than just before freeze-up. Martin (1952) found that the number of feeding lake trout was highest after ice-out and during early summer. Also, a stock that spends the majority of its life constrained by ice, and stressed by overwintering may become most active as soon as the constraining factor disappears. Time of day (daytime or evening) did not affect catch per unit effort which indicates that lake trout were equally active during the daytime as they were during the evening.

There was no significant difference in catch per unit effort among the lake sections, but the middle section did have a higher catch rate. Lake trout are known to enter shallow water to feed (Rawson 1947; Miller and Kennedy 1948; Martin and Olver 1980), and the middle section of Walker Lake contains islands and extensive reefs that provide a great deal of relatively shallow water (Figure 2). It appears that lake trout exhibit a slight, though insignificant, preference for this area.

The spawning substrate used by lake trout varies from sand to boulders (DeRoche 1969; Scott and Crossman 1973; Martin and Olver 1980; Dorr et al. 1981; Wagner 1982; Sly and Widmer 1984) with coarse cobble, free of fine particles, being preferred (Wagner 1982; Sly and Widmer 1984). It was assumed that late in the sampling season lake trout would congregate in areas of cobble-boulder substrate in preparation for spawning. However, the catch per unit effort for the cobble-boulder substrate during the late sampling season was the lowest of all the catch rates by substrate and season. No significant differences among catch per unit effort for substrates or substrates by seasons suggested that lake trout did not have a preference for a particular bottom type, and that this lack of preference was consistent regardless of season.

From cursory examination of 1987 catch data (not included in this thesis), it appeared that stream mouths and straight shorelines had the highest catch per unit effort. The 1988 results showed that the catch per unit effort for the stream mouths and straight shorelines were highest, but these values were significantly different only from the outlet, which had the lowest catch per unit effort. The low catch per unit effort at the outlet may be related to the characteristics of the shelf leading to the outlet proper. This area is extremely shallow, devoid of cover, completely exposed to direct sunlight, and the outflow of the lake gains velocity in this area (Figure 2). Because only four lake trout were captured in this area, it is assumed that these factors preclude the outlet area from being a preferred lake trout habitat. Stream mouths were preferred habitat possibly due to food availablility. The drift entering the lake would not only provide food for lake trout, but would also attract forage species. It appears that straight shorelines had high catch rates purely because they are the predominant feature of the lake's shoreline. Any lake trout moving from one area to another would eventually pass through this shoreline type.

The results of the relative abundance sampling for adult lake trout provided indications of lake trout behavior and their preferred habitats. The period just after ice-out had a higher catch per unit effort than the period before freeze-up, and stream mouth areas had the highest catch per unit effort of all the shoreline types. From superficial observation, these tendencies are reflected by sport fishermen who appeared to concentrate their fishing effort at stream mouths during the early open water season.

Juvenile lake trout

Juvenile lake trout are known to be widely dispersed throughout the pelagic portion of a lake, and are difficult to capture in substantial numbers (Miller and Kennedy 1948; Royce 1951; Martin 1952; Martin and Olver 1980; Peck 1982). In Walker Lake, juvenile lake trout tended to prefer water less than 50 m deep in the middle and north sections. Of the 13 total lake trout captured in pelagic nets, only one was caught in the south section. This section contains the deepest basin in the lake, and has the most pelagic area of the three sections (Figure 2). The north section has a deep basin, but its pelagic area is much less extensive than the south section. The basins in the middle section are not nearly as deep as the others, and its pelagic area is the smallest of the three sections. In spite of the small number captured, it appears that juvenile lake trout were widely dispersed in Walker Lake, and they preferred pelagic zones that were in close proximity to shallow areas.

Fingerling lake trout that were captured in Walker Lake exhibited meristic characters that overlapped those of Dolly Varden (*Salvelinus malma*) Arctic char (D. E. Snyder, Larval Fish Laboratory, Colorado State University, personal communication). The key to juveniles of the subfamily Salmoninae in Morrow (1980) separates lake trout from Arctic char and Dolly Varden by the position of the dorsal fin and the number of fin rays in the dorsal and anal fins. The origin of the dorsal fin for Walker Lake specimens was half of the distance from the snout to the base of the tail. Morrow (1980) states that when the distance from the snout to the front of dorsal fin is about half the distance from the snout to the base of tail, the fish is a lake trout. When this distance is less than half, the fish is an Arctic char/Dolly Varden. However, some reference specimens of lake trout (40 mm TL) from the Larval Fish Laboratory had dorsal origins positioned at less than half the distance from the snout to the base of the tail. Also, Morrow (1980) states that lake trout have eight to 10 dorsal and anal fin rays, and Arctic char/Dolly Varden have 12 to 16 dorsal rays and 11 to 15 anal rays. Some lake trout specimens from the Larval Fish Laboratory have 11 dorsal and anal rays. The specimens from Walker Lake exhibited 11 to 12 dorsal fin rays and 10 anal fin rays. Although the external characters examined are not sufficiently consistent to identify these specimens to species, subsequent comparisons of pyloric caeca counts among Walker Lake specimens and lake trout reference specimens from the Larval Fish Laboratory indicated that some or all of the fingerlings captured in Walker Lake were Arctic char (see Juvenile lake trout, Results, Relative Abundance).

The habitat preference for the fingerlings appeared to be stream mouth areas. However, habitat preference cannot be used to distinguish lake trout from Arctic charr. Johnson (1980) states that fingerling Arctic char can be found in suitable habitat along rocky shorelines or in streams. Lake trout are usually found in deeper water with rocky substrate (Martin and Olver 1980), but four 50 mm lake trout were captured in a small stream entering Great Bear Lake (Johnson 1975b), and Russell (1980) captured three fingerling lake trout (41 to 45 mm) in a tributary stream of Turquoise Lake, Alaska. Since Arctic char/Dolly Varden do not inhabit Great Bear Lake, it is certain that those fingerlings were lake trout. However, because Dolly Varden do occur in Turquoise Lake, it is possible that those fingerlings may not have been lake trout. It is conceivable that the fingerlings captured in Walker Lake were not lake trout; until further taxonomic study their positive identification remains inconclusive.

Age and Growth

Age determination of lake trout is difficult and inexact, particularly with arctic populations (Power 1978). Extreme longevity and slow growth are two factors which create difficulties in the interpretation of bony tissue and the definition of annuli. For example, two tagged lake trout from Great Bear Lake had only grown from 627 to 635 mm and 953 to 962 mm over 8 and 9 years, respectively (Johnson 1975a). At such slow growth rates, it is questionable whether reliable or readable annuli were formed (Johnson 1976). No method for aging arctic lake trout has been validated (McCart et al. 1972; Power 1978).

Various structures have been used to age lake trout including branchiostegal rays (Bulkley 1960), pectoral fin rays (Cuerrier 1951), scales (Cable 1956; Rawson 1961; Eck and Wells 1983), and sagittal otoliths (Falk et al. 1974; Craig and Wells 1975; Moshenko and Gillman 1978; Power 1978; Horler et al. 1984). Branchiosegal and pectoral fin rays have been rarely used; scales and otoliths have been more readily accepted. Comparisons of lake trout ages based on scales and otoliths indicated agreement between the two methods for immature fish (McCart et al. 1972; Johnson 1976; Power 1978; Sharp and Bernard 1988). However, of fish older than 5 years, otoliths are believed to provide more accurate age estimates (McCart et al. 1972). Annuli become so crowded at the edge of the scale that they are impossible to interpret, but otolith annuli are deposited as caps on either side of the sulcus acusticus (central groove), and do not become over crowded (Power 1978). Also, otoliths are not susceptible to the erosion and subsequent loss of annuli characteristic of scales (Healey 1978a). Despite providing more accurate age estimates, otolith ages are still likely to be conservative (McCart et al. 1972; Johnson 1976).

Growth is affected by the interaction of factors such as age, sex, season, climate, reproductive cycle, and population size. However, growth, in either length or weight, slows, and reaches an asymptote sometime after the juvenile stage. When plotted against age, this growth rate exhibits a positive slope during the accelerated growth phase of early life, reaches an inflection point, and then exhibits a deceleration during the slower growth of later life. The result is a logistic growth curve that is asymmetrically sigmoidal (Royce 1984).

There are many methods used to describe this growth process and its resultant curve. The von Bertalanffy equation is widely used, and provides a simple model for predicting the length of a fish from its age (Rosenberg and Beddington 1988; Smith 1988). The relation is based upon growth being the difference between the biological processes of anabolism (elaboration of tissue) and catabolism (breaking down of tissue). The von Bertalanffy model fits fish growth data very well, especially for the period after the inflection point in the absolute growth curve (Ricker 1975; Everhart and Youngs 1981).

Methods

Lake trout used for age and growth analysis were captured from 16 June to 17 September, 1987, and from 13 June to 15 September, 1988. The sampling period in 1987 was part of a nonrandom mark-recapture experiment that focused on the live capture and release of as many lake trout as possible. Therefore, sampling gear was deployed in areas that continually provided high catch rates without consideration to gear placement, time of day, amount of effort, or randomness. The 1988 sampling was strictly designed to evaluate the relative abundance of lake trout and to complement the life history information collected in 1987 (see Methods, Relative Abundance).

During the 1987 season, experimental gill nets (46 x 2.4 m with six equal size panels of 1.3, 1.9, 2.5, 3.8, 5.1, and 6.3 cm mesh) were used extensively in the shoreline areas of the lake. To increase the capture rate, these nets were occasionally chummed with preserved salmon eggs or with pieces of round whitefish. Fishing time for gill nets varied from 0.5 to 8 h. Nets were checked every 0.5 h to minimize mortalities. Deep water areas were not extensively sampled due to low catch rates. Fyke nets (one with a 9 x 0.9 m lead and a second with a 46 x 2.4 m lead) with 3 x 0.5 m wings and minnow traps were used in suitable areas, and baited with preserved salmon eggs and fish pieces. Lake trout were also captured by baited setlines and angling.

The National Park Service required that the number of lake trout mortalities be no more than 100 fish for the entire study. Because medium-sized fish were more easily gilled, most of the mortalities in the experimental gill nets were of lake trout 400-500 mm long. Also, because of their higher sport fishing value, large fish received priority for release. These factors precluded the random collection of fish over all length classes, and resulted in very few samples for certain ages.

The sagittal otoliths were collected from all dead fish and from several fish donated by sport anglers. Otoliths were extracted, cleaned of tissue in the field,and stored dry in scale envelopes. Age was determined by a modification of the break and burn technique (Beamish and Chilton 1982; Chilton and Beamish 1982; Barber and McFarlane 1987; Beamish and McFarlane 1987; Trippel and Beamish 1989). A small, power hand drill was used to grind the broken surface of the otolith prior to burning. This allowed the broken surface of the otolith to be maintained in the same focal plane while being read at 40X to 160X magnification under a binocular microscope.

Otoliths were aged independently by three readers without knowledge of length or weight of the fish. Annuli were distinguished as being distinct, concentric hyaline (dark brown) rings that were continuous around the otolith. Annuli were tallied in the direction of the largest count (Sharp and Bernard 1988). Disagreements were resolved by reevaluation of annuli criteria and discussion among the readers.

Mean length at age was calculated as the average fork length of all aged lake trout in each age class. A Walford plot (Ricker 1975;

Everhart and Youngs 1981) of mean length at age was used to determine the von Bertalanffy growth equation:

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

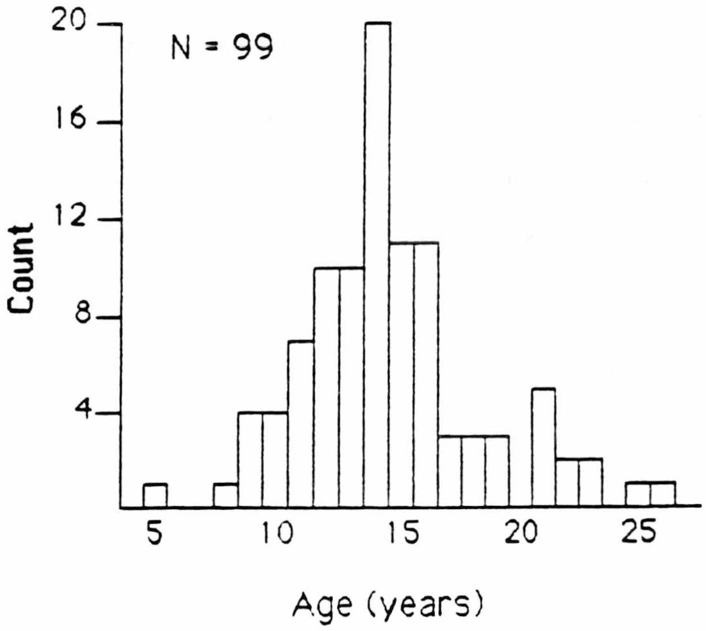
where L_t = length at age t, L_∞ = asymptotic length, t = age (years), t_0 = theoretical age (years) when length was zero, and K = growth coefficient. The regression of the natural log of ($L_\infty - L_t$) versus age at time t was used to determine t_0 (Ricker 1975; Everhart and Youngs 1981). The growth curve (mean length versus age) for lake trout in Walker Lake from 1987 and 1988 was compared with a historical growth curve from 1967. The 1987 and 1988 growth curve was also compared with lake trout growth curves from five other lakes in Alaska.

Results

A total of 99 lake trout were aged with mean length at age ranging from 203 mm at age 5 to 805 mm at age 26 (Table 5). Seventy-eight (79%) of the lake trout were aged between 11 and 19 years with corresponding lengths between 301 and 795 mm. Age 14 fish were the most frequently captured (Figure 6). Very young lake trout were relatively absent from the sample. Fifty-eight (59%) of the samples were in the length class most prone to dying in the gill nets (400-500 mm). The extreme ages were underrepresented in the samples, but were used in the analysis to maintain a maximum sample size.

Table 5.-Ages and lengths of lake trout in Walker Lake, 1987 and 1988.

		Fork length (mm)		
Age	N	mean	range	SD
5	1	203	-	-
8	1	235	-	-
9	4	282	235-322	41
10	4	345	302-387	38
11	7	405	301-453	64
12	10	406	274-540	78
13	10	440	317-565	63
14	20	469	259-657	76
15	11	496	440-668	66
16	11	524	405-724	82
17	3	544	495-608	58
18	3	679	657-716	32
19	3	747	690-795	53
21	5	650	608-690	32
22	2	626	564-687	87
23	2	642	580-704	88
25	1	649	-	-
26	1	805	-	-
Total	99	485	203-805	128



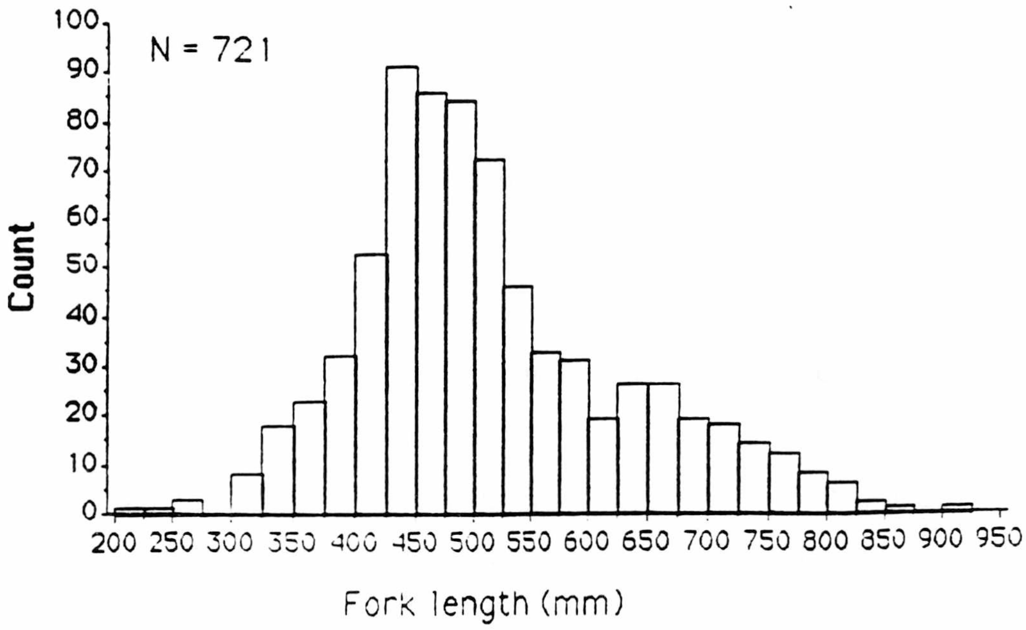


Figure 6.-Age and length frequency of lake trout in Walker Lake, 1987 and 1988.

The Walford plot resulted in an asymptotic length (L_∞) of 1,024 mm (Figure 7 and Table 13, Appendix). The growth coefficient, K, was equal to 0.068 (where K = the negative natural logarithm of the regression slope of the Walford plot), and t_0 was 2.2 years. Therefore, the von Bertalanffy growth equation for lake trout from Walker Lake was:

$$L_t = (1{,}024\ \text{mm})\ (1 - e^{-0.068\ (t\ -\ 2.2)})$$

Discussion

The reported world record lake trout was a 1,270 mm fish captured in the early 1960's from Lake Athabaska, Saskatchewan (Martin and Olver 1980). The fish weighed 46.3 kg, and was estimated, using scales, to be 20-25 years old. The oldest age determined with otoliths for a lake trout was 62 years (Bond 1975). It was 1,005 mm in length and captured in 1973 from Kaminuriak Lake, Manitoba. Lake trout from Alaska were estimated, using otoliths, to be over 40 years old with corresponding lengths ranging from 837 to 934 mm (Craig and Wells 1975; Bendock 1979; Bendock and Burr 1984; Bendock and Burr 1986). Gear selectivity, the restriction on mortalities, and the preferential release of larger fish prevented the collection of age samples for older fish in Walker Lake. The sampled lake trout did not achieve the extreme age of the previous examples, and may be due to environmental conditions that limit the fish's maximum age; sampling bias against older fish, or a difference in aging techniques (see Future study, Summary). However, the large size of a number of released fish

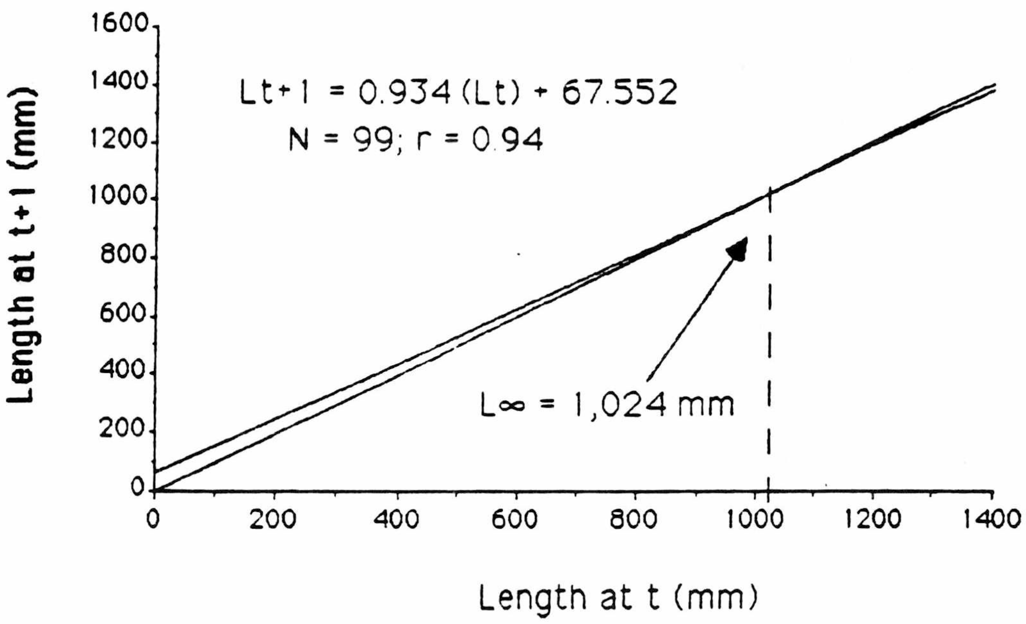


Figure 7.-Walford plot for lake trout in Walker Lake, 1987 and 1988.

(924 mm maximum) suggests that there also may be fish 40 years or older in Walker Lake.

The capture of few young lake trout in Walker Lake is typical for lake trout studies (Craig and Wells 1975; Martin and Olver 1980; Burr 1987a). Young lake trout are sparsely distributed throughout mid-water and deep water areas (Royce 1951; Martin 1952; Martin and Olver 1980; Peck 1982). Despite a concerted effort in these areas during the 1988 relative abundance sampling, only six fish under age 10 were captured. Possible explanations for the low capture rate of young fish are: gear selectivity, different distributions of gear and fish, or low abundance.

The sigmoidal shape of a typical growth curve suggests that the fastest growth rate is attained during the middle period of life. The von Bertalanffy equation assumes the growth rate to be constant throughout life. This constant is K, the growth coefficient, and describes the rate at which the growth curve approaches L_∞, maximum length. Although fish increase in length, K is negative because the rate of growth is declining. The parameter, t_0, is the theoretical age from which K applies. In theory, at age t_0 the length of a fish would be zero, assuming the von Bertalanffy relation is in effect. Theoretically, the growth of Walker Lake lake trout did not follow the von Bertalanffy curve until the fish reached an age of 2.2 years. No studies that used the von Bertalanffy equation to describe the growth of lake trout were available for comparison. For a single population the von Bertalanffy equation can be used to predict lengths and ages within the sampled portion of the population. Length is one of the more easily measured parameters, and by substituting this measurement into the von Bertalanffy equation, the age can be estimated without sacrificing the fish. These predictions should be done only over the corresponding range of lengths and ages that applied to the initial calculation of the equation.

Variability of growth within a population is characteristic of arctic lake trout, especially in older age classes (McCart et al. 1972; Burr 1987a). In Walker Lake the variability of length at age is relatively high for the middle ages, and becomes highest at the oldest ages (Figure 8). The largest standard deviations were for 22 and 23 year old fish. Growth was fastest during early life, and then slowed down considerably after age 20.

Variability in lake trout growth between populations is also characteristic of the species (McCart et al. 1972; Burr 1987a). The comparison of mean length at age growth curves from Walker (N=99), Paxson (N=275, Burr 1989), Summit (N=132, Burr 1988), Glacier (N=189, Burr 1987b), Old John (N=75, Craig and Wells 1975), and Itkillik (N=87, McCart et al. 1972) lakes demonstrates this variability (Figure 9). Fish were captured by a variety of methods including creel census, and all fish were aged by otoliths. Growth curves were fit by eye, and expressed only over the range of available data.

Comparable curves can generally be grouped by similarities in climate as a function of latitude and altitude. Fish from Walker and Old John lakes have similar curves, and both are at approximately the

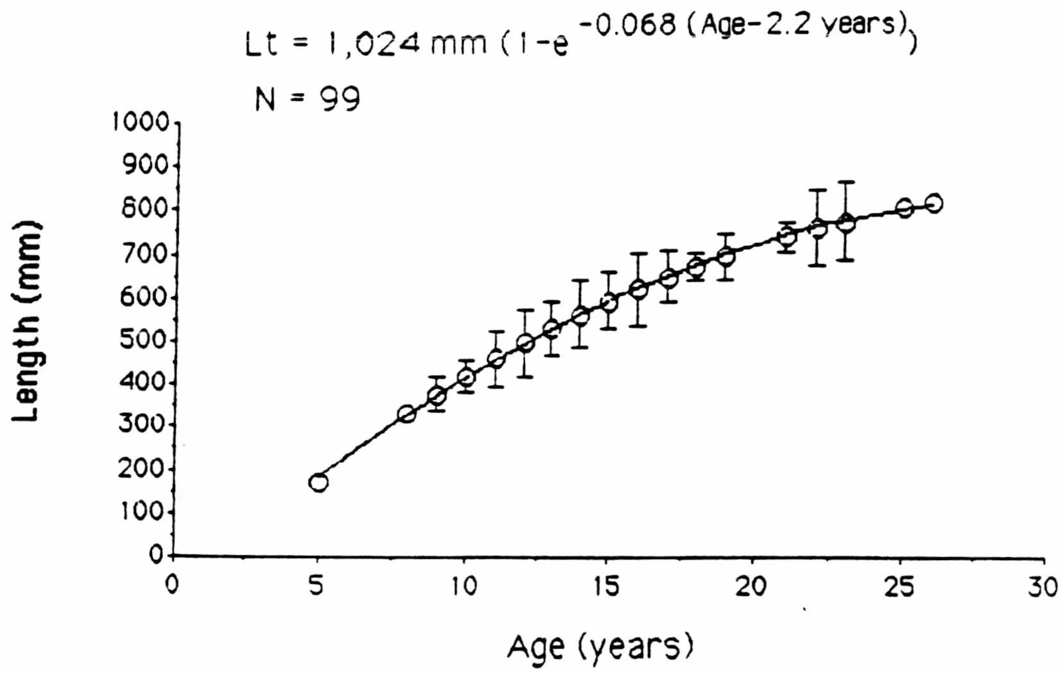


Figure 8.-Mean length-at-age (circles), with standard deviations (bars), and the fitted von Bertalanffy growth curve for lake trout in Walker Lake, 1987 and 1988.

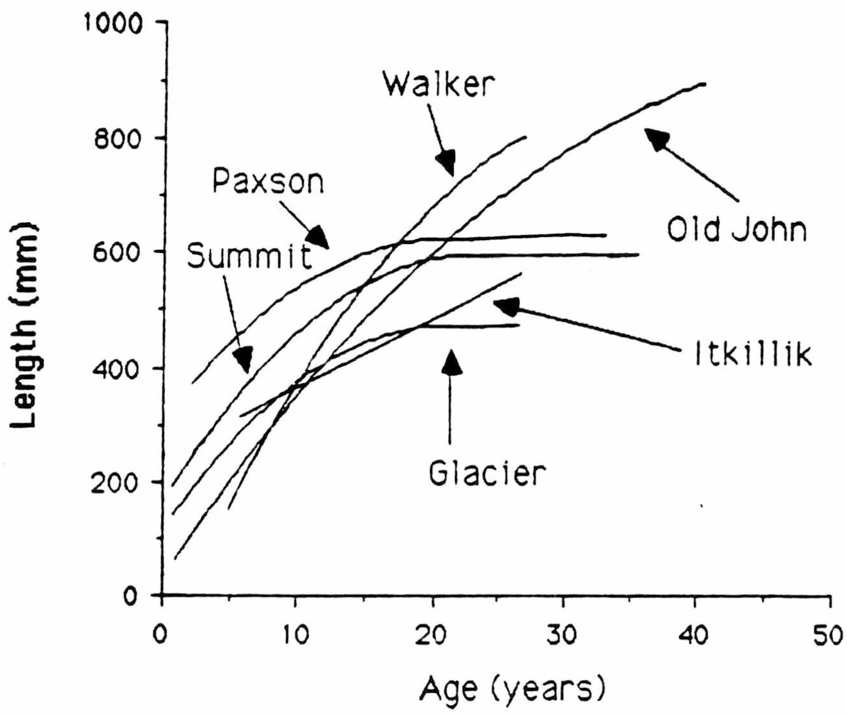


Figure 9 -Growth curves (eye fit) based on mean length-at-age for lake trout in six Alaska lakes.

same latitude, with the elevation of Old John lake being approximately 500 m higher. The curves representing Paxson and Summit lakes are also similar. These lakes are situated within a degree of latitude and within 200 m altitude of each other. Itkillik Lake is 5 degrees farther north than Glacier Lake, but their growth curves are approximately equal. This similarity may be due to Glacier Lake being approximately 400 m higher in elevation than Itkillik. This is an example of ecological altitudinal-latitudinal zonation (Odum 1971; Smith 1974). The faster growth rate during early life for lake trout from Paxson and Summit lakes is probably due to the existence of large numbers of juvenile sockeye salmon (*Oncorhynchus nerka*) that provide a substantial forage base (Burr 1989).

The growth curves for Paxson, Summit and Glacier lakes exhibit a marked leveling off at approximately age 20, while it appears that the other growth curves have not reached a plateau. While there is no quantitative information available on the harvest rates for the three lakes in the Brooks Range, their remoteness probably limits the fishing pressure they receive. In contrast, the three lakes from the Alaska Range are much nearer the state's population centers, and Paxson and Summit lakes are located on the road system. Burr (1987b) found that the maximum sustainable yield recommended by Healey (1978a) of less than 0.5 kg/ha/year of lake trout was being exceeded in these lakes. Environmental constraints limit the maximum size possible for a fish of a given lake, but it appears that fishing pressure has cropped off the larger, older lake trout in the more heavily fished systems. As expected, the growth curves from the more remote lakes do not level off markedly. This may be due to lower exploitation rates or unknown genetic or environmental factors. However, these growth curves are based solely upon lake trout that were sacrificed for estimates of age. Length frequencies for all fish captured (sacrificed and released) in the easily accessible lakes indicate that larger fish do exist in these lakes (Figure 10 and Table 14, Appendix). Therefore, it is possible that older fish do occur in these lakes, and their growth curves do not level off as markedly as depicted.

Healey (1978a) made comparisons of growth curves for temperate and northern lake trout populations. He observed that growth rates for the lake trout populations in the Great Lakes (Huron, Michigan, and Superior) were near the maximums ever recorded during the sea lamprey infestations of the late 1960's and early 1970's. Comparisons of growth curves from before and after extensive commercial fishing in Great Bear and Great Slave Lakes demonstrated that lake trout in both lakes grew more rapidly after exploitation. This suggests that lake trout populations that have experienced high natural mortality or high fishing mortality react in the same way that northern whitefish populations do (Healey 1975). The high mortality rates cause the populations to compensate for increased mortality by increasing their growth rate. Lake trout were captured by several different methods in these studies, and ages were determined from scales in some reports and otoliths in others. Because of these

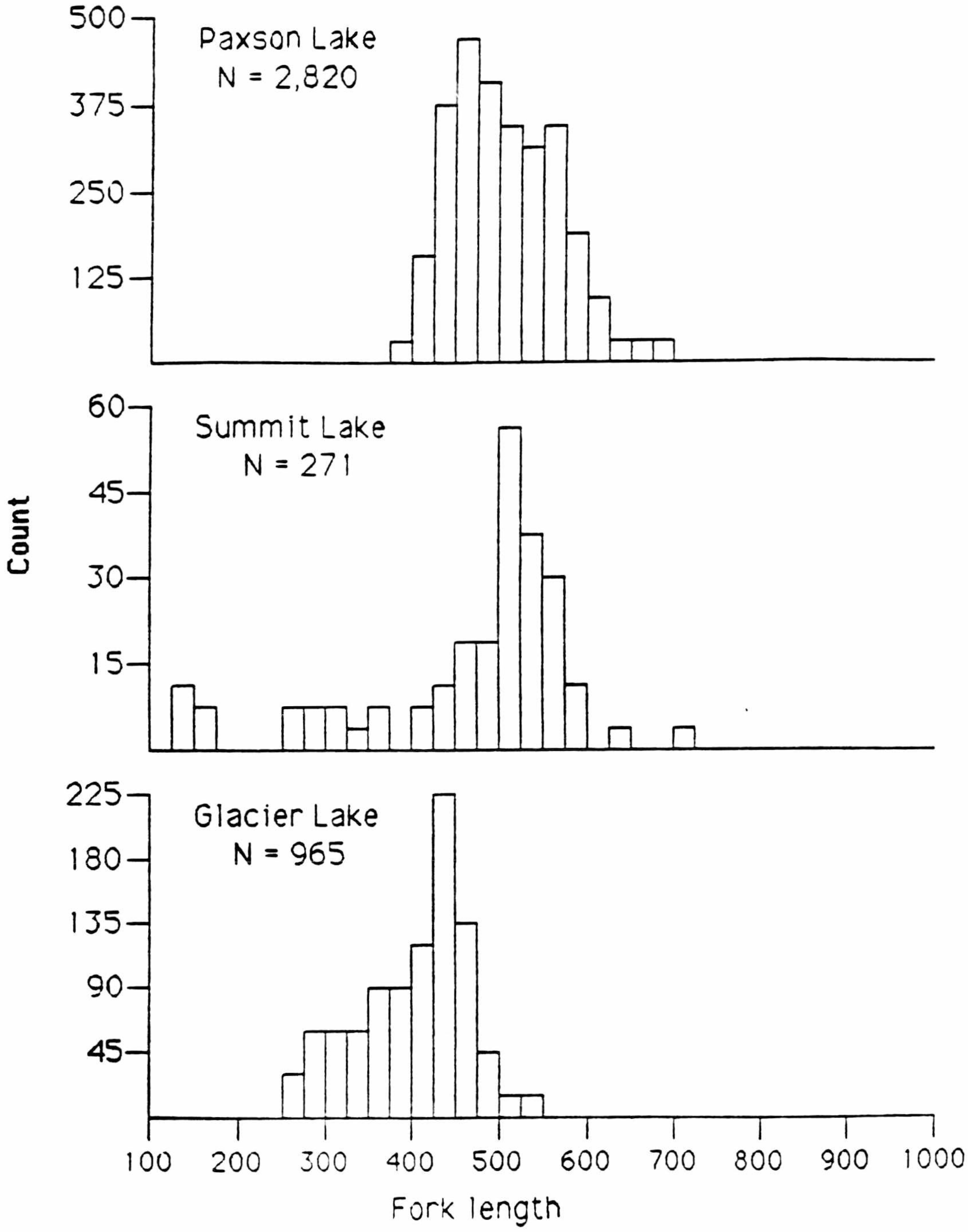


Figure 10.-Length frequency for all lake trout captured in Paxson, Summit and Glacier lakes, 1986-89 (J. M. Burr, Alaska Department of Fish and Game, personal communication).

inconsistencies, detailed comparisons are not appropriate, but the tendency toward higher growth is obvious (Healey 1978a).

A similar historical comparison of lake trout growth rates for Walker Lake also indicates that these lake trout have not been over harvested. Thirteen lake trout were captured by angling and gill netting during two days in 1967 (Roguski and Spetz 1968). These fish were aged by scales, and did not exhibit older age classes (Table 6), and the comparison of mean length at age growth curves suggests that growth has decreased over this time (Figure 11). Accepting Healey's theory about exploitation and the resultant increase in growth, it appears that lake trout in Walker Lake have not experienced significant exploitation over the last 20 years. This reasoning is consistent with the results of the growth curve comparisons from other Alaskan lake trout populations, and tends to confirm that lake trout in Walker Lake have not experienced extensive exploitation. However, because determining ages with scales underestimates lake trout ages (McCart et al. 1972; Johnson 1976; Healey 1978a; Power 1978), and the current study aged fish by otoliths, direct comparison of the growth curves must be done with caution. Also, the 1967 data suffers from limited sampling effort and a very small sample size.

The comparisons of ages and growth curves for lake trout are difficult due to a number of factors. The physical and chemical characteristics of the water, food habits, available forage base, and the individual's genetic potential all can affect a fish's growth. Aging errors are undoubtedly present especially with such a long-lived

Table 6.-Lengths and scale ages from 1967 and lengths and otolith ages from 1987 and 1988 for lake trout in Walker Lake.

	Otolith age			Scale age		
		Fork length (mm)			Fork length (mm)	
Age	N	mean	range	N	mean	range
5	1	203	-	2	376	358-394
7				1	495	-
8	1	235	-	5	509	483-526
9	4	282	235-322	1	533	-
10	4	345	302-387	1	640	-
11	7	405	301-453	2	711	660-762
12	10	406	274-540			
13	10	440	317-565	1	838	-
14	20	469	259-657			
15	11	496	440-668			
16	11	524	405-724			
17	3	544	495-608			
18	3	679	657-716			
19	3	747	690-795			
21	5	650	608-690			
22	2	626	564-687			
23	2	642	580-704			
25	1	649	-			
26	1	805	-			
Total	99	485	203-805	13	556	358-838

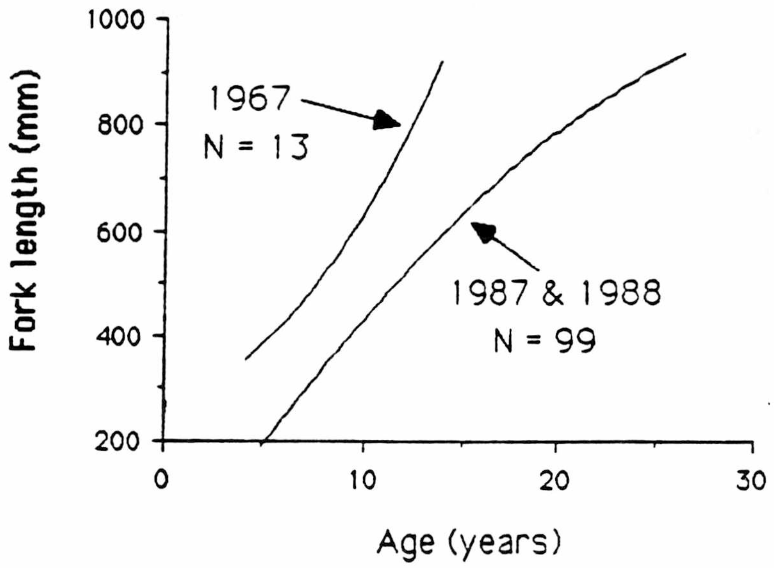


Figure 11.-Growth curves (eye fit) for lake trout in Walker Lake, 1967, and 1987 and 1988.

species. With no age validation for arctic lake trout, otolith readers must rely upon experience and consensus to accurately age these fish. Gear selectivity will influence the shape and slope of the growth curve. If larger, faster growing fish are more susceptible to the gear, the resultant growth curve will exhibit a much higher rate than what is actually occurring. These data are fitted to mean length at age, so there is no allowance for growth rates of individual fish. Also, the small sample sizes may not be truly representative of the population. When making comparisons of growth rates, all these factors must be considered before meaningful interpretation can be made.

Weight-Length Relation and Fish Condition

For a fish that grows with unchanging body form and unchanging specific gravity, its weight varies as the cube of its length, and the weight-length relation is isometric. If weight decreases or increases faster than the cube of length, the shape of the fish changes, and allometric growth occurs. The relation between weight and length can be quantitatively determined, and these values used to predict the weights of measured fish (Everhart and Youngs 1981; Royce 1984). The values from the weight-length relation can also be employed to calculate the degree of condition (robustness) of each fish (Anderson and Gutreuter 1983; Bolger and Connolly 1989). This assumes that heavier fish of a given length are in better shape, and it is a good indicator of general well-being. Other indices such as the hepatosomatic index, body water content,visceral-somatic index, gut index, protein-energy ratio, and caloric values of tissue have been used to evaluate the condition of fish, but these methods require sacrificing the fish and laboratory analysis (Bolger and Connolly 1989).

Calculation of condition factors only requires weight and length measurements. Normal seasonal fluctuations in metabolic balance, maturation, and fullness of the gut are reflected in changes in condition when using weight-length data. Condition factors can be used to compare the relative robustness of a sample of fish with another sample from the same population (Bolger and Connolly 1989).

Methods

The weight-length relation for lake trout from Walker Lake was described by the power function:

$$W = aL^b,$$

where W = wet weight (g), L = fork length (mm), a = intercept, and b = a dimensionless exponent. The relation's parameters were estimated by the functional regression of the geometric mean (GM) (Ricker 1973, 1975). The functional regression is recommended for weight-length analysis, and is derived from the ordinary regression of log weight versus log length (Ricker 1975; Anderson and Gutreuter 1983).

The appropriate method for calculation of a condition factor was determined by comparing the weight-length slope from a hypothetical population with isometric growth (b = 3) to the slope of the Walker Lake weight-length regression. The Student's two-tailed t test (Zar 1984; Neter et al. 1985) was used to determine if a significant difference ($P < 0.05$) existed between the two slopes. A significant difference indicates that the LeCren (allometric) condition factor should be used, whereas a nonsignificant difference indicates that the Fulton-type (isometric) condition factor is appropriate (Anderson and Gutreuter 1983).

An allometric condition factor (Kn) was computed for individual fish as:

$$Kn = W/aL^b$$

For analyzing ratio data such as condition factors, nonparametric statistical methods are more appropriate than are parametric methods (Bolger and Connolly 1989). Condition factors for all captured fish were compared by year, early and late sampling season, and sex with the Mann-Whitney U test (Hollander and Wolfe 1973; Zar 1984). Condition factors of male and female lake trout were combined by season and sex, and compared with the Tukey multiple comparison test (Zar 1984). Condition factors for spawning lake trout were compared to condition factors for non-spawning fish with the Mann-Whitney test. All tests were performed at the 0.05 significance level.

Results

The length frequency histogram for 721 Walker Lake lake trout exhibited a unimodal distribution (Figure 6). Lengths ranged from 203 to 924 mm, and weights ranged from 83 to 8,500 g.

The regression of the log-log transformation of weight and length (Figure 12) resulted in the equation:

$$\log W = 3.109 (\log L) - 5.275$$

$$(r = 0.984)$$

The geometric mean (GM) functional regression (Table 15, Appendix) resulted in the equation:

$$\log W = 3.159 (\log L) - 5.409$$

The slope of the functional regression for weight and length was significantly different than the slope for a population with isometric

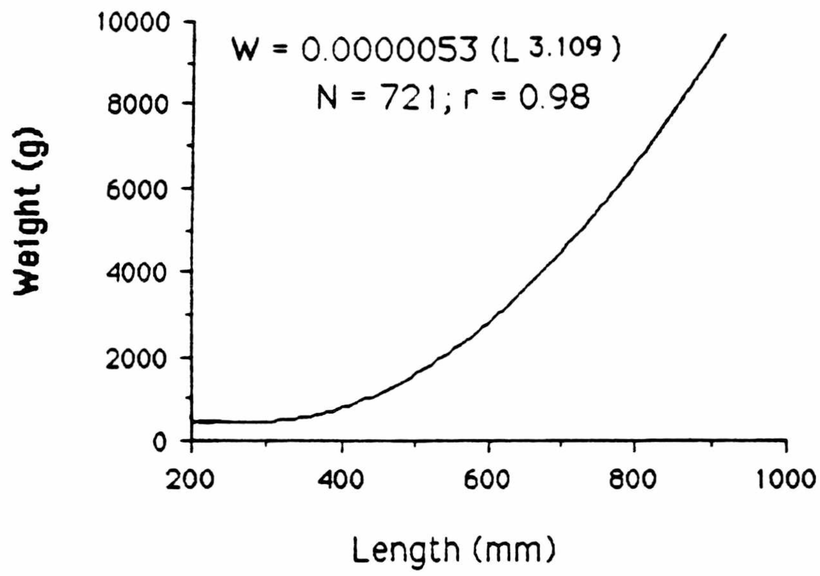


Figure 12.-Weight-length relation, based on log-log regression, for lake trout in Walker Lake, 1987 and 1988.

growth ($P < 0.05$). Walker Lake lake trout display positive allometric growth (weight increases at a faster rate than the cube of length). LeCren condition factors, using the GM regression equation, for the total sample (N = 721) ranged from 0.492 to 1.849 with a mean of 1.006. No significant differences were noted between condition factors from separate years or early and late sampling seasons.

Female condition (N = 32) ranged from 0.625 to 1.349 and male condition (N = 50) ranged from 0.753 to 1.399. There was no significant difference in condition factors between years for either sex. When the condition factors for each sex were pooled for both years, there was no significant difference between sexes. There were no significant differences for the seasons between or within either of the sexes.

Discussion

The weight-length relation for lake trout often varies between different stocks (Martin and Olver 1980). This variability may be dependent upon the environmental, genetic, and behaviorial factors that affect a particular stock. Comparisons of weight-length relations among lake trout stocks are difficult because of differences in measurements. However, for fish of similar fork length ranges, the intercept value for the Walker Lake weight-length relation was much lower than the intercept values for two temperate lakes (Martin and Olver 1980), but was intermediate between values for Itkillik Lake (McCart et al. 1972) and Old John Lake (Craig and Wells 1975), both located in the Brooks Range of northern Alaska (Table 7). The slope of the weight-length relation for Walker Lake lake trout was between the values reported for Itkillik and Old John lakes. The differences between the weight-length relations for different lake trout stocks may be somewhat related to the stocks' geographic location. The higher intercepts for the temperate populations may be related to better habitat in the more southerly regions. The similarities of the slopes for the different stocks suggests that the increase in weight per unit length for lake trout may be constant regardless of the geographic area. The weight-length relations for lake trout in the Brooks Range were similar. The lakes in this area apparently provide equivalent habitat for lake trout, and their weight-length relations reflect this similarity.

These comparisons were made among weight-length relations from lake trout studies with similar fork length ranges. Neither the method of capture nor the method of calculation of the weight-length parameters (ordinary regression or geometric mean functional regression) were described in these studies. Condition factors were not computed for these other populations.

The weight-length relation is very sensitive to variability in weight at a particular length, and this variability affects the shape and slope of the weight-length plot. However, condition factor, a derivative of this relation, adjusts for this variability (Weatherly and Gill 1987). The LeCren condition factor compensates for allometric growth, and provides a better basis for statistical comparisons than do

Table 7.-Weight-length relations for several populations of lake trout with similar length ranges.

State/Province Lake	N	Length range (mm)	Regression a (intercept)	Regression b (slope)
Quebec				
Mistassini	603	180-1020	-2.36	3.25
Oregon				
Odell	478	196-1003	-2.86	2.81
Alaska				
Itkillik	180	129-800	-5.38	3.16
Old John	75	114-903	-4.92	3.06
Walker	721	203-924	-5.41	3.16

tests comparing the parameters of the weight-length relation. With the LeCren method, average fish of all lengths have a condition of 1.0 (Anderson and Gutreuter 1983) (Figure 13).

Because no significant differences were noted in condition factors between years, data were pooled for comparison of condition by sex, length, sampling season, and date of capture. Generally, the condition of lake trout increases with an increase in length, but some lake trout populations possess a relatively constant condition regardless of size (Martin and Olver 1980). Also, in a lake trout population from Toolik Lake north of the Brooks Range, where growth is food limited, condition did not increase as length increased (McDonald and Hershey 1989). Although it is not known if the Walker Lake population is food limited, these fish exhibited a relatively constant condition over all their length ranges (Figure 14). There was no significant relationship between increasing condition with increasing length ($P > 0.10$). Female ($N = 32$) and male ($N = 50$) lake trout did not exhibit significant relationships between their condition factors and fork lengths throughout the field season ($P > 0.20$) (Figure 15).

As spawning season approaches, it is assumed that the weight of a spawning lake trout will increase as its gonads ripen. However, there was no significant relationship for increasing condition over the sampling season for all lake trout sampled ($P > 0.05$) (Figure 16). There were no significant relationships between female or male condition factors and capture dates ($P > 0.20$) (Figure 17).

There were no significant relationships between condition and

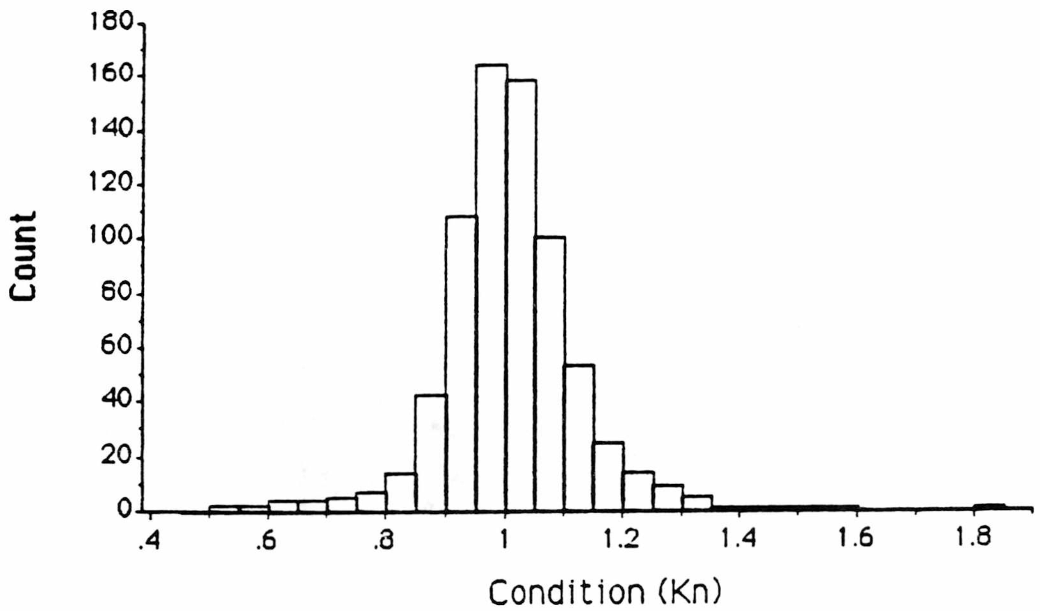


Figure 13.-Condition frequency for lake trout in Walker Lake, 1987 and 1988.

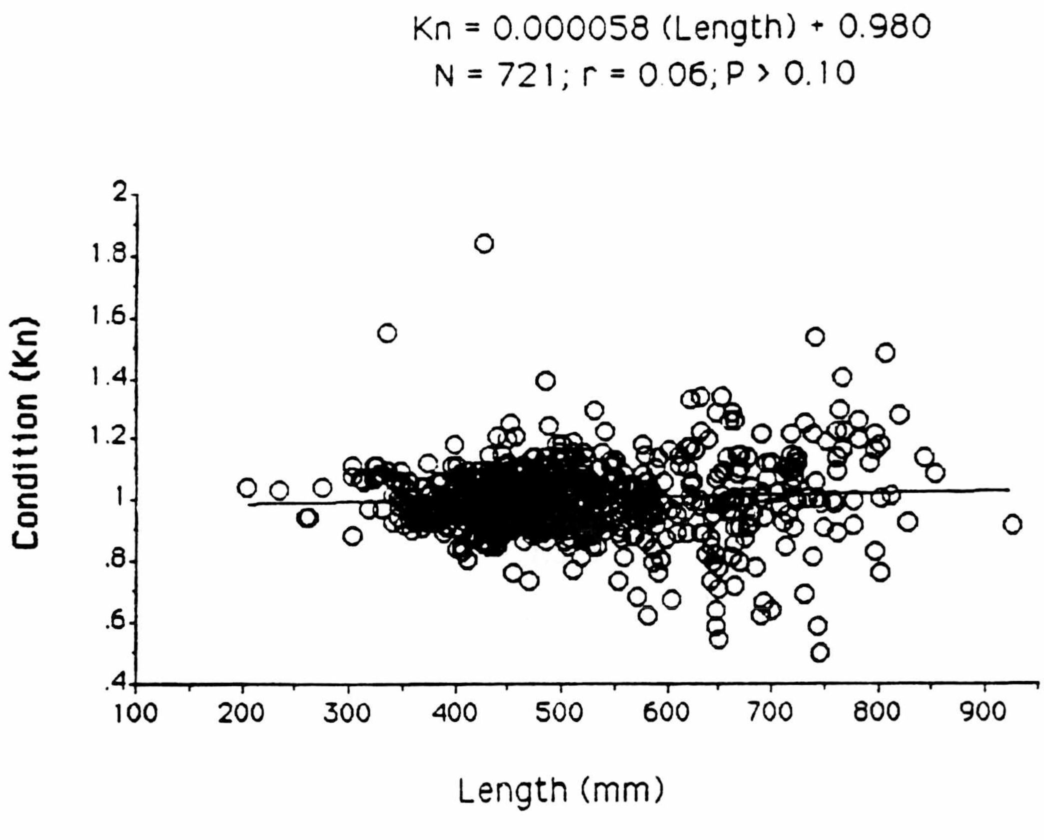


Figure 14.-Condition and length for lake trout in Walker Lake, 1987 and 1988.

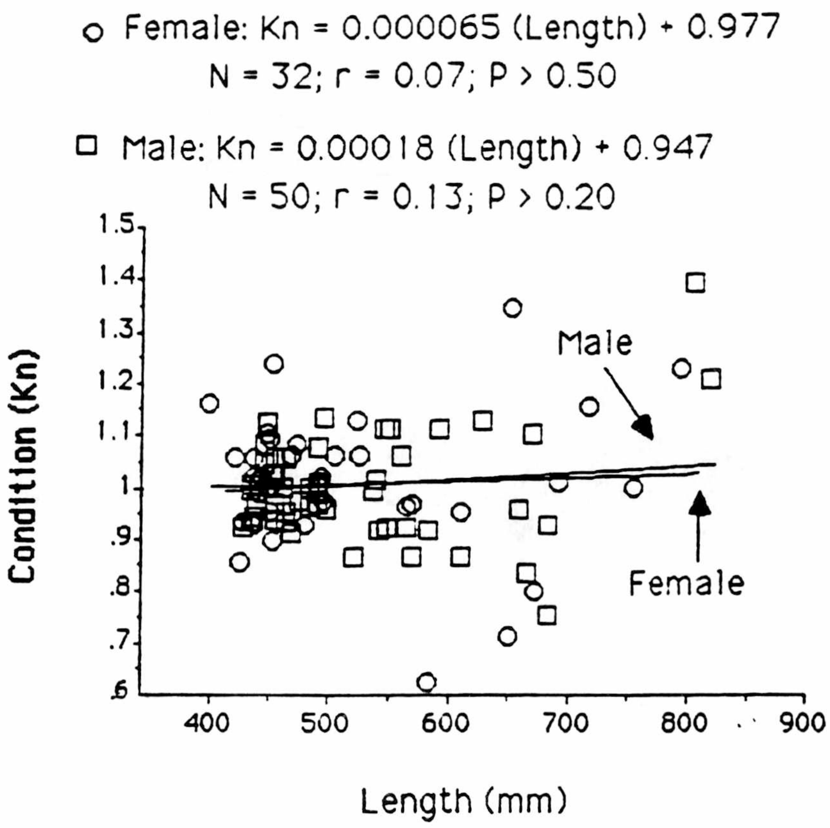


Figure 15.-Condition and length for both sexes of lake trout in Walker Lake, 1987 and 1988.

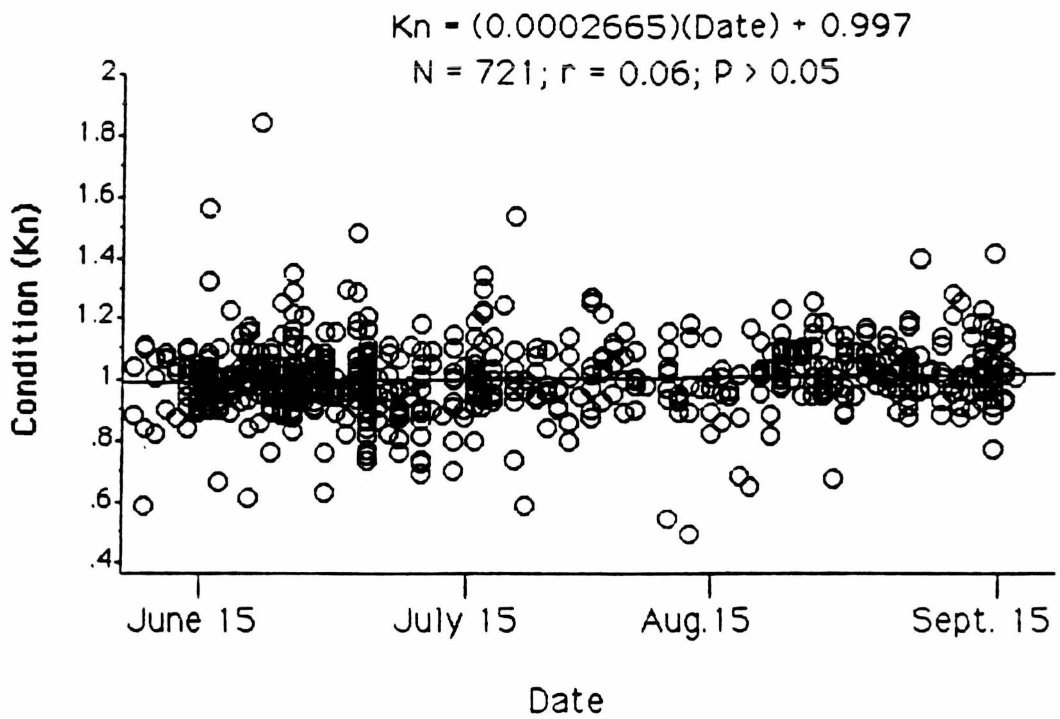


Figure 16.-Condition and date of capture for lake trout in Walker Lake, 1987 and 1988.

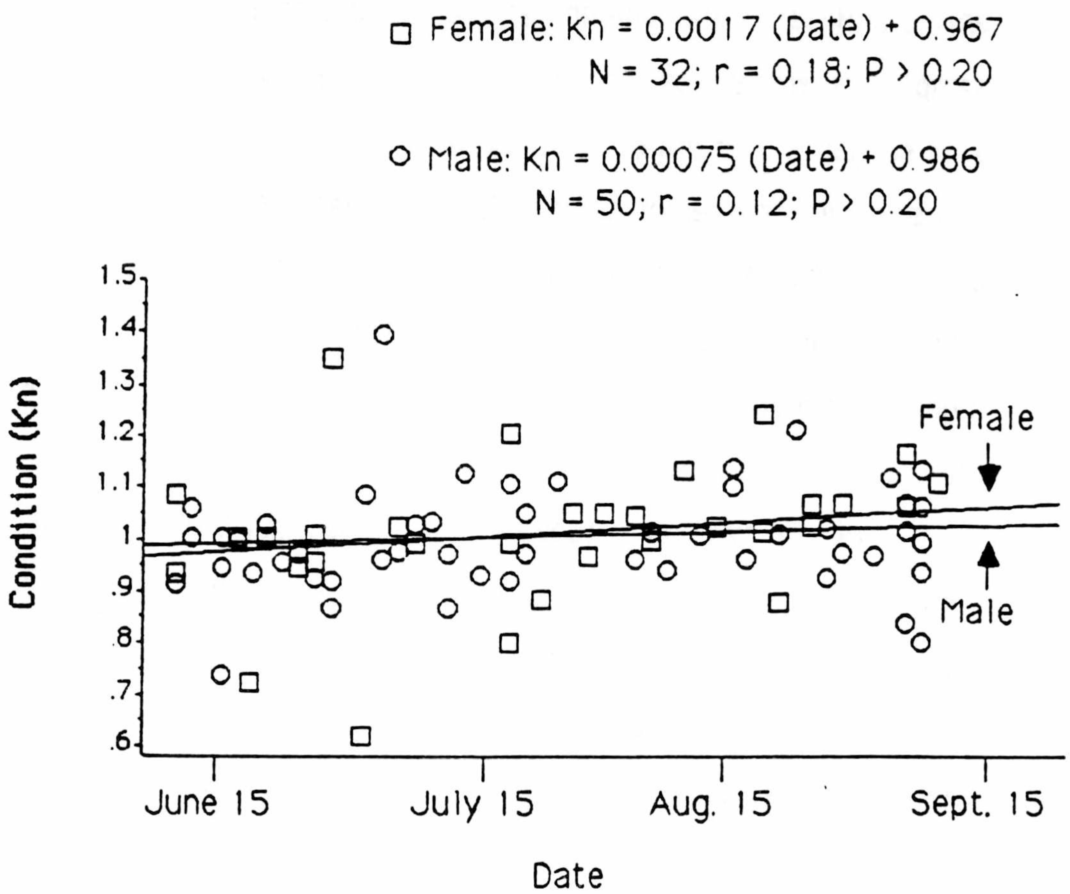


Figure 17.-Condition and date of capture for both sexes of lake trout in Walker Lake, 1987 and 1988.

date of capture within sampling seasons for either sex (P > 0.05). The only significant relationship between condition and fork length within sampling seasons was for males during the early season (P < 0.05). This suggests that male lake trout may gain more weight per unit length during the period prior to 23 July than they do afterward. The condition of females apparently remains constant regardless of their length or date of capture within a sampling season. There were no significant differences in condition factors within or between sexes for the early and the late sampling seasons (P > 0.05).

Over the two year study the only lake trout that were positively identified as being in spawning condition were 13 male fish. These fish were captured during the late sampling season and all released milt when handled. There was no significant relationship between condition of the spawning fish (N = 13) and fork lengths or dates of capture (P > 0.20). There was no significant difference between condition factors of spawning males and other males captured during the late sampling season (P > 0.05). There was no significant difference between condition factors of the spawning fish and other males captured during the complete field seasons (P > 0.05). This suggests that even when males are fully ripe and in prime spawning condition, they do not necessarily gain a substantial amount of weight. This observation was documented by Eschmeyer (1955) for female lake trout. He stated that females actually exhibited a reduction of condition prior to spawning because of a decrease in feeding activity.

Lake trout are considered to be intermittent spawners (Martin and Olver 1980), and it appears that in Walker Lake an insignificant portion of the male and female lake trout spawn in any given two year period (see Discussion, Maturity and Fecundity). If spawning lake trout do display better condition than non-spawners, it appears that the non-spawning fish are in greater proportion than spawning fish. Also, it is possible that an insignificant portion of the spawning population was captured, or that non-spawners were captured selectively.

With the large sample size involved in the weight-length relation and its resultant condition factors, it can be assumed that the population is healthy, and growing normally. However, the sample sizes for sexed fish were relatively small, and preclude broad interpretation about the condition of female and male lake trout.

Maturity and Fecundity

The maturity of an individual can provide significant insight and understanding into the life history and potential productivity of the population. The state of gonad maturation can indicate the current status of reproduction, the size and age at first spawning, the fraction of the stock that is mature, and the general nature of the population's reproductive cycle (Snyder 1983).

Information on maturity in lake trout is scattered and inconsistent, and criteria for assigning mature, immature, or juvenile status is usually not well defined (Healey 1978a). Except for fish in spawning condition, the designation of a fish as mature or immature is somewhat subjective and based upon the experience of the examiner. The maturity status of smaller or younger fish is difficult to distinguish, and determining the sex of immature fish is also difficult (Martin and Olver 1980).

The gonadosomatic index (maturity coefficient) documents the development of the gonads and provides a means of comparing a fish's relative readiness to spawn. The index uses the weight of the gonads expressed as a percentage of body weight (Snyder 1983).

Fecundity is the potential maximum number of eggs that could be laid at spawning as compared to fertility, the actual number of eggs laid. Fecundity is related to length, weight, and age, and can be used to compare spawning intensity between individuals within a stock or to compare separate populations. A combination of fecundity, onset of sexual maturation, sex ratio, and frequency and timing of spawning can all be used to characterize the reproductive capacity of a population, as well as providing guidelines for size restrictions (Snyder 1983).

Methods

Sex was determined by inspection of the fresh gonads from fish collected for age and growth analysis, or by observation of gametes released during handling. Both sexes were classified as mature (able to spawn in the year of capture, or having spawned in a previous year) or immature (never having spawned).

Females were classified as mature if their eggs were larger than a pinhead (1 mm) in diameter. A female with an ovary containing retained eggs from a previous spawning was also considered mature. Immature females had ovaries that were tightly compacted, and granular and contained eggs 1 mm or less in diameter (Martin and Olver 1980). Females with egg diameters greater than 3 mm were considered to be able to spawn in the year of capture (McCart et al. 1972).

Males were classified as mature if the testes were flattened and the maximum width of a testis was equal to or greater than 3 mm. Immature males had testes that were cylindrical and less than 3 mm in diameter. Males were able to spawn in the year of capture if the testis width was greater than 10 mm (Martin and Olver 1980). Fish that could not be sexed were classified as juveniles. The percentage of mature fish for each sex was determined for each age or length class.

Gonads collected during the 1987 sampling season were not weighed fresh, but were preserved and stored in 90% ethanol. Gonads collected in 1988 were weighed fresh, then preserved, and stored in the same manner as the 1987 collections. Preserved weights of the 1988 collections were compared to their fresh weights to obtain conversion factors for estimation of the fresh weights of the 1987 collections. Conversion factors per 100 mm length class for each sex were computed as the average of individual conversion factors for that length class (Table 16, Appendix). No males in the 400 and 800 mm length classes died during 1988 sampling. Therefore, fresh weights of testes were not available for these length classes, and conversion factors for these sizes of fish were calculated as the mean of the conversion factors for the 500 and 600 mm classes.

The gonadosomatic index (Gn) was calculated as:

$$Gn = (G/aL^b) \times 1000$$

where G equals gonad weight (g) and aL^b is the predicted weight from the equation for condition factor (see Methods, Weight-Length Relation and Fish Condition). Gn provides a better basis for comparison than other gonadosomatic indices because it standardizes the weight for fish of the same length, and removes some of the variability associated with individual weights (Anderson and Gutreuter 1983). A gonadosomatic index was not computed for juveniles.

Fecundity was estimated by a gravimetric method where random subsamples of the ovaries were weighed and all the eggs within each subsample were counted. The total number of eggs was determined by multiplying total weight of the ovaries by the mean number of eggs per unit weight (g) in the subsample (Bagenal and Baum 1978; Snyder 1983).

Egg diameter was determined as the mean of a random sample of eggs placed in a 100 mm egg trough. Testis width was measured at the maximum width of a testis laying flat on a measuring board. Conversion factors for 1987 fresh egg diameters and fresh testis widths were calculated in the same manner as gonad weights.

The Mann-Whitney U test (Hollander and Wolfe 1973; Zar 1984) was used to test gonadosomatic indices for significant differences between, years, sexes, and between early (prior to 23 July) and late (after 23 July) sampling seasons. The nonparametric Tukey multiple comparison test (Zar 1984) was used to test for significant differences among the gonadosomatic indices of the combinations of sexes and sampling seasons. Simple linear regression (Zar 1984) was used to test for significant relationships of gonadosomatic indices, fecundity, egg diameter, and testis width with date of capture, fork length, and age. All tests were performed at the 0.05 significance level. Inconsistencies in sample collection caused variation in sample sizes.

Results

Of the 96 lake trout that were sexed. 12% were immature females, 15% were immature males, 21% were mature females, 37% were mature males, and 15% were juveniles (Figure 18; Table 17, Appendix). Immature females ranged in length from 425 to 523 mm with immature males ranging from 428 to 520 mm. Mature females ranged from 422 to 795 mm, and mature males ranged from 435 to 805 mm. Juveniles ranged from 203 to 444 mm. For both females and males, the youngest sexed fish was 11 years old, and the earliest maturity was 12 years for both sexes (Figure 19; Table 18, Appendix). All females older than 16 years were mature, with all males older than 15 years being mature. The oldest juvenile was 14 years old.

Gonads were collected from a total of 55 fish. The gonadosomatic indices for immature females (N = 11) ranged from 5.2 to 12.7 with all fish having eggs of 1 mm in diameter (Table 8). Fecundity ranged from 250 to 2,000 per fish. Mature females (N = 15) had gonadosomatic indices ranging from 2.6 to 66.5 and contained eggs from 2 to 4 mm in diameter. Fecundity ranged from 116 to 10,005 eggs per fish. Fish that were identified as spawning females (N = 3) exhibited gonadosomatic indices ranging from 46.5 to 124.9 with egg diameters from 4 to 5 mm in diameter. Fecundity ranged from 2,618 to 7,442 eggs for each fish.

The gonadosomatic indices for immature males (N = 5) ranged from 2.0 to 5.4 with testis widths from 1 to 2 mm (Table 9). Mature males (N = 18) had gonadosomatic indices ranging from 1.2 to 11.1 with

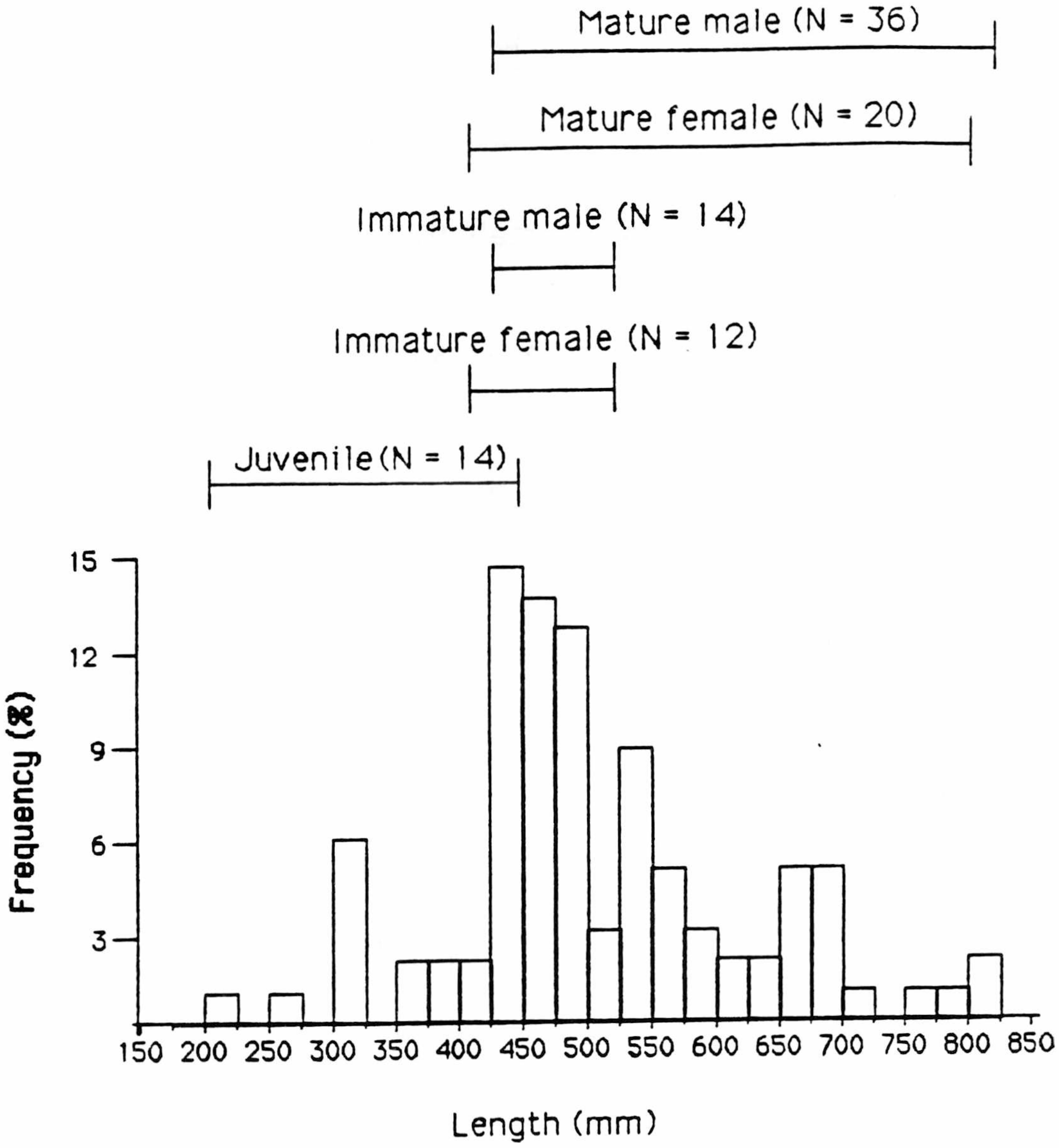


Figure 18.-Overlap of length ranges for mature, immature, and juvenile lake trout in Walker Lake, 1987 and 1988 (N = 96).

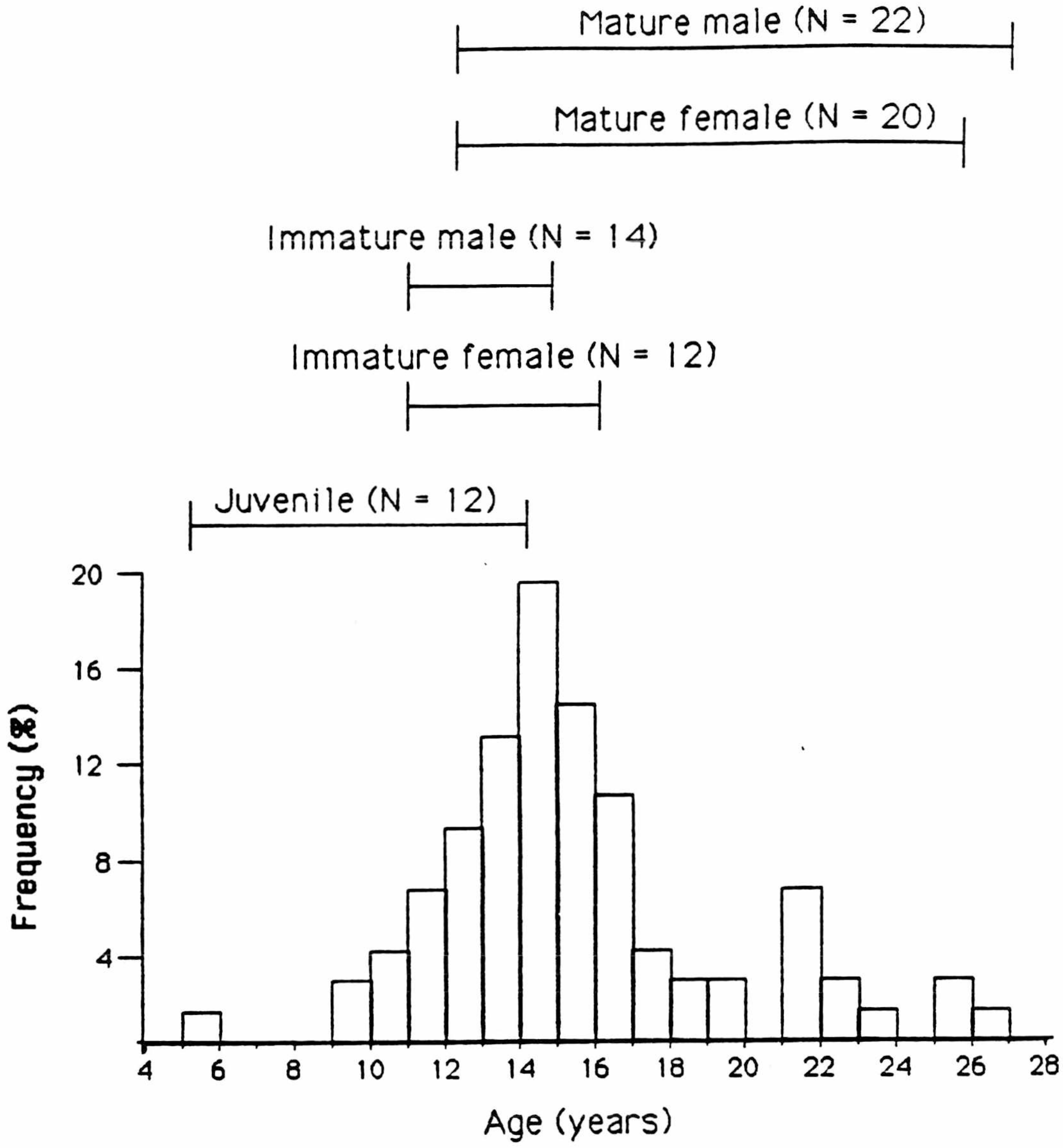


Figure 19.-Overlap of age ranges for mature, immature, and juvenile lake trout in Walker Lake, 1987 and 1988 (N = 80).

Table 8.-Gonadosomatic index (Gn), egg diameter (mm), and fecundity (total eggs per fish) for female lake trout in Walker Lake, 1987 and 1988.

	Immature	Mature	Spawning
N	11	15	3
Length range (mm)	425-494	422-755	651-795
Age range (years)	11-16	12-25	18-25
Gn			
mean	7.8	9.1	79.3
range	5.2-12.7	2.6-13.4	46.5-124.9
Egg diameter			
mean	1.0	2.1	4.3
range	-	2.0-3.0	4.0-5.0
Fecundity			
mean	1,123	3,222	6,688
range	250-2,000	116-8,085	2,618-10,005

Table 9.-Gonadosomatic index (Gn) and testis width (mm) for male lake trout in Walker Lake, 1987 and 1988.

	Immature	Mature	Spawning
N	5	18	3
Length range (mm)	428-456	435-687	546-805
Age range (years)	11-15	12-23	16-26
Gn			
mean	3.3	3.4	49.5
range	1.2-5.4	1.2-11.1	37.3-60.4
Testis width			
mean	1.3	6.5	31
range	1.0-2.0	3.0-10.0	20.0-39.0

testis widths from 3 to 10 mm. Lake trout that were identified as spawning males (N = 3) exhibited gonadosomatic indices from 37.3 to 60.4 and had testis widths from 20 to 39 mm.

There were no significant differences detected between gonadosomatic indices between sampling years, female and male lake trout, or early and late sampling seasons ($P > 0.10$). No significant differences were detected among gonadosomatic indices for pooled sexes and sampling seasons ($P > 0.50$).

There were no significant relationships between gonadosomatic indices and date of capture for female or male lake trout (Table 10). A significant relationship for gonadosomatic indices and fork length existed only for mature females. There was a significant relationship between the gonadosomatic indices and age only for spawning males. For immature females, no significant relationships were detected between fecundity and date of capture, fork length or age, and no significant relationships were detected between egg diameter and the three factors (Table 11). For mature females, the only significant relationships were between fecundity and fork length and age. The only significant relationship detected for male testis width was for fork length in mature fish (Table 12).

The sex ratio was 32 female lake trout captured to 50 males (1:1.6). Fourteen juveniles were captured for a juvenile to female to male ratio of 1:2.3:3.7.

Table 10.-Significance levels (P) for the relationships of gonadosomatic index (Gn) to date of capture, length (mm), and age (years) for lake trout in Walker Lake, 1987 and 1988 (* denotes a significant relationship ($P < 0.05$)).

	N	Gn x Date	Gn x FL	Gn x Age
Females				
immature	11	0.705	0.060	0.717
mature	15	0.619	0.034*	0.164
spawner	3	0.158	0.878	0.543
Males				
immature	5	0.671	0.972	0.159
mature	18	0.337	0.159	0.975
spawner	3	0.399	0.057	0.013*

Table 11.-Significance levels (P) for the relationships of date of capture, length (mm), and age (years) to fecundity (total eggs per fish), and egg diameter (mm) for female lake trout in Walker Lake, 1987 and 1988 (* denotes a significant relationship ($P < 0.05$)).

	Immature	Mature	Spawner
N	11	15	3
Date			
Fecundity	0.594	0.542	0.889
Egg diameter	1.000	0.223	0.0001*
Fork length			
Fecundity	0.104	0.0001*	0.147
Egg diameter	1.000	0.083	0.964
Age			
Fecundity	0.132	0.0001*	0.753
Egg diameter	1.000	0.175	0.386

Table 12.-Significance levels (P) for the relationships of date of capture, length (mm), and age (years) to testis width (mm) for male lake trout in Walker Lake, 1987 and 1988 (* denotes a significant relationship (P < 0.05)).

	Immature	Mature	Spawning
N	5	18	3
Date			
Testis width	1.000	0.710	0.497
Fork length			
Testis width	0.658	0.045*	0.155
Age			
Testis width	0.423	0.061	0.111

Discussion

Length at first maturity for lake trout can vary from 280 mm to 650 mm, and age at first maturity ranges from 4 to 19 years (Martin and Olver 1980). Lake trout from areas north of 60°N generally mature at slightly smaller sizes and older ages (Healey 1978a). Lake trout from Alaska mature at lengths from 308 mm to 526 mm, and the youngest age at maturity ranges from 5 to 20 years (Burr 1987b, 1989). Lake trout from lakes in the Brooks Range reached first maturity between 340 and 500 mm and between 10 and 15 years of age (McCart et al. 1972; Craig and Wells 1975). Length and age at first maturity for lake trout in Walker Lake are consistent with the findings for other northern Alaska populations.

Males generally mature a year earlier than females (Martin and Olver 1980), but both sexes matured at the same age in Walker Lake. The largest members of an age group usually mature first (Kennedy 1954; Martin and Olver 1980). In Walker Lake, of the age classes with overlapping immature and mature fish (ages 12 to 16), the largest fish in each age class were mature males.

The gonadosamatic indices were highly variable with values that overlapped between and within both sexes for immature and mature fish. This suggests that the gonadosomatic index is not a reliable method for identifying immature and mature fish. However, the gonadosomatic index may be applicable for identifying fish that would have spawned during the season of capture. The three spawning females (based on egg diameter) were captured on 24 June (two fish) and 11 July (one fish) and had gonadosomatic indices of 46.5, 66.5 and 124.9, respectively. The highest gonadosomatic index for non-spawning females was 13.4. Spawning males were captured on 30 June, 17 July, and 29 August, and had gonadosomatic indices of 60.4, 37.3, and 39.9. The highest gonadosomatic index for the non-spawning males was 11.1. Egg diameter and testis width are the more accepted methods for determining maturity, but the gonadosomatic index is easier to estimate, and may be useful for identifying spawning lake trout.

As the spawning period nears, the gonad of a lake trout makes up an increasing proportion of body weight (Hanson and Wickwire 1967; Martin and Olver 1980). However, in Walker Lake the lack of significant relationships between the gonadosomatic indices and date ofcapture indicates that the weight of the gonads did not increase significantly as the field season progressed. This may have been caused by a decrease in the feeding activity as spawning season approached (Eschmeyer 1955; Hanson and Wickwire 1967), or it may have been due to very few lake trout reaching spawning condition in any given two year period. Also, very few spawning lake trout were sampled.

Martin (1970) found no consistent association between gonad weight and length for lake trout, while Eschmeyer (1955) described an increase in gonad weight as a fish's length increased. Walker Lake mature females exhibited a significant relationship between the gonadosomatic index and length, but males did not. This is for fish of approximately equal length and age ranges, and suggests that the testes of male lake trout make up a constant percentage of body weight, but ovaries of female lake trout make up an increasingly greater proportion of body weight as length increases. Only spawning males exhibited a significant relationship between gonadosomatic index and age, but the sample size for this group was extremely small.

Although fecundity appears not to be reduced in northern populations (Healey 1978b), fecundity in Alaskan stocks appears to be somewhat lower than in more southerly areas. Mean fecundity for Walker Lake lake trout was 3,216 eggs per female with a range of 116 to 10,005. Other lake trout populations in Alaska with similar length ranges exhibited mean fecundities from 1,710 to 6,633 eggs per female with ranges from 274 to 13,000 (McCart et al. 1972; Craig and Wells 1975; Burr 1987b). Lake trout stocks from more southerly areas with similar fork length ranges exhibited mean fecundities from 996 to 7,943 eggs per female with ranges from 411 to 21,500 eggs per female (Martin and Olver 1980).

Considerable variability exists in fecundity between individual fish of similar length and age (Eschmeyer 1955; Hanson and Wickwire 1967; Martin and Olver 1980). This variability in fecundity was obvious in Walker Lake with several younger and smaller immature fish having more eggs than mature fish. Indeed, these same immature fish had almost as many eggs as one of the spawning fish. Eschmeyer (1955), Hanson and Wickwire (1967), and Healey (1978b) described a strong relationship between fecundity and length, and lake trout in Walker

Lake exhibited this significant relationship. Fecundity also increases significantly with age (Hanson and Wickwire 1967) as was observed in Walker Lake.

In a controlled experiment in the Northwest Territories of Canada, individual fecundity of mature females was significantly higher after exploitation than it was before exploitation (Healey 1978b). An unexploited lake trout population exhibited no correlation between fecundity and exploitation, while exploited lake trout exhibited a significant increase in fecundity. For Walker Lake, the Mann-Whitney test (Hollander and Wolfe 1973; Zar 1984) detected no significant difference between the fecundities of fish captured in 1987 and 1988 ($P > 0.20$). The t-test (Zar 1984) detected no significant difference ($P > 0.20$) between the slopes of the fecundity by fork length plots for each year (Figure 20). This suggests that the population of lake trout in Walker Lake is not being overly exploited. However, both these studies suffer from extremely small sample sizes, and the time period needed to observe fecundity changes is not known.

The size of eggs in spawning female lake trout increases throughout the season with ripe eggs ranging from 4 to 7 mm in diameter at the time of spawning (Martin and Olver 1980). In Alaska egg diameters in spawning females increased from 3 to 5 mm during the open water season (McCart et al. 1972). In northern lake trout populations 5 mm was considered to be the minimum size necessary for spawning (Johnson 1972; McCart et al. 1972; Craig and Wells 1975).

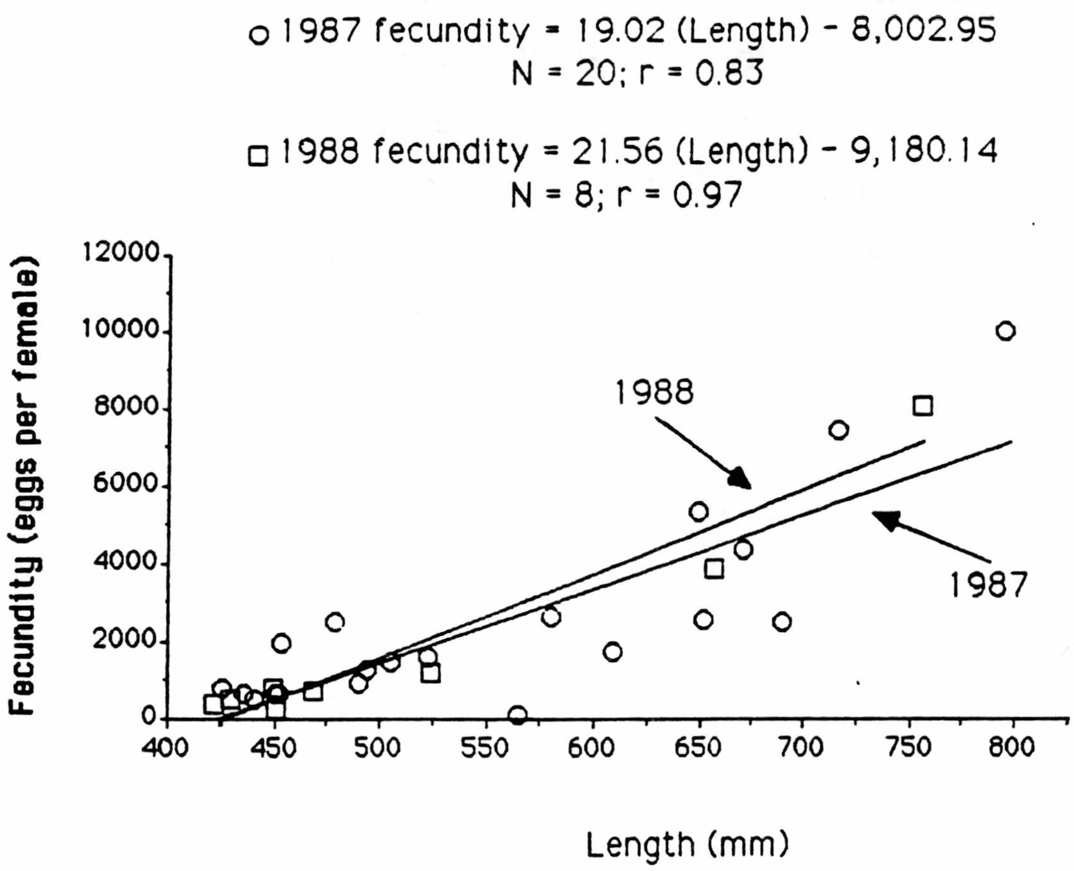


Figure 20.-Fecundity by length for lake trout in Walker Lake, 1987 and 1988.

The three spawning females that were sampled in Walker Lake were captured early in the open water season with egg diameters from 4 to 5 mm. Despite the small sample size, there was a significant relationship between egg diameters and the date of capture for spawning females. This would be expected since the egg diameters of non-spawning females remain in the 1 to 2 range throughout the open water season spawning season (Craig and Wells 1975). No ripe females were captured during the entire study.

Non-consecutive spawning in lake trout is common especially in northern populations (Johnson 1972; Power 1978; Martin and Olver 1980). Females in Great Bear Lake spawned every third year (Miller and Kennedy 1948), and females in Great Slave Lake spawned every other year (Kennedy 1954). A population from an alpine lake in Alberta contained females that might spawn every 4 years (Donald and Alger 1986) while females in Keller Lake, Northwest Territories, may spawn only three times in a lifetime (Johnson 1972). In Walker Lake, except for the spawners, the gonads of mature females contained one or more retained eggs, and it is assumed that these fish spawned in the year before capture. The diameters of the eggs that were not residual were less than 3 mm, which suggests that these females would not have spawned in the year of capture. By assuming these developing eggs would be spawned in the year after capture, it appears that females in Walker Lake spawn at a maximum frequency of once every 2 years. Because previous spawning in males could not be verified, their spawning frequency could not be determined. However, once they were mature, males from an alpine lake in Alberta spawned every year (Donald and Alger 1986).

While no data are available for the sex ratio of an entire stock of lake trout, typical female:male ratios are 1:1 (Martin and Olver 1980). McCart et al. (1972) reported a female to male ratio of 1:1.2 from Itkilik Lake, and Craig and Wells (1975) reported a 1:1 ratio from Old John and Campsite lakes. Burr (1987a, 1988, 1989) reported female to male ratios ranging from 1:0.4 to 2.5:1 for several lakes throughout interior Alaska. While these sex ratios are the best estimates available for the proportions of females and males in lake trout populations, the biases associated with gear selectivity and sampling times and locations are not known.

The ratio of spawning females to non-spawners was 1:3 in Keller Lake (Johnson 1972). In Walker Lake the ratio of spawning females to non-spawners (immature and mature) was 1:8.7, and the ratio of spawning females to non-spawning mature females was 1:5. The ratio of spawning males to non-spawning (immature and mature) males was 1:7.7, and the ratio of spawning males to mature non-spawners was 1:6. These ratios were calculated only for fish that died during sampling, and may not reflect the true ratios. However, it appears that only a small percentage of each sex reaches spawning condition in any 2 year period.

Lake trout populations usually spawn at night with males generally arriving on the spawning grounds first. The spawning season can occur from late August to late November with fish arriving on the spawning grounds as dusk approaches (DeRoche 1969; Martin and Olver 1980). Material ranging from sand to boulders is used as a spawning substrate (DeRoche 1969; Scott and Crossman 1973; Martin and Olver 1980; Dorr et al. 1981; Wagner 1982; Sly and Widmer 1984). Besides the three males with the highest gonadosomatic indices and largest testis widths that died in the nets, 13 other males were confirmed as spawners when they released milt during handling. These fish ranged in length from 454 to 818 mm, and were not sacrificed due to the restriction on mortalities. Five of these 13 were captured in the same set in 1988, and one was captured at the same location in 1987. This site is in a straight shore area with a mixed substrate that appeared suitable for spawning. The fish from 1988 were captured in an evening set (after 1700 hours), but there was no record for the time of the set from 1987. These factors suggest that the location just south of the central peninsula on the east side of the lake may be a spawning area, or at least a staging area for spawning males (Figure 21). The remaining seven males that released milt were captured throughout the middle and south sections of the lake, and three of these fish were captured in evening sets. No spawning fish were captured in the north section. The earliest date that a fish released milt was 5 September, approximately 10 days before the end of each field season. Information from local residents who sport fish at the lake suggests that most spawning activity takes place under the ice during October.

For lake trout in Walker Lake, maturity and fecundity appear to be typical for a northern population. In some samples, there were

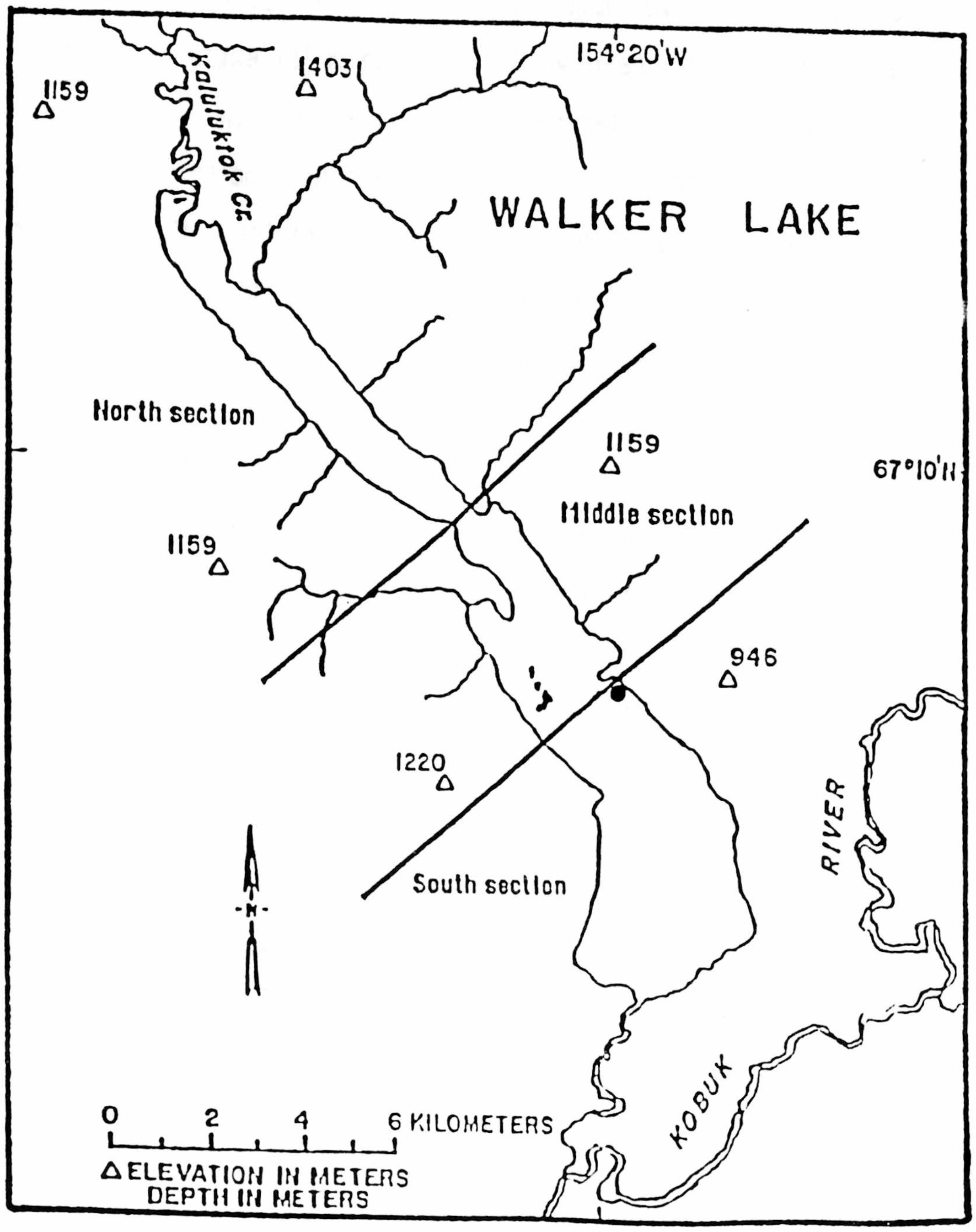


Figure 21.-Possible lake trout spawning location (●) at Walker Lake.

definite trends over date, length, and age for gonad weight, fecundity, egg diameter and testis width. In spite of the extremely small sample sizes, and the irregular methods of collection, these trends indicate how few lake trout actually reach spawning condition in any year.

Because males usually outnumber females in the spawning areas (Martin and Olver 1980), and males appear to ripen earlier than females, the number of potential offspring in any year is most likely limited by the number of spawning females. The number of ripe females influences the number of eggs shed and fertilized, and this affects the abundance of surviving larvae. The abundance of surviving larvae influences the number of fish recruited into the fishery, and the number of recruits influences the number of fish eventually reaching trophy size. The limited number of spawning females, apparent non-consecutive spawning, and the time needed to reach maturity, indicate that the lake trout population in Walker Lake may be very sensitive to harvest rates. An increase in harvest may deplete the spawning stock to a point where reproduction limits the fishery's yield, and could result in recruitment overfishing (OMNR 1983).

Summary

This study of the life history of lake trout in Walker Lake will serve primarily as a baseline for future comparisons. Without sufficient historical data for the lake, there is no information about population trends for assessment of the current vigor of the stock. However, general conclusions from comparisons with other lake trout studies have provided insight into the status of the Walker Lake population. Interpretation of the population's health provides a basis for recommendations concerning the protection and maintenance of the population while allowing a sport fishery. In general, Walker Lake has a typical lake trout population that exhibits the specific characteristics of living under arctic conditions.

Conclusions

No relative abundance studies were available for comparison, but indices from this study indicated that lake trout in Walker Lake are basically unpredictable wanderers with few spatial or temporal patterns. Of the temporal factors that were tested for adult fish, the results indicated that the catch per unit effort was significantly higher after ice-out than before freeze-up. A stock that spends the majority of its life constrained by ice and stressed by overwintering would be expected to be most active as soon as the constraining factor disappears. Adult lake trout were captured at significantly higher rates near stream mouth and straight shoreline areas than at the outlet area. Intuitively, stream mouth areas would be more attractive to opportunistic feeders such as lake trout. The higher catch per unit effort for straight shorelines may have been due to frequent movement of lake trout through this dominant shoreline feature. There were no significant differences in catch per unit effort for the other factors that were tested (time of set, lake section, substrate type and the combinations of factors).

Juvenile lake trout are known to be widely distributed throughout the pelagic portion of a lake. In Walker Lake these fish preferred areas in the water column less than 50 m deep that are close to shallow areas. Because Arctic char also occur in Walker Lake, and their morphological characteristics at small sizes overlap with those of lake trout, fingerlings that were captured by seining could not be positively idenitfied to species. However, subsequent analysis of pyloric caeca indicated that the fingerlings were most likely Arctic char. Significantly more fingerlings were captured at stream mouth areas than at straight shoreline areas; stream mouths may be important rearing areas for both species.

Although the oldest lake trout from Walker Lake was aged at 26 years, several lake trout that were not sacrificed exhibited lengths equal to or larger than the lengths of the oldest fish (28-42 years) from other Alaskan lakes. The modal age was 14 years with the youngest fish aged at 5 years. Few young lake trout are usually captured in lake trout studies, and only six fish under the age of 10 years were captured in Walker Lake.

Northern lake trout populations exhibit a high degree of variability in length at age. The fork length for age 14 fish in Walker Lake ranged from 259 to 657 mm, and 16 year old fish had fork lengths ranging from 405 to 724 mm. The asymptotic length for Walker Lake fish was estimated as 1,024 mm.

Comparisons of growth curves among lake trout from Alaskan lakes indicated that climate, as a function of latitude and altitude, provides a crude index to relative growth rates. Growth rates among populations from the Alaska Range were similar as were those among populations from the Brooks Range. Lake trout at low elevation in the Brooks Range had a growth rate similar to those at a higher elevation in the Alaska Range. This is an example of ecological altitudinal-latitudinal zonation.

The same comparison also indicated that the growth curves for stocks from accessible lakes leveled off at a lower maximum age compared to curves for stocks from remote areas which contained larger, older fish. Undoubtedly, the accessible lakes receive more fishing pressure, and, indeed, other studies found that the recommended maximum sustainable yield of less than 0.5 kg of lake trout per surface hectare per year was being surpassed in these lakes. It appears that the abundance of larger, older fish in the accessible lakes may have been reduced by fishing pressure. It also appears that lake trout in Walker Lake have not experienced such heavy exploitation.

However, large lake trout were captured in the more accessible lakes, but these fish were not sacrificed for estimates of age.

Comparisons of historical growth curves for lake trout populations from other studies indicated that compensatory growth occurred after heavy natural or fishing mortality. A comparison of the growth curve from a study in 1967 with the growth curve from 1987 and 1988 indicated that the Walker Lake population did not exhibit compensatory growth. Although the sample for 1967 was small and the ages were estimated by scales, this conclusion provided further indication that the Walker Lake population is not heavily fished.

A total of 721 lake trout were weighed and measured over the two year study. Lengths ranged from 203 to 924 mm with weights ranging from 83 to 8500 g. The modal length class was 426 to 450 mm. The weight-length relation for Walker Lake fish was similar to relations for lake trout from other Brooks Range lakes. However, the Walker Lake relation was distinct from the weight-length relations for lake trout from temperate lakes.

Allometric condition factors were computed for all captured fish. Although the condition of some lake trout stocks increases with an increase in length, or as spawning season approaches, there was no significant relationship between condition of Walker Lake fish and either of these factors. For sexed fish, the only significant relationship was between condition and fork length for males during the early sampling seasons (13 June to 22 July for both years). This suggests that the weight per unit length of males increases more during the period after ice-out than it does during the period before freeze-up.

Thirteen males that released milt when handled were the only fish that were positively identified as spawners. These fish did not exhibit significant relationships between condition and date of capture or fork length. Also, there were no significant differences in condition between these spawning males and other males during either of the sampling seasons. It appears that even in prime spawning condition, males do not gain a substantial amount of weight. In Lake Superior the condition of female lake trout decreased during spawning season because of a reduction in feeding activity. Male lake trout in Walker Lake may behave in similar manner.

Of the lake trout that were identified to state of maturity, the largest portion were mature males. Male lake trout usually mature a year earlier than females, but in Walker Lake the youngest age at maturity was 12 years for both sexes. All females older than 15 years, and all males older than 14 years were mature. Length at first maturity was 422 mm for females, and 435 mm for males. All fish larger than 525 mm were mature. Lake trout in Alaska mature at ages 5 to 20 years, and mature at lengths from 308 to 526 mm. For lake trout, the largest members in an age group usually mature first. In Walker Lake mature males were the largest fish in age classes that contained both immature and mature fish. Juveniles ranged in length from 203 to 444 mm, and the oldest juvenile was aged at 14 years.

Sex ratios (female to male) for Alaskan lake trout range from 1:0.4 to 1:2.3. The ratio of females to males for Walker Lake fish was 1:1.6.

Gonadosomatic indices were highly variable between and within stages of maturity for both sexes which suggests that they may not be a dependable indicator of maturity. However, the gonadosomatic indices for fish that were considered to be able to spawn in the year of capture were much higher than for non-spawning fish. Therefore, the index may be valuable for identifying spawners. Females exhibited a significant relationship between the gonadosomatic index and fork length, but males did not. This suggests that the weight of the ovaries of females may increase as length increases, but male testes constitute a constant proportion of body weight regardless of length. Spawning males exhibited a significant relationship between gonadosomatic index and age, and indicates that for males that will spawn in the year of capture, age influences gonad weight more than length or date of capture.

Mean fecundity per female in Walker Lake was 3,216 eggs with individual fecunditites ranging from 116 to 10,005 eggs. Mean fecundities for other Alaskan lake trout populations ranged from 1,710 to 6,633 eggs with individuals containing from 274 to 13,000 eggs. Fecundity is highly variable among lake trout of similar lengths and ages, and several smaller and younger immature fish from Walker Lake contained more eggs than larger and older mature fish. Fecundity generally increases with length and age, and lake trout in Walker Lake exhibited significant relationships for each of these factors. Individual fecundity has been documented to increase due to exploitation. No significant difference was detected between the fecundities of fish captured in 1987 and the fecundities of fish captured in 1988. Although the sample sizes are small, and little time had elapsed between sampling years, this suggests that Walker Lake lake trout had not been heavily fished during the study period.

In Alaska spawning females contain eggs with diameters that increase from 3 to 5 mm during the open water season with 5 mm being the minimum diameter necessary for spawning. The spawning females from Walker Lake were captured early in the open water season with eggs from 4 to 5 mm in diameter. Spawning male lake trout have testis widths greater than 10 mm, and Walker Lake spawning males had testis widths ranging from 20 to 39 mm.

Non-spawning females outnumbered spawning females in Keller Lake, Northwest Territories by a ratio of 3:1. In Walker Lake non-spawning fish (immature and mature) of both sexes outnumbered spawning fish by approximately 10 to one. The ratio of mature non-spawners to spawners for both sexes was seven to one.

Intermittent spawning is common in northern populations of lake trout. Residual and developing eggs that were found in some females indicated that the spawning frequency for females in Walker Lake is a maximum of once every 2 years. After reaching maturity, males from an alpine lake in Alberta spawned every year. However, in

Walker Lake it was not possible to verify that males had spawned in previous years, and spawning frequency could not be determined.

Lake trout populations spawn from late August to late November with fish arriving on the spawning grounds as dusk approaches. Spawning substrate for lake trout consists of material ranging in size from sand to large boulders. From 5 to September to the end of the field season, 13 males that released milt during handling were captured at Walker Lake. Six of the males that released milt were captured at the same location with five of the six being captured in nets set after 1700 hours. The bottom material at this site was classified as mixed substrate (equal amounts of material greater than and less than 64 mm in diameter), and appeared to be suitable for spawning. The remainder of the spawning males were captured throughout the lake at differing times. This suggests that this location may be a spawning area, or at least a staging area for spawning males. No ripe females were captured in either of the field seasons.

While the results of this study provide valuable insight into the life history of lake trout in Walker Lake, several aspects must be clarified for the information to be completely meaningful. With limited budget, time, and personnel it was difficult to effectively sample such a nomadic species in such a large lake. During the 1987 season, randomness was compromised by an effort to capture as many lake trout as possible without regard to time, gear, or sampling methods. However, the 1988 sampling used a rigid design that was stratified by temporal and spatial factors, and used standardized gear and methods. Strata for relative abundance sampling were subjectively chosen and described, and resulted in unequal sample sizes that may have biased the statistical analyses.

The restriction on the number of mortalities, and the preferential release of large fish resulted in small sample sizes, and somewhat biased data for age, growth and maturity related indices. Despite ages that were estimated by interpretation of otolith annuli by three independent observers, aging errors were certainly present. Ages were determined at the time of capture with no adjustment for growth during the season. Mean lengths for the von Bertalanffy equation and growth curve comparisons did not allow for individual growth rates, and these data were undoubtedly influenced by gear selectivity, also.

The slope and intercept from the weight-length regression were used to calculate the predicted weight for the condition factor, and did not provide for individual variation. Fish from both extremes of length and weight were underrepresented in the sample, and may have biased the results toward the medium sizes.

Determination of maturity was somewhat subjective, and largely based upon the experience of the observer. Conversion factors for gonad weights, egg diameters, and testis widths may have influenced relationships and their interpretation. Gonadosomatic indices were based upon a predicted body weight for each length, and did not allow for individual variation. Extrapolation of the mean number of eggs in subsamples of the ovaries may have produced error in the computation of fecundity. In spite of the study's limitations, the results of the research are meaningful, and will provide a representative baseline for future comparisons.

Management

Commercial overfishing has depleted lake trout populations in northern areas (Keleher 1972; Regier and Loftus 1972). Eutrophication and the introduction of exotics, combined with overfishing, have devastated stocks in more southern regions (Berst and Spangler 1972; Christie 1972; Christie et al. 1972; Colby et al. 1972; Hartman 1972; Lawrie and Rahrer 1972; Martin and Fry 1972; Regier and Loftus 1972; Wells and McLain 1972; Youngs and Oglesby 1972). However, because Walker Lake is remote, and is within a designated wilderness area of Gates of the Arctic National Park (USDI 1986), the lake apparently has been immune from these pressures. The only foreseeable source of future stress for lake trout would come from the lake's sport fishery.

Lake trout exhibit slow growth, late maturity, and low production, especially in northern areas (Kennedy 1954, McCart et al. 1972; Craig and Wells 1975; Healey 1978b). These fish are easily captured by angling, and there is no question that angling pressure alone can cause declines in arctic lake trout populations (McCart et al. 1972; Ryder and Johnson 1972; McDonald and Hershey 1989). These factors make lake trout vulnerable to overexploitation (Martin and Olver 1980).

Overexploitation, by definition, occurs when:

> Because of fishing, the yields from a fishery resource no longer can be maintained at or near peak potential, or there is good reason to believe that the resource is predisposed to collapse (OMNR 1983).

While there is no evidence indicating that lake trout in Walker Lake have been overexploited, the identification of overexploitation has always been plagued by delayed recognition, hesitant action, and long recovery time (OMNR 1983). Typically the historical data needed to make baseline comparisons were not available, and the depletion of the fishery was not evident. Only after the resilience of a stock was destroyed, would it become obvious that overexploitation had occurred, and that controlling measures should have been implemented earlier (Loftus 1976; OMNR 1983). Once overexploitation is identified, an oligotrophic lake may be required to "lie fallow" for about 15 years before restoration to its former condition is reached (Ryder and Johnson 1972).

Until recently, the minimum bag and possession limits for lake trout throughout Alaska were 10 fish under 20 inches (500 mm), with the regulations for some areas allowing an additional two fish of 20 inches or more (Burr 1986). During 1986, because of a lack of historical data, and a statewide increase in sport fishing effort and harvest, the Alaska Department of Fish and Game began researching the life history and sport harvest of lake trout. From these studies the Department determined that maximum harvest levels for some of the more accessible lakes were being exceeded. These populations could not sustain such high levels of exploitation without major effects on population numbers and size structure. To prevent the degradation of these stocks, more stringent regulations were adopted for the entire state. Harvest on the most heavily fished lakes was restricted to two fish per day, and two in possession with an 18 inch (450 mm) size limit (Burr 1986). While these lake trout populations may not have been overexploited, the new regulations signified a heightened awareness of the fragility of Alaskan lake trout stocks. The new restrictions have reduced the possibility that overexploitation would occur, and have also provided a chance for depleted stocks to recover.

The conclusions of the Walker Lake study suggest that its lake trout have not been overexploited. The current regulations for lake trout in the Walker Lake area restrict the harvest to four fish per day, four in possession with no size limit. These regulations may be adequate, but to ensure that the population remains healthy, and that it provides a quality fishing experience, it may be prudent to restrict harvest even more, and adopt the regulations of the heavily harvested lakes. If a limit of two fish per day, two in possession, and an 18 inch length restriction can maintain quality fishing on heavily fished lakes, it undoubtedly would maintain the fishery on a remote lake. This caution would provide time to evaluate the fishery, and would undoubtedly lower the probability of the lake becoming overexploited. If errors in management were to be made, it is preferable to err on the conservative side.

Future study

The lake trout population in Walker Lake appears to be healthy and relatively unstressed, and a subsequent study of the fish's life history is not needed in the near future. Since the only foreseeable stress on the population would come from angling, it is obvious that its influence must be quantitatively evaluated. Therefore, a creel survey is imperative for understanding the use and harvest trends of the lake's fishery.

The only means of access to Walker Lake during the open water season is by aircraft. Because the lake is large, and there are no specific access points, it would be very difficult for a creel investigator to accurately sample the fishery. However, it may be possible to use the guides from the lake's only fishing lodge as creel clerks. Collection of data by the guides would provide a reproducible, high quality sample of the exploited portion of the population at a relatively low cost (Yaremchuk 1986). Data would have to be collected from every fish hooked during a client's angling session, but all angling sessions would not have to be sampled. Initially, the only information needed would be number of fisherman, hours fished, number and species released and retained, length of all captured fish, and area of the lake fished. Periodically, trained personnel could sample the creel as a check on the guide's information, and collect age and weight data (Yaremchuk 1986). Also, to complement their own creel information, guides could count and possibly interview other anglers on the lake.

An accurate creel survey should identify harvest rates, and any changes in the population's size or age structure. However, the completion of a baseline study, the recent implementation of these new regulations, and the possible creel survey provide an enviable opportunity to identify population trends of an arctic population of lake trout. After these regulations have been in place for 5 to 10 years, the results of a subsequent life history study could be compared to the baseline information. By waiting a substantial amount of time, any effects caused by the regulations would become observable, and any declines in the population probably would not have had time to become uncontrollable. Also, the effects of the removal of fish for the baseline study would have been moderated. The trends observed from the studies would provide the most accurate and meaningful information available, and could be used to amend the current management strategy.

The ideal follow-up study would mimic the baseline study in every method and detail. However, to increase efficiency and decrease cost, several elements of the original study should be modified. Shoreline nets should be set in the exact locations, dates, and times, but pelagic sampling should be deleted due to the little information provided by these sets. Seining should be attempted at all times of the sampling season, and expanded into unsampled areas including upstream reaches of creeks. A concerted effort should focus on distinguishing fingerling lake trout from Arctic char. Also, from cursory examination of the catch data, it appeared that most of the lake trout that died were captured in the 2.5 cm mesh. Smaller mesh may reduce incidental mortalities, and provide a better opportunity to control the sizes and numbers of fish sacrificed. Further examination of the data indicated that the gill net that was attached to the shore captured the majority of the fish, and that the majority of the catch was in the lower half of the net. This indicates that future sampling could be streamlined by using one 2.5 m deep gill net that was set from the shore.

Age and growth information should be analyzed in the same manner with strict duplication of the age determination process. Recent reports usually include age data based on otoliths, but the exact techniques have differed, or have not been described. The ages of fish from Paxson, Summit, and Glacier lakes were determined by surface readings of the otoliths with supplemental grinding performed to identify the outer annuli (J. M. Burr, Alaska Department of Fish and Game, personal communication). The aging techniques for fish from Old John and Itkillik lakes were simply described as "the otolith method" (McCart et al. 1972; Craig and Wells 1975), while this baseline study used the break and burn method. Any otolith method undoubtedly provides more accurate age estimates than scales. However, different aging methods may influence the interpretation of annuli, and makes it difficult to directly compare age structures between populations. A precise standardization of aging techniques would decrease variability between populations, and allow more meaningful comparisons to be made.

A two year study would be optimum, but data from a single season should be adequate for comparison to the baseline. If sampling needed to be streamlined even more so, the most information per unit effort would be supplied by sampling during the spawning season. This schedule would involve extending the sampling season well into October. Sampling late in the season would increase the information concerning length, weight, age, and relative abundance of spawners. It would also provide complementary information about spawning timing, condition, numbers, ratios, and locations as well as improve the other indices concerned with maturity. Regardless of study schedule or duration, 100 total mortalities appear to provide sufficient information without harmfully affecting the population. A creel survey and follow-up life history study would not only protect the lake trout stock in Walker Lake, they could serve as a basis for management for similar lakes within Gates of the Arctic National Park and Preserve.

Epilogue

The lake trout and its waters provide the type of lake community that is generally accepted to be the most esthetically pleasing (Loftus and Regier 1972). However, the essence of such ecosystems, i.e., the transparency and purity of the water, the beautiful organisms, clean sand and stones, is easily despoiled by the direct and indirect effects of humans. With an inevitable increase in access to oligotrophic lakes, and the associated increase in sport fishing, none of these waters is exempt from the deleterious effects of humankind (Ryder and Johnson 1972). Many inaccessible lakes have had their salmonid populations stressed by ardent anglers with further depletions caused by contamination of habitat. There is little optimism about ever returning these lakes to an oligotrophic state (Ryder and Johnson 1972).

Unless appropriate management measures are taken and pollution arrested, salmonid communities in oligotrophic lakes seem destined for extinction (Ryder and Johnson 1972). A policy that would conserve and maintain viable communities should be readily acceptable to all society (Regier and Power 1980). Perhaps Walker Lake can be an example of this policy.

Literature Cited

Anderson, R. O., and S. J. Gutreuter. 1983. Length, weight, and associated structures. Pages 283-300 *in* L. A. Nielsen, and D. L. Johnson, editors. Fisheries Techniques. American Fisheries Society. Bethesda, Maryland.

Bagenal, T. B., and E. Baum. 1978. Eggs and early life history. Pages 165-201 *in* T. Bagenal, editor. Methods of assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford, England.

Barber, W. E., and G. A. McFarlane. 1987. Evaluation of three techniques to age Arctic char from Alaskan and Canadian waters. Transactions of the American Fisheries Society 116: 874-881.

Beamish, R. J., and D. E. Chilton. 1982. Preliminary evaluation of a method to determine the age of sablefish. Canadian Journal of Fisheries and Aquatic Sciences 39: 277-287.

Beamish, R. J., and G. A. McFarlane. 1987. Current trends in age determination methodology. Pages 15-42 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Behnke, R. J. 1980. A systematic review of the genus *Salvelinus*. Pages 441-480 *in* E. K. Balon, editor. Charrs: Salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers, The Hague, Netherlands.

Bendock, T. N. 1979. Inventory and cataloging of Arctic area waters. Alaska Department of Fish and Game. Annual Performance Report 1978-1979, Juneau, Alaska.

Bendock, T. N., and J. M. Burr. 1984. Inventory and cataloging of Arctic area waters. Alaska Department of Fish and Game, Annual Performance Report 1983-1984, Juneau, Alaska.

Bendock, T. N., and J. M. Burr. 1986. Arctic area trout studies. Alaska Department of Fish and Game, Federal aid in fish restoration and anadromous fish studies, Juneau, Alaska.

Bergman, M. A., and H. E. Welch. 1985. Spring meltwater mixing in small arctic lakes. Canadian Journal of Fisheries and Aquatic Sciences 42: 1789-1793.

Berst, A. H., and G. R. Spangler. 1972. Lake Huron: effects of exploitation, introductions, and eutrophication on the salmonid community. Journal of the Fisheries Research Board of Canada 29: 877-887.

Bolger, T., and P. L. Connolly. 1989. The selection of suitable indices for the measurement and analysis of fish condition. Journal of Fish Biology 34: 171-182.

Bond, W. A. 1975. Data on biology of lake whitefish and lake trout from Kaminuriak Lake, District of Keewatin, Northwest Territories. Department of Environment, Fisheries and Marine Service, Data Report Series Number CEN/D-75-4, Winnipeg, Manitoba.

Bulkley, R. V. 1960. Use of branchiostegal rays to determine age of lake trout. Transactions of the American Fisheries Society 89(4): 344-350.

Burr, J. M. 1986. Lake trout stock status: A report to the Alaska Board of Fisheries. Unpublished. Available at Alaska Department of Fish and Game, Division of Sport Fish, 1300 College Road, Fairbanks, Alaska 99701.

Burr, J. M. 1987a. Synopsis and bibliography of lake trout in Alaska. Alaska Department of Fish and Game, Fishery Manuscript Number 5, Juneau, Alaska.

Burr, J. M. 1987b. Stock assessment and biological characteristics of lake trout populations in interior Alaska, 1986. Alaska Department of Fish and Game, Fishery Data Series Number 35, Juneau, Alaska.

Burr, J. M. 1988. Stock assessment and biological characteristics of lake trout populations in interior Alaska, 1987. Alaska Department of Fish and Game. Fishery Data Series Number 66, Juneau, Alaska.

Burr, J. M. 1989. Stock assessment and biological characteristics of lake trout populations in interior Alaska, 1988. Alaska Department of Fish and Game, Fishery Data Series Number 99, Juneau, Alaska.

Cable, L. E. 1956. Validity of age determination from scales and growth of marked Lake Michigan lake trout. U. S. Fish and Wildlife Service, Fishery Bulletin 107, Washington, D. C.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Department of Fisheries and Oceans Canadian Special Publication of Fisheries and Aquatic Sciences 60, Ottawa.

Christie, W. J. 1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. Journal of the Fisheries Research Board of Canada 29: 913-929.

Christie, W. J., J. M. Fraser, and S. J. Nepszy. 1972. Effects of species introductions on salmonid communities in oligotrophic lakes. Journal of the Fisheries Research Board of Canada 29: 969-973.

Colby, P. J., G. R. Spangler, D. A. Hurley, and A. M. McCombie. 1972. Effects of eutrophication on salmonid communities in oligotrophic lakes. Journal of the Fisheries Research Board of Canada 29: 975-986.

Craig, P. C., and J. Wells. 1975. Fisheries investigations in Chandalar River region, northeast Alaska. Pages 67-75 *in* P. C. Craig, editor. Fisheries investigations in a coastal region of the Beaufort Sea. Arctic Gas Biological Report Series 34, Calgary, Alberta.

Cuerrier, J. P. 1951. The use of pectoral fin rays for determining age of sturgeon and other species of fish. The Canadian Fish Culturist 11: 10-18.

DeRoche, S. E. 1969. Observations on the spawning habits and early life of lake trout. Progressive Fish Culturist 31: 109-113.

Donald, D. B., and D. J. Alger. 1986. Stunted lake trout from the Rocky Mountains. Canadian Journal of Fisheries and Aquatic Sciences 43: 608-612.

Dorr, J. A., D. B. O'Connor, N. R. Foster, and D. J. Jude. 1981. Substrate conditions and abundance of lake trout eggs in a traditional spawning area in southeastern Lake Michigan. North American Journal of Fisheries Management 1: 165-172.

Eck, G. W., and L. Wells. 1983. Biology, population structure and estimated forage requirements of lake trout in Lake Michigan. U. S. Fish and Wildlife Service, Technical Paper Number 111, Washington, D. C.

Eschmeyer, P. H. 1955. The reproduction of lake trout in Lake Superior. Transactions of the American Fisheries Society 84: 47-74.

Everhart, W. H., and W. D. Youngs. 1981. Principles of fishery science. Comstock Publishing Associates, Ithaca, New York.

Falk, M. R., D. V. Gillman, and L. W. Dahlke. 1974. Data on the biology of lake trout from Great Bear and Great Slave Lakes, Northwest Territories, 1973. Canada Department of the Environment, Fisheries and Marine Service Data Report Series CEN/D-74-4, Winnipeg, Manitoba.

Hanson, J. A., and R. H. Wickwire. 1967. Fecundity and Maturity of lake trout in Lake Tahoe. California Fish and Game 53: 154-164.

Hartman, W. L. 1972. Lake Erie: effects of exploitation, environmental changes, and new species on the fishery resources. Journal of the Fisheries Research Board of Canada 29: 899-912.

Healey, M. C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. Journal of the Fisheries Research Board of Canada 32: 427-448.

Healey, M. C. 1978a. The dynamics of exploited lake trout populations and implications for management. Journal of Wildlife Management 42: 307-328.

Healey, M. C. 1978b. Fecundity changes in exploited populations of lake whitefish and lake trout. Journal of the Fisheries Research Board of Canada 35: 945-950.

Hollander, M., and D. A. Wolfe. 1973. Nonparametric statistical methods. John Wiley and Sons, New York.

Horler, A., M. E. Jarvis, and R. A. C. Johnston. 1984. Creel census study on Fox, Marsh and Tagish Lakes in the Yukon Territory, 1983. Canada Department of Fisheries and Oceans, Yukon River Basin Study Project 61, Whitehorse, Yukon Territory.

Hubert, W. A. 1983. Passive capture techniques. Pages 95-122 *in* L. A. Nielsen, and D. L. Johnson, editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Johnson, L. 1972. Keller Lake: characteristics of a culturally stressed salmonid community. Journal of the Fisheries Research Board of Canada 29: 731-740.

Johnson, L. 1975a. Physical and chemical characteristics of Great

Bear Lake, Northwest Territories. Journal of the Fisheries Research Board of Canada 32: 1971-1987.

Johnson, L. 1975b. Distribution of fish species in Grear Bear Lake, Northwest Territories, with reference to zooplankton, benthic invertebrates and environmental conditions. Journal of the Fisheries Research Board of Canada 32: 1989-2004.

Johnson, L. 1976. Ecology of arctic populations of lake trout and lake whitefish, Arctic char and associated species in unexploited lakes of the Canadian Northwest Territories. Journal of the Fisheries Research Board of Canada 33: 2459-2488.

Johnson, L. 1980. The Arctic charr. Pages 15-98 *in* E. K. Balon, editor. Charrs: Salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers, The Hague, Netherlands.

Jones, J. R., J. D. LaPerriere, and B. D. Perkins. 1990. Limnology of Walker Lake and comparisons with other lakes in the Brooks Range, Alaska. Verhandlungen Internationale Vereinigung fur Theoritische Ange Wandte Limnologie. 24: *in press*.

Keleher, J. J. 1972. Great Slave Lake: effects of exploitation on the salmonid community. Journal of the Fisheries Research Board of Canada 29: 741-753.

Kennedy, W. A. 1954. Growth, maturity and mortality in the relatively unexploited lake trout of Great Slave Lake. Journal of the Fisheries Research Board of Canada 11: 827-852.

Lawrie, A. H., and J. F. Rahrer. 1972. Lake Superior: effects of exploitaton and introductions on the salmonid community. Journal of the Fisheries Research Board of Canada 29: 765-776.

Loftus, K. H. 1976. Science for Canada's fisheries rehabilitation needs. Journal of the Fisheries Research Board of Canada 33: 1822-1857.

Loftus, K. H., and H. A. Regier. 1972. Introduction to the proceedings of the 1971 symposium on salmonid communities in oligotrophic lakes. Journal of the Fisheries Research Board of Canada 29: 613-616.

Martin, N. V. 1952. A study of the lake trout in two Algonquin Park, Ontario, lakes. Transactions of the American Fisheries Society 81:111-137.

Martin, N. V. 1970. Long-term effects of diet on the biology of the lake trout and the fishery in Lake Opeongo, Ontario. Journal of the Fisheries Research Board of Canada 27:125-146.

Martin, N. V., and F. E. J. Fry. 1972. Lake Opeongo: effects of exploitation and introductions on the salmonid community. Journal of the Fisheries Research Board of Canada 29: 795-805.

Martin, N. V., and C. H. Olver. 1976. The distribution and characteristics of Ontario lake trout lakes. Ontario Ministry of Natural Resources Research Report 97: 1-30.

Martin. N. V., and C. H. Olver. 1980. The lake charr. Pages 205-277 *in* E. K. Balon, editor. Charrs: Salmonid fishes of the genus *Salvelinus*. Dr. W. Junk Publishers, The Hague, Netherlands.

McCart, P., P. Craig, and H. Bain. 1972. Report on fisheries investigations in the Sagavanirtok River and neighboring drainages. Alyeska Pipeline Service Company, Anchorage, Alaska.

McDonald, M. E., and A. E. Hershey. 1989. Size structure of a lake trout population in an arctic lake: influence of angling and implications for fish community structure. Canadian Journal of Aquatic Sciences 46: 2153-2156.

Miller, R. B., and W. A. Kennedy. 1948. Observations on the lake trout of Great Bear Lake. Journal of the Fisheries Research Board of Canada 74: 176-189.

Moshenko, R. W., and D. V. Gillman. 1978. Creel census and biological investigation on lake trout from Great Bear anbd Great Slave Lakes.

Northwest Territories, 1975-76. Canada Department of Fisheries and Environment, Fisheries and Marine Service Report Number 1440, Winnipeg, Manitoba.

Morrow, J. W. 1980. The freshwater fishes of Alaska. Alaska Northwest Publishing Company, Anchorage Alaska.
Neter, J., W. Wasserman, and M. H. Kutner. 1985. Applied linear statistical models. Irwin, Incorporated, Homewood, Illinois.

Odum, E. P. 1971. Fundamentals of ecology. W. B. Saunders Company, Philadelphia.

OMNR (Ontario Ministry of Natural Resources). 1983. The identification of overexploitation. Strategic planning for Ontario fisheries working group number 15. Toronto.

Peck, J. W. 1982. Extended residence of young-of-the-year lake trout in shallow water. Transactions of the American Fisheries Society 111: 775-778.

Power, G. 1978. Fish population structure in Arctic lakes. Journal of the Fisheries Research Board of Canada 35: 53-59.

Rawson, D. S. 1947. Great Slave Lake. Pages 45-68 *in* Northwest Canadian fisheries surveys. Fisheries Research Board of Canada

Bulletin 72. Ottawa.

Rawson, D. S. 1961. The lake trout of Lac la Ronge, Saskatchewan. Journal of the Fisheries Research Board of Canada 18: 423-462.

Reanier, R. E., and P. M. Anderson. 1986. A bathymetric study of nine lakes in the south-central Brooks Range: A report to the National Park Service. Unpublished. Available at Gates of the Arctic National Park and Preserve, P. O. Box 74680, Fairbanks, Alaska 9970.

Regier, H. A., and K. H. Loftus. 1972. Effects of exploitation on salmonid communitites in oligotrophic lakes. Journal of the Fisheries Research Board of Canada 29: 959-968.

Regier, H. A., and G. Power. 1980. Wild trout and a charr watch. Pages 130-134 *in* W. King, editor. Wild Trout Two. Trout Unlimited and Federation of Fly Fishermen, Vienna, Virginia.

Ricker, W. E. 1973. Linear regressions in fishery research. Journal of the Fisheries Research Board of Canada 30: 409-434.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Department of Fisheries and Oceans. Fisheries Research Board of Canada Bulletin 191. Ottawa.

Roguski, E. A., and C. E. Spetz. 1968. Inventory and cataloging of the sport fish and sport fish waters in the Interior of Alaska. Alaska Department of Fish and Game, Dingell-Johnson Annual Report of Progress, 1967-68, Volume 9, Juneau, Alaska.

Rosenberg, A. A., and J. R. Beddington. 1988. Length-based methods of fish stock assessment. Pages 83-103 *in* J. A. Gulland, editor. Fish population dynamics. John Wiley and Sons, New York.

Royce, W. F. 1951. Breeding habits of lake trout in New York. U. S. Fish and Wildlife Service, Fishery Bulletin 52, Washington, D.C.

Royce, W. F. 1984. Introduction to the practice of fishery science. Academic Press, New York.

Russell, R. 1980. A fisheries inventory of waters in the Lake Clark National Monument area. Alaska Department of Fish and Game, Juneau, Alaska.

Ryder, R. A. 1972. The limnology and fishes of oligotrophic glacial lakes in North America (about 1800 A.D.). Journal of the Fisheries Research Board of Canada 29: 617-628.

Ryder, R. A., and L. Johnson. 1972. The future of salmonid communities in North American oligotrophic lakes. Journal of the Fisheries Research Board of Canada 29: 941-949.

Schindler, D. W., H. E. Welch, J. Kalff, G. J. Brunskill, and N. Kritsch. 1974. Physical and chemical limnology of char lakes, Cornwallis Island, 75° north latitude. Journal of the Fisheries Research Board of Canada 31: 585-607.

Scott, W. B., and E. J. Crossman. 1985. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184, Ottawa.

Sharp, D., and D. R. Bernard. 1988. Precision of estimated ages of lake trout from five calcified structures. North American Journal of Fishery Management 8: 367-372.

Sly, P. G., and C. C. Widmer. 1984. Lake trout spawnig habitat in Seneca Lake, New York. Journal of Great Lakes Research 10: 168-189.

Smith, R. L. 1974. Ecology and field biology. Harper and Row, New York.

Smith, T. D. 1988. Stock assessment methods: the first fifty years. Pages 1-33 *in* J. A. Gulland, editor. Fish population dynamics. John Wiley and Sons, New York.

Snyder, D. E. 1983. Fish eggs and larvae. Pages 165-198 *in* L. A. Nielsen, and D. L. Johnson, editors. Fisheries Techniques. American Fisheries Society, Bethesda, Maryland.

Thomasson, K. 1956. Reflections on arctic and alpine lakes. Oikos 7: 56-72.

Trippel, E. A., and F. W. H. Beamish. 1989. Lake trout growth potential predicted from cisco population structure and conductivity. Canadian Journal of Fisheries and Aquatic Sciences 46: 1531-1538.

USDI (United States Department of Interior, National Park Service). 1986. Gates of the Arctic National Park and Preserve-General management plan/land protection plan/wilderness suitability review. Available at Gates of the Arctic National Park and Preserve, P. O. Box 74680. Fairbanks, Alaska 99707.

Van Whye, G. L., and J. W. Peck. 1968. A limnological survey of Paxson and Summit Lakes in interior Alaska. Alaska Department of Fish and Game. Informational Leaflet 12. Juneau. Alaska.

Wagner. W. L. 1982. Lake trout spawning habitat in the Great Lakes. Michigan Department of Natural Resources. Fisheries Research Report Number 1904. Lansing. Michigan.

Weatherley, A. H., and H. S. Gill. 1987. The biology of fish growth. Academic Press, London.

Welch, H. E. 1985. Introduction to limnological research at Saqvaqjuac, north Hudson Bay. Canadian Journal of Fisheries and Aquatic Sciences 42: 494-505.

Welch, H. E., and M. A. Bergmann. 1985a. Water circulation in small arctic lakes in winter. Canadian Journal of Fisheries and Aquatic Sciences 42: 506-520.

Welch, H. E., and M. A. Bergmann. 1985b. Winter respiration of lakes at Saqvaqjuac, north Hudson Bay. Canadian Journal of Fisheries and Aquatic Sciences 42: 521-528.

Wells, L., and A. L. McLain. 1972. Lake Michigan: effects of exploitation, introductions, and eutrophication on the salmonid community. Journal of the Fisheries Research Board of Canada 29: 889-899.

Williams, F. T. 1966. Inventory and cataloging of sport fish and sport fish waters of the Copper River and Prince William Sound drainages, and the upper Susitna River. Alaska Department of Fish and Game. Annual Performance Report, 1965-66. Project F-5-R-7, 7(14-A). Juneau, Alaska.

Wohlschlag, D. E. 1953. Some characteristics of the fish populations in an arctic Alaskan lake. Pages 19-29 *in* I. L. Wiggins, editor. Current Biological Research in the Alaska Arctic. Stanford University Publications, Stanford, California.

Wong, B. 1973. Limnological and biological survey of Hottah Lake, Northwest Territories. Environment Canada Fisheries and Marine Service, Technical Report Number 7, Ottawa.

Yaremchuk, G. C. B. 1986. Results of a nine year study (1972-1980) of the sport fishing exploitation of lake trout on Great Slave and Great Bear lakes, Northwest Territories: the nature of the resource and management options. Department of Fisheries and Oceans, Canadian Technical Report of Fisheries and Aquatic Sciences Number 1436, Winnipeg, Manitoba.

Youngs, W. D., and R. T. Oglesby. 1972. Cayuga Lake: effects of exploitation and introductions on the salmonid community. Journal of the Fisheries Research Board of Canada 29: 787-794.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Incorporated, Englewood Cliffs, New Jersey.

Appendix

Table 13.-The von Bertalanffy equation from least squares regression for lake trout in Walker Lake, 1987 and 1988.

$L_{t+1} = 67.552 + (0.934)(L_t),$

$r = 0.940$

L_∞ = (intercept of L_{t+1} vs. L_t) / (1-slope) =

$67.552 / (1-0.934) = 1{,}023.52 = 1{,}024$ mm;

$K = -\ln$ slope $= -\ln(0.934) = 0.068;$

t_0 = [(intercept of $\ln(L_\infty - L_t)$ vs. t) - $\ln L_\infty$] /

K (slope of ($\ln L_\infty - l_t$) vs. t) =

$(7.053 - 6.930) / 0.055 = 2.2$ years

Table 14.-Frequency by length class (25 mm) for all lake trout captured in Paxson. Summit. and Glacier lakes, 1986-89 (J. M. Burr, Alaska Department of Fish and Game, personal communication).

Length class	Frequency		
	Paxson	Summit	Glacier
100	-	-	1
125	-	10	1
150	-	9	2
175	-	1	2
200	-	-	2
225	-	1	5
250	1	6	35
275	1	6	63
300	-	8	53
325	5	5	52
350	8	7	89
375	38	1	93
400	148	6	126
425	373	13	219
450	462	20	130
475	399	20	47
500	334	56	9
525	315	38	10
550	337	30	4
575	201	13	3
600	102	2	5
625	27	5	2
650	20	1	5
675	17	1	4
700	5	4	3
725	5	-	-
750	6	1	-
775	2	2	-
800	5	1	-
825	2	1	-
850	2	2	-
875	2	1	-
900	2	-	-
925	1	-	-
Total	2,820	271	965

Table 15.-The GM functional regression of the weight-length relation for lake trout in Walker Lake, 1987 and 1988 (from Ricker 1975).

Ordinary regression of log W on log L

$y = b(x) + a$

$\log W = 3.109 (\log L) + (-5.275)$

$(r = 0.984)$

GM functional regression of log W on log L

$y = v(x) + a$

$v = b/r$

$= 3.109 / 0.984$

$= 3.159$

$a = (\text{mean of } \log W) - (v)(\text{mean of } \log L)$

$= (3.12) - (3.159)(2.70)$

$= -5.409$

$\log W = 3.159 (\log L) + (-5.409)$

Table 16.-Conversion factors (CF) from 1988 samples for calculating fresh gonad weight (FG) from preserved gonad weight (PG) for 1987 samples of lake trout in Walker Lake.

	Female		Male	
Length class (mm)	N	Conversion factor	N	Conversion factor
400-499	6	1.531	0	1.353*
500-599	1	1.143	1	1.373
600-699	1	1.318	1	1.333
700-799	1	1.310	-	-
800-899	-	-	0	1.353*

* mean of CF for 500 and 800 male length classes

Conversion factor (CF) calculation for each length class:

FG/PG = CF for an individual fish

Σ(individual CF)/N = length class CF

Table 17.-Percent maturity by length class (25 mm) and sex for lake trout in Walker Lake, 1987 and 1988.

Length (mm)	N	Percent immature female	Percent immature male	Percent mature female	Percent mature male	Percent juvenile
200	1					100
225	1					100
300	6					100
350	2					100
375	2					100
400	2	50		50		
425	15	20	47	13	7	13
450	14	36	36		28	
475	13	15	8	23	54	
500	4	25	25	50		
525	9			11	89	
550	5			20	80	
575	3			33	67	
600	2			50	50	
625	2			50	50	
650	5			60	40	
675	5			20	80	
700	1			100		
750	1			100		
775	1			100		
800	2				100	
Total N	96	12	15	21	37	15

Table 18.-Percent maturity by age and sex for lake trout in Walker Lake, 1987 and 1988.

Age (years)	N	Percent immature female	Percent immature male	Percent mature female	Percent mature male	Percent juvenile
5	1					100
9	2					100
10	3					100
11	5	20	60			20
12	7		43	14	14	29
13	10	20	30		30	20
14	15	40	7	33	13	7
15	11	18	36		46	
16	8	13		37	50	
17	3			100		
18	2			100		
19	2			50	50	
21	5			60	40	
22	2				100	
23	1				100	
25	2			100		
26	1				100	
Total N	80	15	18	25	27	15