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[No.] 111 Biology, Population Structure, and Estimated Forage Requirements of Lake Trout in Lake Michigan

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UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

Contents

Biology, Population Structure, and Estimated Forage Requirements of Lake Trout in Lake Michigan[1]

by

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Abstract

Data collected during successive years (1971–79) of sampling lake trout (*Salvelinus namaycush*) in Lake Michigan were used to develop statistics on lake trout growth, maturity, and mortality, and to quantify seasonal lake trout food and food availability. These statistics were then combined with data on lake trout year-class strengths and age-specific food conversion efficiencies to compute production and forage fish consumption by lake trout in Lake Michigan during the 1979 growing season (i.e., 15 May–1 December). An estimated standing stock of 1,486 metric tons (t) at the beginning of the growing season produced an estimated 1,129 t of fish flesh during the period. The lake trout consumed an estimated 3,037 t of forage fish, to which alewives (*Alosa pseudoharengus*) contributed about 71%, rainbow smelt (*Osmerus mordax*) 18%, and slimy sculpins (*Cottus cognatus*) 11%. Seasonal changes in bathymetric distributions of lake trout with respect to those of forage fish of a suitable size for prey were major determinants of the size and species compositions of fish in the seasonal diet of lake trout.

The lake trout (*Salvelinus namaycush*) was the most valuable commercial species in Lake Michigan from 1890 to the mid-1940's, when it began a rapid decline in abundance that led to its extinction by the mid-1950's (Wells and McLain 1973; Baldwin et al. 1979). Smith (1968) attributed the decline to overfishing and predation by the sea lamprey (*Petromyzon marinus*), which invaded the lake in the 1930's. After control efforts had greatly reduced lamprey abundance (Smith 1968), a rehabilitation program aimed at reestablishing self-sustaining lake trout populations in Lake Michigan was begun in 1965. Under this continuing program, an annual average of 2.3 million lake trout were released in the lake during 1965–79, mostly as yearlings (some as fingerlings). Although the planted fish have provided a sizable recreational fishery, the original objective of the rehabilitation program has not been attained: significant reproduction has not yet occurred.

Before its decline, the lake trout was the dominant predator in the offshore waters of Lake Michigan, although the burbot (*Lota lota*), another piscivorous species, was probably fairly abundant (Wells and McLain 1973). According to Van Oosten and Deason (1938), the food of the native lake trout in the early 1930's consisted mainly of deepwater sculpins (*Myoxocephalus thompsoni*), slimy sculpins (*Cottus cognatus*), and coregonines (*Coregonus* spp.). Although individual species of coregonines eaten by the trout generally were not identified by Van Oosten and Deason, it seems highly probable that most were lake herring (*C. artedii*) and ciscoes (several species of *Coregonus* closely related to *artedii*), as judged by their great abundance at that time in Lake Michigan and also by their prominence in the diet of Lake Superior lake trout (Dryer et al. 1965). Rainbow smelt (*Osmerus mordax*), which were introduced into the lake's watershed in 1912 (Van Oosten 1937), became important in the diet of Lake Michigan lake trout by the early 1940's (Van Oosten 1947). Alewives (*Alosa pseudoharengus*), another exotic forage species, also occupied the lake before the demise of the native lake trout, but probably arrived too late to be of much consequence as food. They were first identified from Lake Michigan in 1949 as they gradually spread through the upper Great Lakes from long-established populations in Lake Ontario.

The forage base in Lake Michigan had changed vastly, however, by the time the lake trout rehabilitation program began there. Lake herring and all species of ciscoes except the bloater (*C. hoyi*) were reduced either to extinction or to low levels of abundance by overfishing and sea lamprey predation (Smith 1968). Alewives, on the other hand,

[1]Contribution 596 of the Great Lakes Fishery Laboratory.

possibly benefiting from an absence of predators and a lack of significant competition from native planktivores (lake herring and ciscoes), became exceedingly abundant (Brown 1972). Since the 1960's, the alewife generally has been the overwhelmingly dominant prey species (Hatch et al. 1981; E. H. Brown, Jr., unpublished manuscript), although its abundance has fluctuated markedly. In 1967, alewives suffered an enormous die-off, presumably because they had exceeded Lake Michigan's carrying capacity for the species (Brown 1972). During the die-off, thousands of tons of dead alewives accumulated along beaches, creating a monumental nuisance (Brown 1972). Millions of dollars were spent to remove the decaying fish from beaches, and more millions in expected tourist dollars were lost by the lake's resort communities (Tody 1979). Alewife populations have since fluctuated at more moderate levels of abundance (Hatch et al. 1981; E. H. Brown, Jr., unpublished manuscript).

A desire to control the alewife and provide sport fishing opportunities led State agencies, pioneered by the State of Michigan, to plant large numbers of piscivorous salmonids (aside from lake trout) in Lake Michigan. Stocking of coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) began in 1966 and 1967, respectively. Demands by the sport fishery grew, and plantings of Pacific salmon and other salmonines, primarily steelhead trout (*Salmo gairdneri*) and brown trout (*S. trutta*), steadily increased (Fig. 1). About 14 million trout and salmon were planted in 1978. Predation by the growing salmonine stocks produced by these large plantings may have contributed to the failure of alewives to regain their former level of overabundance.

Although predation does not yet appear to have had a deleterious effect on alewives and other prey species, there is a distinct possibility that it might if salmonine stocking continues to increase. If predation does have a serious effect, a protracted loss of valuable fish resources could result. Increases in stocking rates of salmon and trout should thus be guided by a knowledge of the capacity of prey populations to absorb increased predation. As a beginning toward acquiring this knowledge, the Great Lakes Fishery Laboratory is collecting data on stock size, recruitment, and annual production of Lake Michigan's major forage fish species, placing special emphasis on alewives. When combined with information on amounts consumed by predators, these data should be useful in estimating the number of predators that can be sustained. However, obtaining meaningful estimates of annual consumption by predators will require a series of studies that characterize and quantify predation by each of the five major species of piscivorous salmonids now present in Lake Michigan. Because of physiological and behavioral differences, each species is probably unique with respect to the way in which it uses, and thus affects, the forage base.

In this paper we deal specifically with the lake trout—its vital statistics, food, and seasonal interactions with forage fish populations in Lake Michigan. We (1) characterize lake

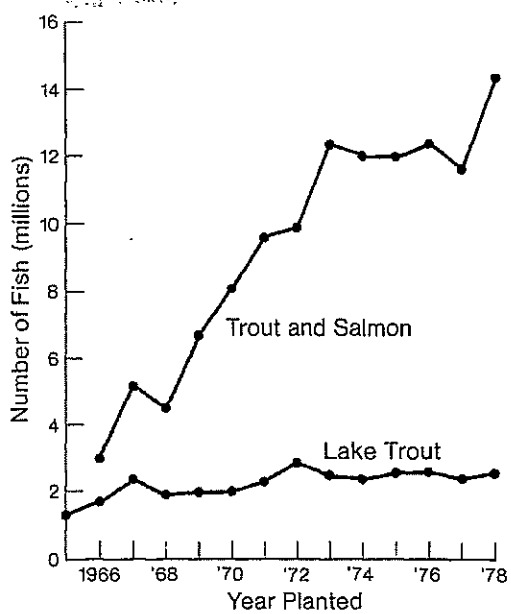

Fig. 1. Numbers of lake trout and total numbers of trout and salmon planted in Lake Michigan each year, 1965–78.

trout growth, maturity, and mortality; (2) estimate stock size and annual production for lake trout in 1979; (3) describe seasonal and bathymetric distributions of lake trout and forage fish species; (4) examine the effects of seasonal changes in food availability on the diet of lake trout; and (5) estimate the degree of use of prey fish stocks by lake trout populations at the levels existing in Lake Michigan during the late 1970's.

Field and Laboratory Methods

To obtain predator and prey data for this study, we sampled lake trout with gill nets and forage fish with trawls from the U.S. Fish and Wildlife Service R/V *Cisco*. The gill nets were 1.83 m high and were fished in standard gangs made up of equal amounts of eight mesh sizes (stretched measure) ranging from 6.35 to 15.27 cm by 1.27-cm increments. A standard trawl had a headrope of 11.9 m and cod-end mesh of 1.27 cm. All nets were fished on bottom. The gill nets were fished in southeastern Lake Michigan off Saugatuck, Michigan, each fall (late September or early October) during 1971–79, and in spring (mid-May) and summer (early August) in 1976. They were fished in the west-central part of the lake off Port Washington, Wisconsin, each fall during 1977–79, and in spring and summer 1977. The trawls were used in all sampling periods at Saugatuck in 1976 and Port Washington in 1977. For the purposes of this paper, we assumed that data collected off Saugatuck and Port Washington were representative of physical conditions and of lake trout and forage fish populations in the east and west halves, respectively, of Lake Michigan proper.

During 1971–75, all gill nets, each gang of which contained 91.3 m of each mesh size, were set along the contour where bottom temperature was about 10° C, the preferred temperature of lake trout (Martin 1952). When bottom temperatures were lower than 10° C at all depths (an occasional situation when hypolimnial water upwelled into shallow parts of the study areas), the nets were set where the water was warmest. Nets were always lifted the day after they were set. An average of nine gangs, or 6,588 linear meters, of gill nets were fished each fall during the 5-year period.

Gill net sampling procedures were altered considerably after 1975. From 1976 to the end of the study in 1979, the amount of each mesh size in a gang was reduced to 30.5 m to facilitate the handling of more gangs each day so that sampling could be conducted at a greater number of depths. In each sampling period, gill nets were routinely fished along four or more parallel transects. The transects were separated by a 1.6-km interval and each encompassed the primary depth range of lake trout at that time (determined by preliminary gillnetting). A maximum of eight and a minimum of five gangs, spaced at about equal depth intervals, were fished along each transect. The shallowest sets were usually at depths of either 5.5 m (the minimum for safe vessel operation) or 9.2 m, and the deepest at 55 or 64 m. During the seasonal studies (i.e., Saugatuck 1976 and Port Washington 1977, when the nets were set in spring, summer, and fall), nets set at the same depths within successive transects were fished alternately along or across the contour to examine the effects of gill net orientation on lake trout catches. In 1978 and 1979, however, all nets were fished along the contour because changes in gill net orientation produced no significant differences in the number or size of lake trout caught during the seasonal studies. All nets fished in the surveys were set during daytime and lifted after about 24 h.

Field processing of lake trout in the gill net samples included determination of total length (mm), weight (g), sex, and stage of maturation; examination for clipped fins (as an aid in aging the fish); and, during the seasonal studies, the removal of stomachs for food analysis. Each planting of lake trout had been marked with distinguishing finclips (one or more fins removed), mainly to facilitate the aging of fish that were later captured. However, because a particular finclip was generally repeated every 3 to 5 years, nearly every mark was borne by more than one age group in the population. Growth rates of individual fish varied widely, and size ranges of older age groups overlapped so widely that we were often unable to age the larger fish, even by considering both finclip and length. We therefore removed scales from all lake trout 600 mm long or longer and aged these fish by the scale method.

Trawls used in the forage fish surveys were towed at a series of depths at the beginning of each sampling period during the seasonal studies and occasionally again near the end. The tows, which usually lasted 10 min, were made along the contour at 4.6-m depth intervals from 5.5 to 36.6 m, and at 9.2-m intervals from 36.6 to 91.5 m. Fish of each species in the trawl samples were counted and weighed (total weight). Lengths were recorded for subsamples of alewives, smelt, and slimy sculpins.

The contents of lake trout stomachs were examined in the field. When the state of digestion permitted, fish in the stomachs were identified, counted, and measured (total length). Weights of the individual forage fish found in the stomachs were later estimated on the basis of weight-length regressions computed for each species from trawl collections. Fish in an advanced stage of digestion were recorded as unidentified fish remains. A notation was made of the presence in the stomachs of invertebrates, identified to the lowest taxon practicable.

Experiments on lake trout food conversion efficiencies were conducted at the Great Lakes Fishery Laboratory. In these experiments, lake trout of three age categories (II, IV, and mature fish VII and older) were held in the laboratory from June 1970 to June 1971 at a temperature of 10° C and fed slimy sculpins ad libitum. The experiments were run in replicate (i.e., two groups of fish for each age class), and each fish was identified by a unique brand to enable the measurement of individual growth rates. The fish were weighed twice monthly, and mean growth efficiencies for each age group were calculated at the end of the study.

The results of the food conversion experiments served as a basis for estimating consumption of forage fish by Lake Michigan lake trout. However, in consideration of the single-species diet and constant temperature used in these experiments, we made estimates only for age groups of lake trout that were primarily piscivorous and only for the portion of the year when water at or near 10° C was available to them, i.e., a 200-day period extending from 15 May to 1 December, as indicated by mean surface temperature of Lake Michigan from May to November (Carr et al. 1973). This period should also approximate the growing season for lake trout in Lake Michigan. The biomass of forage fish consumed was estimated by calculating production, or flesh elaborated, during this period by each piscivorous age class of trout and dividing by the corresponding age-specific growth efficiency. Biomasses of principal forage species represented in the total prey biomass consumed were then estimated from their relative proportions by weight in the diet of trout from each sampling location during the spring, summer, and fall surveys. In making these estimates, we assumed that all forage species were of equal value by weight as food — an assumption which, at least on the basis of energy content, should be reasonable (Rottiers and Tucker 1982) — and that the numbers of lake trout on the east and west sides of Lake Michigan were equal.

Vital Statistics of Lake Trout

Growth

We examined possible differences in the growth of lake trout related to age and season when the fish were planted, sex, genetic strain, geographical area, and year. Only fish planted in spring as yearlings were used in the growth calculations; those planted in fall as young of the year were not considered because many were reared in the hatchery under special conditions (for experimental purposes) and their growth in earlier years differed somewhat from that of fish planted in spring. In all growth analyses, data for both sexes were pooled because growth rate of males and females did not differ significantly.

Although at least five genetic strains of lake trout were planted in Lake Michigan in 1965–79, and each may have a unique growth pattern, fish of the eastern Lake Superior and Green Lake strains (most planted in spring as yearlings) accounted for over 98% of the total stocked (Brown et al. 1981). Therefore, descriptions and evaluations of growth are focused entirely on these two strains. Although no Green Lake fish were planted after 1977, both strains were represented in every year class planted in Lake Michigan in 1966–77. Comparisons of their rates of growth are difficult, however, because plants of the two strains before 1970 were usually spaced so far apart geographically that samples taken at a specific site, such as Saugatuck, failed to include one strain or the other in sufficient numbers to enable statistically valid comparisons. Also, beginning with the 1970 plant, the Green Lake and Lake Superior strains were not assigned distinguishing finclips (although the three less frequently planted strains were). The only useful data from our study for comparing growth of the two strains involved the 1968 year class. Green Lake fish of this year class were stocked in the extreme southern part of the lake and Lake Superior fish farther north, but both were taken in considerable numbers at Saugatuck during 1972–74.

Comparisons of growth were limited to age groups III to V (Table 1) because too few older Green Lake fish of the 1968 year class were captured off Saugatuck. At age IV, fish of the Lake Superior strain were significantly ($P < 0.05$) larger than those of the Green Lake strain, but differences in length and weight were not significant for ages III and V. Similar inconsistencies were observed by Rybicki and Keller (1978) in comparisons of sizes of the two strains at ages VI–VIII of the 1965 year class and ages V–VIII of the 1967 year class, in series of samples taken near Ludington and Port Sheldon, Michigan. Fish of the two strains did not differ significantly in length and weight at capture ($P < 0.05$) at any age for the 1965 year class nor at ages V and VII for the 1967 year class; however, for fish of the 1967 year class, those of the Lake Superior strain were significantly larger and heavier at age VI and those of the Green Lake strain were significantly longer (though not heavier) at age VIII. The data of Rybicki and Keller (1978) and those of the present study collectively suggest that growth rates of the two strains were generally similar. Therefore, the following comparisons of the growth of lake trout from different geographic areas and of different year classes at specific sampling locations should not be seriously affected by the varying but largely unknown proportions of fish of each strain in the samples.

Table 1. *Comparisons at different ages of mean lengths and weights of lake trout of Green Lake and Lake Superior strains of the 1968 year class. All fish were caught in standard gill net sets off Saugatuck in fall, 1972–74. Significant differences between means ($P < 0.05$) are indicated by asterisks.*

Strain and age	Length (mm)	Weight (g)	Number of fish
Green Lake			
III	472	1,075	10
IV	549*	1,546*	9
V	629	2,475	10
Lake Superior			
III	480	1,050	87
IV	599*	2,141*	64
V	637	2,496	31

On the basis of the fall sampling off Saugatuck, growth rates of lake trout of successive year classes generally declined after the mid to late 1960's (Table 2). This trend was temporarily reversed in 1975 for age groups III–V (Fig. 2). However, fish of these age groups showed the greatest decreases in average size over the period 1971–79. Age III fish of the 1968 year class averaged 91 mm longer and more than 500 g heavier than those of the 1975 year class (Table 2), and the differences were even more pronounced for age groups IV and V: age IV fish of the 1967 year class were 130 mm longer and over 1 kg heavier than those of the 1974 year class, and age V fish of the 1966 year class were 100 mm longer and 1.4 kg heavier than those of the 1974 year class. Although their data were inconclusive for age group III, Rybicki and Keller (1978) reported similar changes in growth rates for lake trout of ages IV and V that were collected in northern and northeastern Lake Michigan. Their data, which covered the period 1969 to 1975, showed fish of age groups IV and V declining in size from 1969 to 1974, and then recovering strongly in 1975. Thus, at least through 1974, the decline in growth of young lake trout in Lake Michigan appeared to be lakewide.

In each year during 1977–79, fish of a given age group from Port Washington were nearly always longer and heavier than their counterparts from Saugatuck (Table 3). (Minor exceptions were fish of ages VI and IX in 1977 and X in 1978.) The statistical significance ($P < 0.05$) of the size advantage of Port Washington over Saugatuck fish for most ages in 1978, and the consistency of the advantage

Table 2. *Mean lengths (mm) and (in italics) weights (g) at capture of spring-stocked lake trout of different age groups and year classes collected with standard gill nets off Saugatuck during each fall, 1971–79. Numbers of fish are shown in parentheses.*

Year class	Age											
	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
1976	306	416										
	221	*659*										
	(3)	(24)										
1975	308	389	479									
	255	*536*	*1,036*									
	(11)	(70)	(115)									
1974	324	402	470	581								
	288	*560*	*922*	*1,890*								
	(41)	(23)	(63)	(36)								
1973	324	414	502	613	662							
	267	*645*	*1,165*	*2,233*	*2,755*							
	(32)	(92)	(33)	(65)	(111)							
1972	356	461	538	641	674	701						
	397	*864*	*1,538*	*2,579*	*2,973*	*3,387*						
	(27)	(54)	(65)	(94)	(185)	(163)						
1971	345	453	599	634	689	695	709					
	341	*830*	*2,187*	*2,535*	*3,155*	*3,236*	*3,360*					
	(97)	(28)	(15)	(51)	(28)	(34)	(23)					
1970	322	430	547	665	693	713	727	737				
	274	*675*	*1,639*	*2,784*	*3,274*	*3,497*	*3,764*	*3,936*				
	(87)	(109)	(18)	(72)	(134)	(39)	(46)	(64)				
1969	344	443	548	618	686	716	731	752	770			
	362	*787*	*1,501*	*2,402*	*3,125*	*3,634*	*3,847*	*4,235*	*4,338*			
	(45)	(68)	(67)	(16)	(168)	(112)	(50)	(21)	(17)			
1968		480	599	637	705	732	741	766	779	803		
		1,050	*2,141*	*2,496*	*3,527*	*3,988*	*4,075*	*4,283*	*4,523*	*4,939*		
		(87)	(64)	(31)	(7)	(87)	(59)	(15)	(9)	(26)		
1967			601	657	667	698	718	729	755	781	772	
			2,199	*2,789*	*2,930*	*3,514*	*3,715*	*3,979*	*4,202*	*4,735*	*4,338*	
			(113)	(232)	(172)	(50)	(133)	(76)	(20)	(7)	(4)	
1966				681	720	743	754	776	764	770	823	830
				3,299	*3,792*	*4,226*	*4,383*	*4,831*	*4,486*	*4,373*	*5,518*	*5,300*
				(318)	(154)	(144)	(37)	(46)	(20)	(6)	(7)	(1)

(though not usually significant) in the other years, clearly suggests that lake trout on the west side of Lake Michigan grew faster than those on the east side.

For use in estimating lake trout production, general expressions of length at age (Von Bertalanffy growth equation) and of weight at length were developed from mean empirical lengths and weights at age of each of the 14 cohorts of lake trout represented in the population at the start of the 1979 growing season. The Von Bertalanffy growth equation was $L_t = 913.31\ (1 - \exp[-0.1863(t - 0.1676)])$, and the weight-length relation was $\log W = 3.1785 \log L - 5.5259$, where L = total length in millimeters, W = weight in grams, and t = age in years. Length and weight at age I were taken from hatchery records provided by the Great Lakes Fishery Commission, in which mean values were listed for the 1978 year class at time of planting in spring 1979. Values for ages II–V were established from a series of trawl tows conducted specifically for this purpose in May 1979, with an experimental high-rise trawl that measured 18.3 m across the headrope. However, because the adults (primarily age VI and older) characteristically occupy the warmer surface waters near shore in spring (as described later), neither bottom-set gill nets nor the high-rise trawl were fully effective in catching them. Consequently, instead of sampling the adults before the 1979 growing season, we based the mean lengths and weights at age for these older age groups on the sizes they had attained near the end of their previous growing season, as determined by gill net samples taken in fall 1978. Inasmuch as all the samples mentioned were collected off Saugatuck, mean lengths and weights at age for lake trout lakewide may have been underestimated because of the trend toward a faster growth rate for lake trout on the west than on the east side of Lake Michigan.

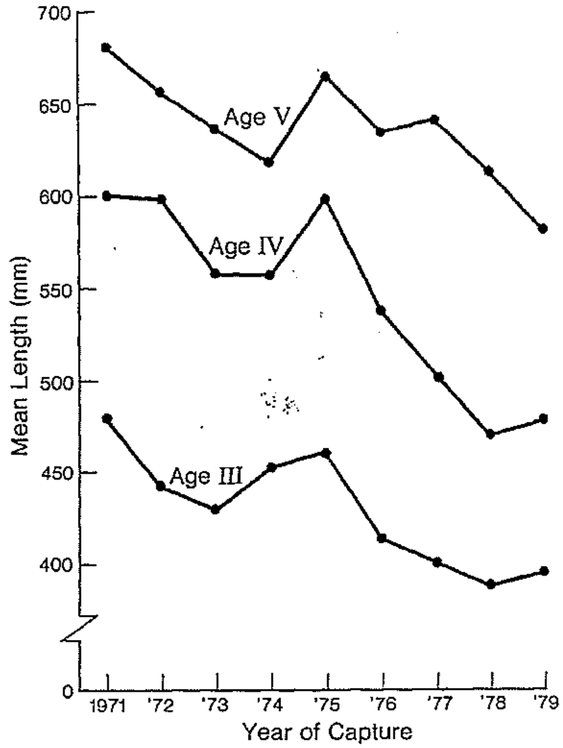

Fig. 2. Mean total length at capture of lake trout of ages III, IV, and V collected in standard gill nets off Saugatuck each fall, 1971–79.

Maturity

Lake trout were judged to be mature if the appearance of their sex organs at time of capture indicated that they would have spawned during the upcoming spawning season. However, determination of size and age at maturity was based only on samples taken in late September and early October off Saugatuck and Port Washington. Judgment as to whether these fish (collected about a month before the spawning season) were mature was much more certain than for fish collected in spring and summer. Minimum total length at maturity was about 450 mm for males and 550 mm for females. Most males longer than 575 mm and most females longer than 600 mm were mature. Minimum ages at maturity were III for males and IV for females.

Fish planted in the 1960's generally reached maturity at an earlier age than did those stocked in later years. For example, 99% of the males and 97% of the females of the fast-growing 1966 year class were mature at age V, compared with 93% of the males and 40% of the females in the much slower-growing 1973 year class. As a further example, although 79% of the males and 26% of the females of the 1967 year class were mature at age IV, none of either sex in the slower-growing 1974 year class were mature at that age. On the basis of assigned values of 2 for mature and 1 for immature, maturity was more strongly correlated with length (r = 0.824 for males and 0.827 for females) than with age (r = 0.663 for males and 0.753 for females). Thus, as noted by Healey (1978), "fish which mature late do not necessarily mature at a different size than fish which mature early."

Table 3. *Mean lengths (mm) and (in italics) weights (g) at capture of lake trout collected with standard gill nets in fall 1977–79 off Saugatuck and Port Washington. Significant differences ($P < 0.05$) in mean lengths or weights for the two areas for a given age and sampling year are indicated by asterisks.*

	1977		1978		1979	
Age	Saugatuck	Port Washington	Saugatuck	Port Washington	Saugatuck	Port Washington
III	402	438*	389	435*	416	418
	560	*717**	*536*	*713**	*659*	*658*
IV	503	534*	470	515*	479	501*
	1,165	*1,378*	*922*	*1,208**	*1,036*	*1,145*
V	641	649	613	638*	581	596
	2,579	*2,610*	*2,233*	*2,433**	*1,890*	*2,006*
VI	689	687	674	690*	662	680*
	3,155	*3,066*	*2,973*	*3,178**	*2,755*	*3,130**
VII	713	742	695	720*	701	706
	3,497	*3,789*	*3,236*	*3,517**	*3,387*	*3,483*
VIII	731	741	727	762*	709	736
	3,847	*3,854*	*3,764*	*4,252**	*3,360*	*4,077**
IX	766	759	752	770	737	746
	4,283	*3,706*	*4,235*	*4,403*	*3,936*	*4,255*
X	—	—	779	776	770	774
	—	—	*4,523*	*4,621*	*4,338*	*4,639*

Table 4. *Numbers of lake trout of different ages taken per 305 linear meters of standard gill nets fished off Saugatuck each fall, 1976–78.*

Year	II	III	IV	V	VI	VII	VIII	IX	X	XI
1976	2.77	4.69	3.28	5.31	5.47	4.65	2.54	2.50	0.74	
1977	0.77	2.74	2.50	8.39	5.65	2.50	3.10	0.83	0.89	0.24
1978	0.12	4.12	4.76	2.72	9.88	2.32	1.95	1.14	0.73	0.93

Mortality

Mortality rates for the adult portion of the stock were estimated from the fall gill net samples collected off Saugatuck during 1976–78. Although lake trout taken at this location in the fall were not fully vulnerable to the standard gangs of gill nets until age VI (Table 4), the size distributions in catches indicated that the nets sampled adult lake trout (primarily age VI and older) representatively with respect to age, and thus provided data from which estimates of adult mortality could be derived. Length frequencies of lake trout 600 mm long or longer (i.e., adults) were not strongly skewed in the catches of any of the mesh sizes (Fig. 3) and in the aggregate appeared to be normally distributed across the adult size range. Furthermore, comparisons of mean lengths of adults captured in each mesh size off Saugatuck during fall revealed no significant differences in within-year means at the 95% confidence level (as judged by analysis of variance). Mortality rates could not be determined for adult lake trout on the west side of the lake, however, because our catches off Port Washington were highly variable between years and often obviously underrepresented certain age groups in the adult population. This variability was probably related to annual changes in the frequency and duration of upwellings of cold water, which are much more common on the west shore than on the east.

We calculated weighted mean mortality rates for adult fish on the east side of Lake Michigan for the periods 1976–77 and 1977–78, using the following formula:

$$A = 1 - \frac{X_1 + \ldots + X_n}{X_0 + \ldots + X_{n-1}}$$

where A = annual mortality rate; $X_1 + \ldots + X_n$ = catches per unit of gill net effort for age groups VII through XI; and $X_0 + \ldots + X_{n-1}$ = catches per unit of effort for age groups VI through X in the previous year. Estimated annual mortality rates for the adult portion of the stock were 0.52 during 1976–77 and 0.46 during 1977–78, averaging 0.49 for the two years combined. The resulting mean annual survival rate of 0.51 falls about midway within the range of 0.40 to 0.60 reported by Rybicki and Keller (1978) for age V and older lake trout from several areas of northern and northeastern Lake Michigan.

Because immature lake trout were not completely vulnerable to the gill nets (Table 4), estimates of the mortality rates of these young fish had to be derived from trawl catches. On the basis of data from intensive sampling with the 11.9-m trawl (Great Lakes Fishery Laboratory, unpublished data) off Grand Haven, Michigan, in 1972–74, we estimated a mean annual mortality rate of 0.57 for age II lake trout in southeastern Lake Michigan. This estimate was then combined with that of 0.37 for lake trout of the same age in northern Lake Michigan (Rybicki and Keller 1978) to produce an estimated lakewide annual mor-

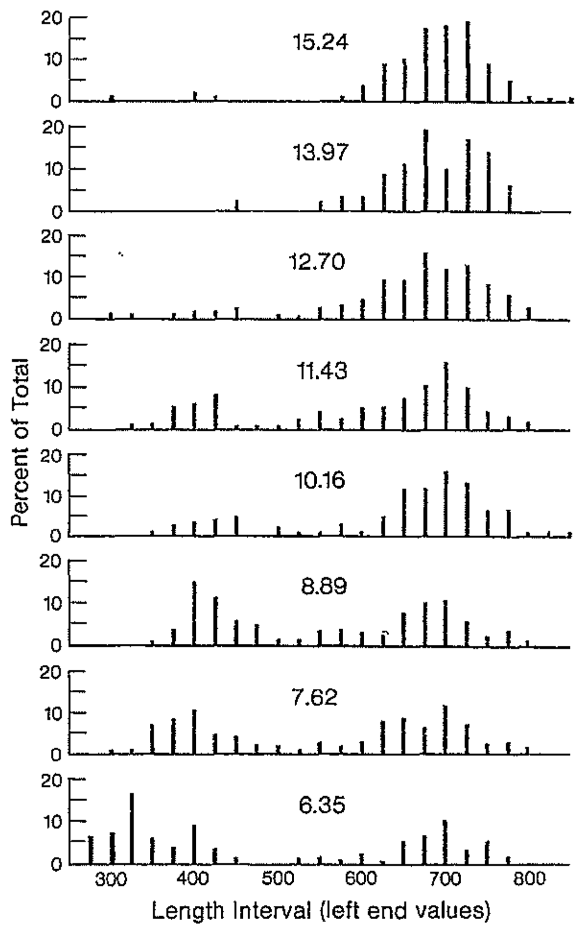

Fig. 3. Length–frequency distributions (by 25-mm intervals, total length) of lake trout caught in standard gill nets by mesh size (centimeters, stretched measure; number near center of each panel) during fall 1976 off Saugatuck.

Table 5. *Estimated biomass of forage fish consumed and production by each age class of lake trout in Lake Michigan during the 1979 growing season (15 May–1 December), and statistics used in making computations. G = instantaneous growth rate. See text for details.*

Age	Biomass of age class (t): Start of year	Start of growing season	End of growing season	Mean during growing season	G	Production (t)	Food conversion efficiency	Forage consumed (t)
I[a]	–	41.0	264.4	152.8	2.222	339.5		
II[b]	200.1	157.4	251.1[c]	204.3	0.716	146.3		
			366.4	308.8	0.487	150.4	0.265	567.5
III	288.8	227.2	318.2	272.7	0.695	189.5	0.265	715.1
IV	333.5	262.3	296.3	279.3	0.480	134.1	0.204	657.4
V	275.2	275.2	203.1	239.2	0.350	83.7	0.204	410.2
VI	188.8	188.8	127.8	158.3	0.264	41.8	0.124	337.1
VII	133.8	133.8	85.3	109.6	0.203	22.2	0.124	179.0
VIII	99.5	99.5	60.7	80.1	0.160	12.8	0.124	103.2
IX	48.5	48.5	28.6	38.6	0.127	4.9	0.124	39.5
X	24.2	24.2	13.9	19.1	0.101	1.9	0.124	15.3
XI	14.1	14.1	8.0	11.1	0.082	0.9	0.124	7.3
XII	7.4	7.4	4.1	5.8	0.066	0.4	0.124	3.2
XIII	5.1	5.1	2.8	4.0	0.054	0.2	0.124	1.6
XIV	1.8	1.8	1.0	1.4	0.044	0.1	0.124	0.8
Totals	1,620.8	1,486.3	1,780.8			1,128.7		3,037.2

[a]Arbitrarily assigned a 15 May planting date for computing production.
[b]Statistics associated with a diet of primarily invertebrates (15 May–30 September; upper number of each pair) and fish (1 October to 1 December; lower number).
[c]Not included in total.

tality rate of 0.47 for age II fish. Data were not available to support mortality estimates for immature fish of other age groups.

Stock Size and Annual Production in 1979

We estimated the number of lake trout in Lake Michigan at the start of the 1979 calendar year by predicting the number of survivors remaining from each year class planted in the lake from 1966 to 1978. (Mortality of fish planted in 1965—the beginning of the stocking program in Lake Michigan—was high and fish were virtually eliminated from the population by age IX [Rybicki and Keller 1978]. None were collected during our study and we concluded that none remained.) In making the predictions, we used the relation $N_t = N_0 e^{-Zt}$, for each year class, where N_t = number of survivors at beginning of 1979, N_0 = number initially stocked, Z = instantaneous mortality rate, and t = number of years spent in the lake.

An overall annual mortality rate of 0.48 ($Z = 0.6539$), the average of the very similar rates estimated for the age II trout (0.47) and adults (0.49), was applied across all ages in predicting survivors. The projected numbers of survivors at each age were then multiplied by the predicted mean weights at age to obtain the respective biomasses (Table 5). These calculations over all year classes combined placed the estimated total biomass of the standing stock as of 1 January 1979 at 1,621 metric tons (t).

Except as noted below, the following mathematical expressions, taken primarily from Ricker (1975) and Chapman (1968), were applied to each year class of lake trout to estimate cohort production during the 1979 growing season: $P = G\bar{B}$, where P = the total amount of fish flesh produced during the growing season (i.e., 15 May to 1 December), G = age specific instantaneous growth rate, and $\bar{B} = (B_1 + B_2)/2 = (B_1[1 + \exp(G - Z^*)])/2$, where B_1, B_2 = cohort biomass at the beginning and end of the growing season, respectively, and Z^* = fraction of Z that occurs during the growing season.

In estimating production, we assumed constant growth rates through the growing season for all ages except II. Growth of age II lake trout increased markedly in the fall (Fig. 4), reflecting a change from a primarily invertebrate diet to one consisting mainly of young-of-the-year alewives that become available at this time of year. To account for this dietary switch and resultant change in growth, we estimated production by age II lake trout separately for the periods of 15 May to 1 October and 1 October to 1 December.

The production estimates were also based on the assumption that mortality of lake trout of ages I–IV was spread evenly throughout the year, and that mortality among fish of the older age groups was confined to the growing sea-

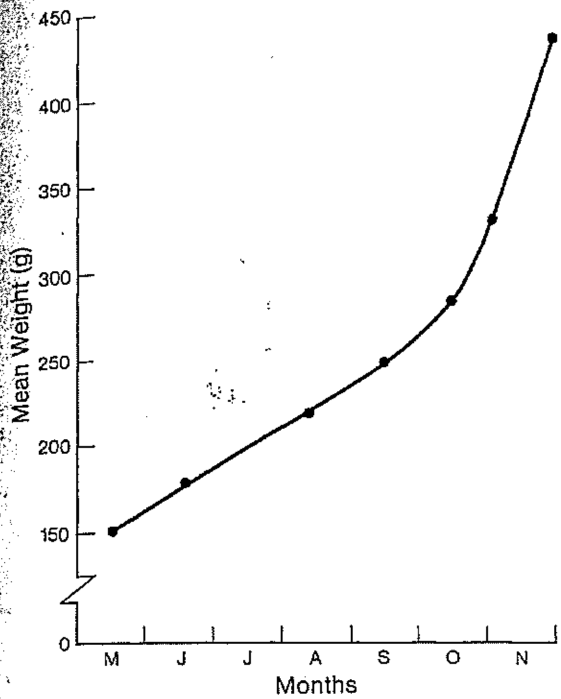

Fig. 4. Seasonal growth in weight of age II lake trout in Lake Michigan, based on trawl catches off Grand Haven, Michigan, during 1974. Curve was drawn by inspection.

son. By age V, lake trout were fully vulnerable to the large Lake Michigan sport fishery (R. Poff and M. Patriarche, personal communications) and had reached a size that is highly susceptible to sea lamprey predation (Pycha 1980). Mortality of fish of the older age groups that results from these principal sources is probably most intense during the 15 May to 1 December interval that we have accepted as representing the growing season (Rybicki and Keller 1978; Kitchell and Breck 1980).

Total lake trout production estimated for the 1979 growing season in Lake Michigan was about 1,129 t (Table 5). The combined effects of high mortality and rapid growth concentrated most of this production within the younger age groups (Fig. 5). Fish of ages I–V, for example, accounted for 85% of the biomass produced by the entire population.

Seasonal Changes in Bathymetric Distribution

Forage Fish

The most comprehensive study of seasonal depth distributions of forage fish in Lake Michigan (we refer here only to the species that are significant in the diet of lake trout—i.e., alewives, smelt, and slimy sculpins) was conducted in the vicinity of Saugatuck in 1964 by Wells (1968). He found that young-of-the-year alewives were highly pelagic in summer, occupying epilimnial waters, but that by fall large numbers (though probably not all) were on bottom, at depths less than 55 m. Yearlings were essentially pelagic, but were occasionally on bottom in all seasons. Older alewives occupied depths greater than 64 m in winter; they began a gradual shoreward movement in late winter or early spring, and most were concentrated near shore during their spawning season in June and July. After spawning, these older fish moved to greater depths as the seasons progressed. Young-of-the-year smelt were pelagic until fall, when many moved to the bottom, where they were most common at depths of 18 to 27 m. Some yearling smelt were pelagic, and some were on bottom. Older smelt were distributed on bottom from 18 to 31 m in midwinter, but they began to move shoreward in late winter and were in extremely shallow water for spawning by mid-April. In summer and fall they were mainly at depths of 9 to 37 m. The yearling smelt on bottom were generally at somewhat shallower depths than were the older fish, except during the spawning season. Slimy sculpins were abundant at depths of 18 to 64 m in winter and early spring, but began a

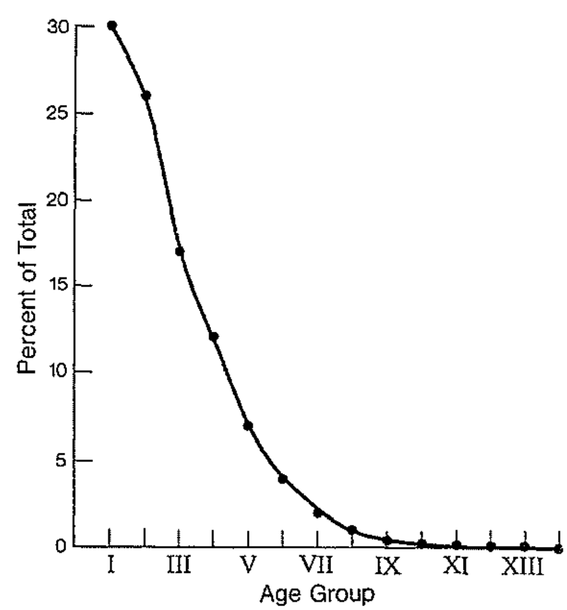

Fig. 5. Percent contribution of each age group to estimated total lake trout production in Lake Michigan in 1979.

Table 6. *Mean numbers of young-of-the-year (YOY), yearling, and adult (age II and older) alewives and rainbow smelt, and all ages of slimy sculpins, taken per 10-min trawl tow at different depth intervals off Saugatuck (1976) and Port Washington (1977), by season.*

Locality, season, and depth (m)	Species, and age category						
	Alewife			Smelt			Slimy sculpin
	YOY	Yearling	Adult	YOY	Yearling	Adult	All ages
Saugatuck							
Spring							
<18		48	490		10	8	0
18<36		65	176		10	8	1
36<55		269	658		0	5	1
55<73		44	327		0	0	33
73≤92		2	36		0	0	112
Summer							
<18		407	316		66	40	0
18<36		17	250		2	6	0
36<55		0	350		1	10	6
55<73		0	147		0	0.3	243
73≤92		0	12		0	0	92
Fall							
<18	545	0	0	3	0	0	0
18<36	1,198	0	0	1	3	9	0
36<55	55	119	61	59	46	143	0
55<73	0	160	233	0	1	34	96
73≤92	0	7	582	0	0	0	40
Port Washington[a]							
Spring							
18<36		0.3	3		0	0	0
36<55		373	1,001		42	335	0
55<73		282	871		4	68	14
73≤92		58	322		1	2	17
Summer							
18<36		49	140		7	39	0
36<55		25	16		1	21	4
55<73		26	71		0	0	11
73≤92		15	53		0	0	19
Fall							
18<36	0	0	0	0	0	0	0
36<55	1,610	2	3	9	31	2	0
55<73	166	32	274	4	30	220	5
73≤92	7	9	375	0.3	0.3	6	49

[a]Obstructions on bottom prevented trawling at depths less than 18 m.

gradual movement away from shore as nearshore bottom waters warmed and by late fall most were concentrated at depths of 43 to 73 m.

The seasonal depth distributions of forage fish in southeastern Lake Michigan as determined in the present study were similar to those described by Wells (1968) and summarized above, except that slimy sculpins showed a less definite spring-to-fall movement into deeper water (Table 6). Our data indicated that alewives and smelt tended to occupy greater depths on the west than on the east side of the lake, although for each of these species seasonal movements were similar on the two sides. The spring distribution of alewives off Port Washington was not determined accurately because bottom obstructions in the sampling area prevented trawling in water shallower than about 18 m. Visual observation indicated that large, dense schools of alewives, mostly yearlings, were in water shallower than 18 m during the spring sampling period. At the time, a moderate die-off of alewives, also mainly yearlings, was occurring along most of Lake Michigan's western shore. Although our data did not indicate a strong spring-to-fall movement of sculpins into deeper water on either side of the lake, the spring catches may have underrepresented the shallow-water population, and a movement into deeper water may have occurred as the seasons progressed. All trawl surveys in previous years (Great Lakes Fishery Laboratory, unpublished data) have indicated such seasonal movements of slimy sculpins.

Lake Trout

The depth distribution of lake trout changed with life stage. For fish of age groups susceptible to our experimental gill nets (II and older), the smaller (and younger) lake trout were generally at greater depths than larger ones, regardless of sampling location or season of year (Fig. 6). Dryer and King (1968) also reported a decline in mean length with increasing depth for Lake Superior lake trout, and Martin (1952) found that small lake trout in Lake Louisa and Redrock Lake, Ontario, were in deeper water than that occupied by larger trout. Evidently, size segregation by depth is common among lake trout populations and may be a general attribute of the species.

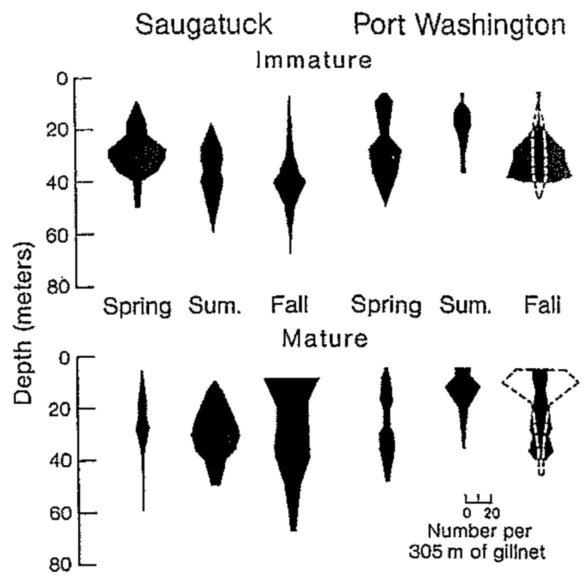

Fig. 7. Seasonal depth distributions of mature and immature lake trout sampled with standard gill nets off Saugatuck in 1976 and Port Washington in 1977 (solid lines) and 1978 (broken lines).

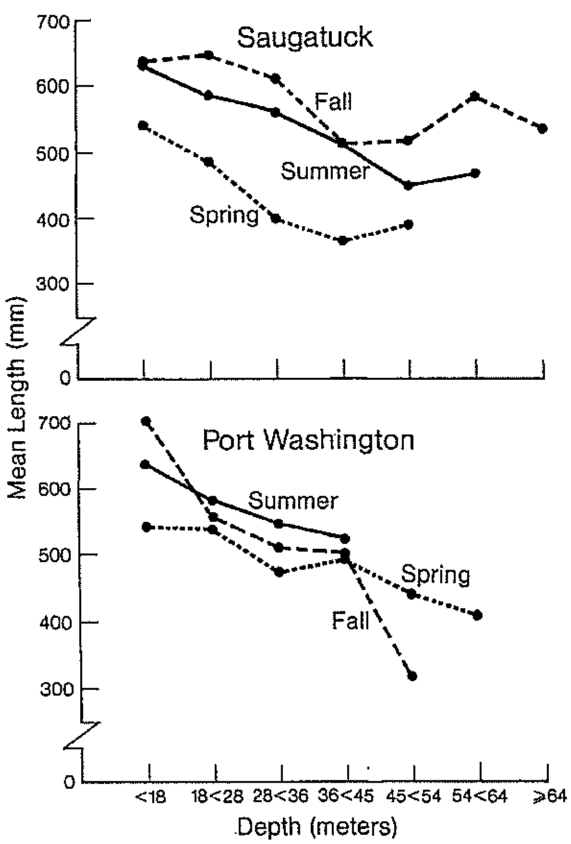

Fig. 6. Mean lengths of lake trout taken in standard gill nets in spring, summer, and fall at different depths off Saugatuck (1976) and Port Washington (1977).

In spring, adult lake trout seek the warmest water available until nearshore temperature exceeds the 10° C that they prefer. Off Saugatuck, lake trout have been taken in late April close to shore from water that was only 1 m deep (R. Owens, personal communication). As the surface waters further offshore grow warmer, however, some adults move offshore and occupy midwater levels. The scarcity of adults in catches at all depths off Saugatuck in spring (10–27 May) 1976 (Fig. 7) most likely resulted from their having been off bottom in warmer surface waters; during that period, local sport fishermen reported catching large lake trout in midwater over bottom depths ranging from 9 to 18 m. Evidence that adult lake trout are sometimes pelagic in spring was also provided by their incidental capture from midlevels in small-mesh gill nets used to determine vertical distribution of alewives off Saugatuck on 24–30 May 1973 (Great Lakes Fishery Laboratory, unpublished data). These nets were fished obliquely from the surface to a bottom depth of about 24 m. Of the four lake trout caught in these nets at midlevel (3 to 6 m below the surface), all were mature, whereas two caught on the bottom were both immature. Once a strong thermocline developed in early or midsummer, adult lake trout seemed to become more bottom-oriented off Saugatuck and concentrated wherever the 10° C water stratum reached the bottom. Later, as the water cooled in fall, they congregated at inshore depths of 18 m or less before spawning.

Immature lake trout off Saugatuck were more bottom-oriented in spring than were the adults. They were abundant on the bottom at depths of 20 to 40 m in spring and then moved to progressively deeper water in summer and fall (Fig. 7). Immature and adult fish were spatially segregated in spring primarily by differences in their locations in the water column, and in summer and fall by differences in depth distributions on bottom, the immature trout being at greater depths than the adults.

Lake trout off Port Washington were found at greater depths in spring, when the water was relatively cold, than in other seasons. These trout moved shoreward as warming progressed in spring, and did not return to deeper water in summer because prevailing westerly winds normally kept the shallows from becoming excessively warm. Judging by the gill net catches, adult and immature lake trout off Port Washington occupied about the same depths in spring and summer (Fig. 7), but the catches may not have given an altogether accurate indication of the distribution of adults. Some adults may have been in warmer surface waters or sometimes may even have been inside the shallowest depth that we fished (5.5 m), seeking the 10° C water that often lies in a narrow band next to the western shore in spring and summer. Significant numbers of these large lake trout have indeed been observed during electrofishing operations in shallow water along the Wisconsin shore in July (P. Schultz, personal communication).

Fall lake trout distribution off Port Washington was difficult to determine on the basis of the 1977 data because thermal conditions were unusual. During fall sampling in 1977, persistent and strong southeast winds thickened the epilimnion along the western shore, and bottom water temperatures at most depths sampled rarely fell below 12° C (Table 7). Adult lake trout taken on bottom in this warm water were widely scattered (Fig. 7). Immature trout, however, were concentrated on bottom at depths of 20 to 40 m in surprisingly great abundance, considering the high water temperatures (Fig. 7). Observations made under more nearly normal thermal conditions off Port Washington in fall 1978 (Table 7, Fig. 7) suggested, however, that in most years adult lake trout on the west side of Lake Michigan, as on the east side, occupy shallow, nearshore water in fall and immature trout occupy deeper water.

Table 7. *Mean bottom-water temperatures (° C) at different sampling depths during seasonal lake trout studies at Saugatuck in 1976 and Port Washington in 1977, and during a fall study at Port Washington in 1978.*

	Locality and season						
	Saugatuck			Port Washington			
Depth (m)	Spring	Summer	Fall	Spring	Summer	Fall	Fall (1978)
6				6.1	7.6	14.2	8.9
9	9.1	17.2	14.9	5.6	6.2	13.9	7.2
13		17.0			6.2	13.7	
18	7.6	14.7	14.4	4.5	5.5	13.9	6.6
22	6.4			4.2	5.2	13.4	
28	6.6	10.3	13.0	4.1	4.5	13.7	6.1
31	6.1	8.9		3.9	4.5	12.3	
37	6.1	8.2	11.5	3.9	4.2	9.1	5.7
40	5.8	7.6	9.9	3.8		7.7	
46					4.2	4.7	5.7
49	5.7	6.6	7.5	3.8			
59		4.1	4.7				
68			4.5				

Seasonal Changes in Lake Trout Diet and Availability of Food

Diet

Although alewives were by far the most important forage species lakewide, their importance in comparison with smelt and sculpins differed according to geographic area, age of lake trout, and season. At Saugatuck, lake trout fed more on alewives and less on sculpins as they became older (Fig. 8). As the seasons progressed from spring to fall, trout that fed heavily on sculpins (primarily age III) at the beginning of the growing season gradually shifted to other forage species. Smelt were not important in the diet of lake trout off Saugatuck until fall and then only among the two youngest piscivorous age groups, II and III (Fig. 8).

Lake trout on the west side of Lake Michigan ate relatively more smelt than did those on the east side. In spring, alewives decreased and smelt increased in the diet with increasing age of the lake trout, until smelt became more important than alewives by age V (Fig. 8). In older fish, alewives again became the most important food. This pattern was much the same in summer and fall, except that the age by which lake trout ate more smelt than alewives was IV rather than V. Off Port Washington, as off Saugatuck, slimy sculpins generally declined in importance in the diet as the age of lake trout increased (Fig. 8). But the distinct, steady decline in importance of slimy sculpins from spring to fall that characterized the diet of 3- and 4-year-old lake trout off Saugatuck did not occur off Port Washington. For example, in the diet of 3-year-olds from Port Washington, sculpins were almost insignificant in the spring, increased in importance in summer, and then declined in fall.

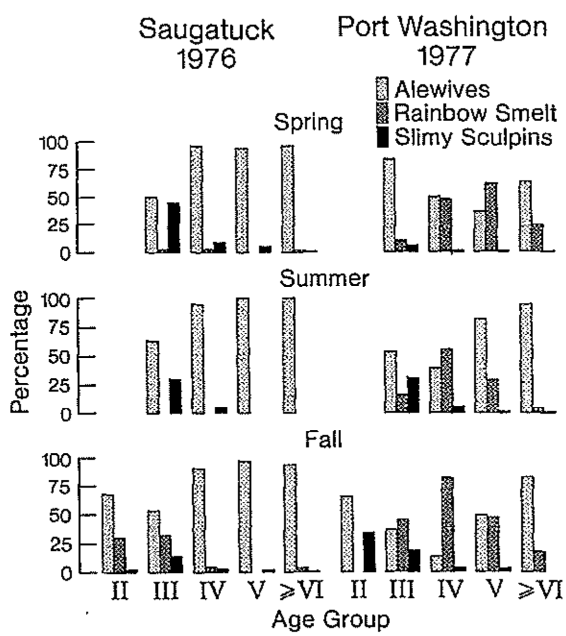

Fig. 8. Percentage by weight of alewives, rainbow smelt, and slimy sculpins in the diet of Lake Michigan lake trout by sampling locality, season, and age of trout.

Availability of Food

Seasonal changes in depth distributions of lake trout and their prey strongly affected the use of forage by the lake trout population. In southeastern Lake Michigan, depth ranges of the lake trout and alewife populations almost completely overlapped in spring (Fig. 7, Table 6). Age III lake trout then fed on both yearling and small adult alewives, and the older, larger trout fed almost exclusively on the adults (Table 8). Once the lake became thermally stratified, however, immature alewives remained in the epilimnion and thus were largely unavailable to the lake trout until fall. As an apparent consequence, mean weights of alewives found in lake trout stomachs were generally much higher in summer than in spring or fall (Fig. 9). How-

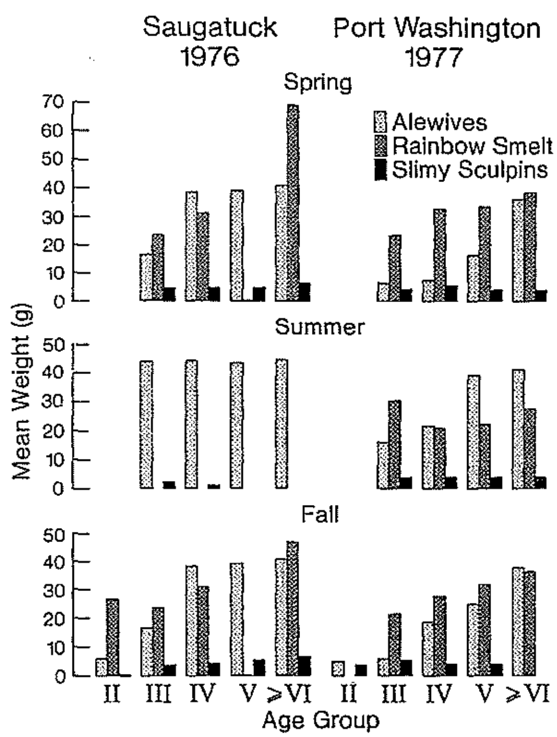

Fig. 9. Mean weights of alewives, rainbow smelt, and slimy sculpins in the diet of Lake Michigan lake trout by sampling locality, season, and age of trout.

Table 8. *Estimated numbers (thousands) of young-of-year (YOY), yearling, and adult (age II and older) alewives and rainbow smelt eaten by each piscivorous age group of lake trout on the east and west sides of Lake Michigan during the spring, summer, and fall periods of the lake trout growing season in 1979. Ages of alewives and smelt eaten by the trout were estimated by comparing the lengths of these forage species in the seasonal diet of the trout with seasonal lengths of known-age fish (Great Lakes Fishery Laboratory, unpublished data).*

Age of lake trout and season	Side of lake, forage species, and age category of forage species											
	East						West					
	Alewives			Smelt			Alewives			Smelt		
	YOY	Yearling	Adult	YOY	Yearling	Adult	YOY	Yearling	Adult	YOY	Yearling	Adult
II												
Fall	29,178	1,651	1,552	0	815	2,388	34,033	0	0	0	0	0
III												
Spring	0	1,137	885	0	0	68	0	8,265	0	0	48	226
Summer	0	185	2,170	0	0	0	3,717	884	915	0	0	868
Fall	9,763	240	485	0	0	1,247	7,213	194	382	479	1,203	1,315
IV												
Spring	0	107	1,278	0	0	64	0	3,451	126	0	0	882
Summer	0	0	3,247	0	0	0	1,407	160	1,119	1,022	511	2,514
Fall	1,005	174	2,088	0	0	192	577	59	307	0	1,102	2,400
V												
Spring	0	0	912	0	0	0	0	604	252	0	0	684
Summer	0	55	2,106	0	0	0	112	0	1,824	102	64	535
Fall	2,683	501	1,262	0	0	0	414	280	762	0	195	886
VI and older												
Spring	0	0	1,518	0	0	41	0	159	1,213	0	0	389
Summer	0	0	3,562	0	0	0	0	124	3,437	0	39	232
Fall	1,340	194	2,641	0	0	166	239	77	2,412	0	0	595
Total												
Spring	0	1,244	4,593	0	0	173	0	12,479	1,591	0	48	2,181
Summer	0	240	11,085	0	0	0	5,236	1,168	7,295	1,124	614	4,149
Fall	43,969	2,760	8,028	0	815	3,993	42,476	610	3,863	479	2,500	5,196
Grand total	43,969	4,244	23,706	0	815	4,166	47,712	14,257	12,749	1,603	3,162	11,526

Table 9. *Qualitative index (in percent) of the seasonal importance of invertebrates (I) and fish (F) in the diet of lake trout of different ages, expressed as a percentage of the combined number of times, on a presence or absence basis, each prey category was found in trout stomachs that contained food.*[a] *(No yearling lake trout were caught in gill nets.)*

	Season								
	Spring			Summer			Fall		
Location, gear, year, and age	No. fish	I	F	No. fish	I	F	No. fish	I	F
Grand Haven and Saugatuck									
Trawl									
1974									
I	5	100	0	33	94	6	117	65	35
II	30	97	3	*57*	*64*	*36*	130	21	79
Saugatuck									
Gill net									
1976									
II	—	—	—	29	62	38	67	18	82
III	210	5	95	102	50	50	109	18	82
IV	272	0	100	63	8	92	74	4	96
≥V	132	0	100	279	0	100	234	0	100
Port Washington									
Gill net									
1977									
II	—	—	—	—	—	—	36	8	92
III	137	3	97	38	32	68	126	1	99
IV	259	0	100	89	9	91	59	0	100
≥V	198	0	100	176	0	100	87	0	100

[a]Derivation of the indices is illustrated with an example (relevant numbers are italicized in the second row of data in the body of the table): Among age II lake trout collected by trawl in summer 1974, 57 contained food. In field analyses, we encountered invertebrates in 37 stomachs and fish in 21 (1 stomach contained both). Total encounters with invertebrates and fish, on a presence or absence basis, were thus 58. The indices in the tables are the quotients of 37/58 and 21/58 multiplied by 100, or 64 and 36%, respectively.

ever, despite the abundance of adult alewives on bottom throughout the lake trout's summer depth range (Fig. 7, Table 6), probably only the largest age III lake trout were able to ingest such large prey. Smaller trout in that age group must have either continued to feed on what sculpins were available (Fig. 8) or reverted to an invertebrate diet, as suggested by the increased occurrence of invertebrates in their diet in summer (Table 9). By fall, many young-of-the-year alewives were available on bottom (Table 6) and even the smallest age II lake trout were able to eat the largest of these.

On the basis of the Port Washington sampling, all age groups of alewives appeared to be available to lake trout along the western shore of Lake Michigan during spring (young-of-the-year, of course, excepted), summer, and fall (Fig. 7, Table 6). Lake trout of ages III and IV fed heavily on yearling alewives in spring (Table 8). As we mentioned earlier, many yearling alewives at this location were weakened and moribund in spring 1977, and would have been easy prey for the trout. Age V lake trout also ate mainly yearling alewives in spring, but included significant numbers of adults in their diet; adult trout (age VI and older) fed primarily on adult alewives (Table 8).

Yearling and even young-of-the-year alewives were common in the diet of lake trout along the western shore in summer (Table 8). Trawl catches showed that yearlings were on bottom at all depths during the summer sampling period off Port Washington (Table 6); we could not determine from the catches whether young-of-the-year alewives were also on bottom because the fish were still too small to be retained by the trawl. We do not know why immature alewives in summer were in the hypolimnion on the west side of Lake Michigan but restricted to the epilimnion on the east side. Perhaps the prevailing westerly winds kept the epilimnion on the west side of Lake Michigan so thin in summer that some immature alewives were forced to live in the hypolimnion. By fall, young-of-the-year alewives were abundant on bottom on the west side of Lake Michigan and were readily available to 2- and 3-year-old lake trout (Table 8). Older lake trout, however, generally ate adult alewives in both summer and fall.

Off Port Washington, most of the smelt eaten by lake trout of all ages during all seasons were adults (Table 8). Among forage fish eaten by lake trout of age IV during all seasons and by those of age V in spring and age III in fall, smelt accounted for a greater proportion by weight (Fig. 8) than their relative abundance in relation to that of alewives would lead one to expect (Table 6). Either our trawl captured alewives more efficiently than smelt, or the trout were feeding selectively. Possibly many age IV and most age III lake trout were not large enough to readily ingest adult alewives, which are rather deep-bodied. Smelt are more elongate, and these trout could probably swallow much larger smelt than alewives in terms of body weight. Although only 2- and 3-year-old lake trout ate significant amounts of smelt off Saugatuck (and then only in fall), these trout also fed primarily on the adults, but in amounts that were more commensurate with their abundance in the environment (Tables 6 and 8).

The decline of sculpins in the diet of small immature lake trout (age III) from spring to fall (Fig. 8) off Saugatuck probably resulted partly from a movement of sculpins to deeper water as the seasons progressed and partly from increased abundance of alternate prey, i.e., young-of-the-year alewives (Table 6). The near lack of sculpins in the diet of young lake trout in spring at Port Washington could have been related to low availability of this forage species, but, as mentioned earlier, it seems possible that sculpins were available in reasonable numbers. We believe it more likely that sculpins were scarce in the diet because the young lake trout had available to them unusually large numbers of yearling alewives, many of which were dying and presumably highly vulnerable to predation in spring 1977. Data from Wright (1968) showed that a similar departure from normal feeding habits of young lake trout occurred on the east side of Lake Michigan during the massive lakewide alewife die-off of 1967.

Use of Prey Fish Stocks by Lake Trout

As explained earlier, production by each cohort of lake trout extant in 1979 was divided by the corresponding age-specific food conversion efficiency to estimate the biomass of forage fish consumed by the trout. Because the conversion efficiencies were derived for lake trout on a strictly fish diet, consumption estimates pertained only to lake trout old enough to be basically piscivorous—age II during the last 2 months of the growing season (i.e., 1 October to 1 December), and age III and older through the entire growing season. Among these age groups, the only possible exception to nearly complete piscivory involved the age III fish, which in summer may have relied significantly on invertebrate forage (Table 9). Lake trout of the ages mentioned consumed an estimated 3,037 t of forage fish and converted them into 643 t of trout biomass during the 1979 growing season (Table 5). Alewives composed about 71% by weight of the total forage fish eaten lakewide (Table 10), followed by rainbow smelt (18%) and slimy sculpins (11%).

Stewart et al. (1983) developed an energetics-based population model for Lake Michigan lake trout that enabled them to consider shifts in diet from one of purely invertebrates to a mixture of invertebrates and fish and finally to purely fish, and to account for seasonal and ontogenetic changes in energy densities of predator and prey and in predator activity levels during the year. From lake trout stocking records and mortality rates, and from preliminary seasonal food data that we provided, they estimated that Lake Michigan's lake trout population consumed about 8,061 t of alewives in all of 1979. This estimate is about 3.8 times the 2,146 t that we projected for the 1979 growing season alone, a period in which all but about 25% of the year's total should have been consumed (D. Stewart, personal communication).

The large discrepancy between the two estimates was related partly to differences in estimated annual mortality and growth rates of lake trout in Lake Michigan and partly to differences in the types of assumptions that were used to bridge various information gaps. For example, Stewart et al. (1983) used lower annual mortality and higher growth rates for lake trout in their simulations than the rates we estimated, and they also assumed seasonal mortality schedules that differed from ours for some age groups of lake trout. Their estimates of annual mortality of lake trout were 0.37 for ages I–III, 0.44 for age IV, and 0.47 for ages ≥V, compared with our estimate of 0.48 for all age groups. As an example of the higher growth rates estimated by Stewart et al., lake trout across ages II–X in their simulations were 7 to 28% heavier (depending on age) in May 1979 than those in our model (D. Stewart, personal communication).

Their estimates were based on data from Rybicki and Keller (1978) that were collected in 1975 and earlier, mostly in the northern and central parts of Lake Michigan, whereas ours were based on data collected after 1975 and from more southern regions of the lake. Therefore, year-to-year and geographic variation could have accounted for some of the differences in the estimates of growth and mortality rates of Lake Michigan lake trout. Because consumption estimates are extremely sensitive to these parameters, a simple substitution of the lake trout growth and mortality rates used by Stewart et al. in our calculations would result in an annual estimate of alewife consumption of about 7,100 t.

For several reasons, however, we believe that our estimates of forage fish consumption by Lake Michigan lake trout during the 1979 growing season are minimum values. We did not, for example, account for consumption by age I lake trout that feed heavily on young-of-the-year alewives in late summer and early fall. In addition, we may have used growth and mortality rates of lake trout that, on a lakewide basis, could have resulted in an underestimate of lake trout stock size and production. Finally, by applying gross food conversion efficiencies derived from ad libitum rations in the laboratory to lake trout in the wild, we may have overestimated conversion efficiencies for Lake Michigan lake trout and thus underestimated consumption. Rations in the wild are probably less than ad libitum and conversion efficiencies are probably lower as well.

Table 10. *Estimated quantity (metric tons) of alewives, rainbow smelt, and slimy sculpins eaten by lake trout of each piscivorous age group on the east and west sides of Lake Michigan in each season during the lake trout's growth period (15 May–1 December) in 1979.*

Age group (lake trout) and prey species	Side of lake and season								Grand total
	East				West				
	Spring	Summer	Fall	Total	Spring	Summer	Fall	Total	
II									
Alewife	0	0	193	193	0	0	187	187	380
Smelt	0	0	85	85	0	0	0	0	85
Sculpin	0	0	7	7	0	0	97	97	104
Total	0	0	285	285	0	0	284	284	569
III									
Alewife	34	106	69	209	55	88	46	190	399
Smelt	2	0	40	42	7	26	57	90	132
Sculpin	30	59	18	107	4	51	24	79	186
Total	66	165	127	358	66	165	127	359	717
IV									
Alewife	53	144	106	303	30	59	17	106	409
Smelt	2	0	6	8	29	84	96	209	217
Sculpin	5	7	5	17	2	8	4	14	31
Total	60	151	117	328	61	151	117	329	657
V									
Alewife	36	94	70	200	14	77	36	127	327
Smelt	0	0	0	0	24	16	34	74	74
Sculpin	2	0	2	4	*	1	3	4	8
Total	38	94	72	204	38	94	73	205	409
VI–XIV									
Alewife	61	158	115	334	48	149	100	297	631
Smelt	1	0	5	6	15	7	22	44	50
Sculpin	1	0	1	2	*	1	0	1	3
Total	63	158	121	342	63	157	122	342	684
Grand total	227	568	722	1,517	228	567	723	1,519	3,036[a]

*Less than 0.5.
[a]Less than total in Table 5 and that quoted in text because of rounding error.

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