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Growth, Maturation, and Production of Northern Pike in Three Michigan Lakes

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Abstract

Differences in the age at first maturation, as well as timing and magnitude of growth (body and gonad) were examined for northern pike *Esox lucius* from three lakes in Michigan. The lakes varied in latitude (42 to 46°N), ice-free season (210 to 248 days), and total mortality (Z = 0.28 to 0.85). Body and gonad calorific equivalents were similar among all three lake populations. Male and female northern pike from all lakes and age classes 1–3 had significant accumulation of somatic energy during summer and winter and depletion of reserves over spawning. Testicular growth occurred entirely in the summer, whereas ovarian growth occurred mainly over winter. Females invested 6- to 18-fold more energy into gonads than did males. Total winter growth was significant in both sexes and all lakes. Individual body and gonad growth over the first 3 years of life for northern pike varied little among lakes. Age at first maturation varied significantly among lakes; the earliest maturation occurred in the lake of intermediate latitude, the latest in the southernmost lake. These differences did not correspond well with length of the growth season. However, there appears to be a relationship between total mortality (due to differences in fishing intensity) and proportion of fish mature at age 1. Increased fishing intensity may have induced higher total mortality rates, earlier ages at first reproduction, and higher total energy allocations to reproduction at earlier ages among these populations. Latitudinal differences in climate had little or no apparent effect on growth and reproductive characteristics of the populations.

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Because temperature has such a strong effect on the metabolism of poikilothermic animals, ichthyologists commonly believe that growth rates of fish are constrained largely by the length of the summer growing season in temperate regions (Tesch 1971; Gerking 1972). The lengths of growing seasons usually vary inversely with latitude, so annual growth should decline in a range of habitats from south to north. There is evidence that this occurs (Gerking 1966; Morin et al. 1982), but the relationship can be subtle. For example, Miller and Kennedy (1948) found that maximum lengths of northern pike *Esox lucius* did not vary over 19 degrees of latitude, but southern fish grew faster and matured earlier than did northern fish. From this work, it appeared that the annual growth increment varied in response to the length of the ice-free season. However, Diana and Mackay (1979) demonstrated that northern pike in Alberta grew nearly as much during the winter as the summer. The ability of fish to grow over winter would have serious implications for theories linking climatic gradients with fish growth. The winter growth of northern pike could be explained by at least two mechanisms: (1) an unusual adaptation of that Alberta population to severe climate conditions; or (2) a general ability of northern pike to grow during winter.

As the length of winter increases, fish may adapt either by growing during a different season, such as winter, or by growing less. Several studies suggest that northern populations of a species have higher metabolic rates at lower temperatures (Venables et al. 1977) and lower preferred temperatures (Hall et al. 1978) than southern populations, indicating adaptation to climatic conditions. These data support the possibility of mechanism (1), but some laboratory data on pike growth support the potential of mechanism (2) (Casselman 1978a; Diana 1982). The present study was undertaken to evaluate the generality of winter growth by northern pike. Growth patterns of fish were examined for three lakes near the southern extreme of the natural distribution of northern pike, where winter conditions are much less severe than in Alberta.

Not only can animal growth change with climate, but the life history pattern of a species also may vary. Leggett and Carscadden (1978) reported that American shad *Alosa sapidissima* from the predictable temperature regimes of southern rivers were predominantly semelparous (spawned once, then died), whereas those from less predictable northern rivers had a much higher incidence of iteroparity (repeat spawning). Latitudinal trends in age at first maturation were found by Schaffer and Elson (1975) for the iteroparous Atlantic salmon *Salmo salar*. These life-history adaptations are somewhat surprising, because Atlantic shad and Atlantic salmon of different stocks intermix freely in the Atlantic Ocean (Leggett 1977); therefore, all of this variation is due to the selective nature of the riverine environment on spawning and early survival. One might predict even larger differences among isolated populations of fish in lakes, because seasonal food availability and weather predictability will affect growth and reproductive success of a limited gene pool of animals throughout their entire life history. However, few comparative studies of this sort have been conducted.

In addition to climatic gradients, edaphic factors (Moyle 1956; Ryder and Kerr 1978) and fishing intensity (Healey 1975) may cause alterations in the growth of fish. Northern pike in Minnesota commonly occur in mesotrophic or eutrophic lakes with total phosphorus concentrations less than 0.1 mg/liter (Moyle 1956). Variations in growth of northern pike in response to different levels of primary productivity have not been analyzed. Variations in primary productivity undoubtedly would affect the species and densities of forage fish available, and thereby affect growth of northern pike even over small geographic areas (Carlander et al. 1978). Similarly, increased fishing intensity has been shown to cause a decline in age at first maturation and an increased growth rate in lake whitefish *Coregonus clupeaformis* populations (Healey 1975), and these responses are believed to be common in many species (Ricker 1975).

The purpose of this study was to evaluate the generality of winter growth and the relationships among total growth, age at first spawning, climatic conditions, and fishing pressure for several northern pike populations. If winter growth of northern pike is a specific adaptation to severe (cold) climatic regimes, one would expect little or no winter growth near the southern extreme of the range. I compared northern pike growth in three lakes in Michigan to evaluate climatic effects on timing of growth near the southern edge of natural pike distribution, as well as to evaluate differences in growth and their relation to fishing pressure, which also varied among the lakes. Four specific questions were addressed. (1) Do these northern pike populations commonly exhibit winter growth? (2) Does the timing or magnitude of growth vary with latitude near the edge of a fish's distribution? (3) Does age at first maturation vary with latitude? (4) Does fishing pressure have any impact on the life history and growth of northern pike?

TABLE 1.—*Physical and biological data for three study lakes in Michigan.*

Variable	Murray Lake	Houghton Lake	Lac Vieux Desert
Latitude	43°	44°24′	46°8′
Longitude	83°30′	84°50′	89°
Surface area (hectares)	15	8,112	1,740
Mean depth (m)	4.2	2.0	2.8
Maximum depth (m)	9.1	6.7	11.6
Thermocline depth (m)	8.1	[a]	[a]
Maximum surface temperature (C)	28	24	25
Annual means			
Ice-free period (days)	248	223	210
Degree-days >14 C	409	311	213
Degree-days >4 C	2,233	1,865	1,729
Degree-days >0 C	3,669	3,479	3,165
Instantaneous total northern pike mortality (Z)	0.28	0.85	0.45

[a] Houghton Lake and Lac Vieux Desert had no thermoclines.

Methods

Northern pike were collected from Murray Lake, Houghton Lake, and Lac Vieux Desert (Table 1). The lakes vary in surface area, although all are relatively shallow. Two of the lakes have no summer stratification, whereas Murray Lake stratifies within 1 m of the bottom. Thus, no thermal refuges exist in which fish can avoid warm midsummer water temperatures.

Mean monthly air temperatures for 1932–1971 were taken from data compiled at weather stations near the three lakes (Strommen 1971). Air temperatures were used as an index of water temperature (McCombie 1959), and although any bias was not estimated for the Michigan lakes, it was assumed to be constant. The average annual degree-days over 14 C (Frost and Kipling 1967), 4 C, and 0 C then were calculated (Table 1).

Northern pike were gillnetted in October 1979, March 1980, and May 1980. Attempts were made to sample 50 fish each time. The sampling intervals allowed direct estimation of growth over winter (October to March) and the spawning season (March to May), and an indirect measure of growth over summer. Fish were frozen immediately after collection and stored at −25 C. When fish were thawed, gross body weights were measured to 1 g and standard lengths to 0.5 cm. The left cleithral bone was removed for aging. Gonads were removed from each fish, weighed to 0.1 g, dried at 80 C to constant weight, then reweighed to 0.1 g. Four fish from each sex and age class (when possible) were selected from each sample for calorific analysis. The body (entire fish without gonads or stomach contents) was ground in a Hobart meat grinder, then subsampled for about 100 g of wet tissue. Somatic samples were weighed to 0.1 g, dried at 80 C to constant weight, and reweighed to 0.1 g. Dried tissue (somatic and gonad) was pulverized in a coffee grinder, and stored in vials at −25 C for calorific analysis.

Calorific equivalents (kcal/g dry weight) were determined with a Phillipson microbomb calorimeter by methods outlined in Paine (1971). Approximately 40 mg of sample were burned for each analysis. Replicate samples were run for each fish. Fourteen calorimetry runs with benzoic acid standard yielded a calibration of 0.92 ± 0.06 (mean ± 2 SD), or an error factor of 6.5%. Corrections were made for burnt fuse only, not for sulphur or nitric-acid content.

The somatic energy content was the product of individual wet weight and group means for proportion dry matter and calorific equivalent. The gonad energy content was the product of individual gonad dry weight and the group mean calorific equivalent. Growth over a given time was considered the difference between the mean energy content of a tissue from fish collected at the beginning and end of a time period. Significant growth was assumed to occur when the two sizes were significantly different ($P < 0.05$). Total growth (in kcal) of a fish over several years includes body growth (which is accumulated over that time) and gonad growth (which is built up then mostly lost seasonally). Therefore, total production by individual northern pike over the first 3 years of life was estimated by summing mean somatic energy for age-3 fish in March with mean gonad energy for age-1, -2, and -3 fish in March.

Northern pike were aged from annuli on the dried, unmagnified cleithral bones under reflected light (Casselman 1978b). Approximately 5% of the fish could not be aged in this manner, due to irregular or misplaced bones. These were classed with similar-sized fish from the same sample that had been aged. Annuli are readily apparent and completely formed at the termination of the spawning season (before June) probably in response to the negative body growth associated with spawning. The birthday of fish from all lakes was assumed to be 1 June, when annuli were all complete.

Total-mortality rates for the fish populations were estimated from catch-curve analysis of the aged fish (Ricker 1975). The age-frequency data for northern pike collected were unbiased in Murray Lake and Lac Vieux Desert because all caught fish were kept, but the Houghton Lake collections were biased because larger individuals were kept and several smaller ones released to allow more complete representation of older fish. This makes the mortality estimate conservative. However, the rate still was calculated to allow minimum mortality values to be compiled and compared among all three lakes.

Age at first maturation was estimated from gonad condition of fish collected in October and May. Testes were fully developed by October, so a direct determination of maturity (ripe condition) and immaturity (minimum development) could be done then. The size of ripe ovaries had increased considerably by October, and fish could be classed as maturing (producing ova) and immature (ovaries of minimal size) at that time. By March, both sexes were either immature or fully mature. The estimates of proportion mature for each age, sex, and lake are maximal because the sex of several immature individuals could not be determined by gonadal appearance and these fish had to be excluded from analysis.

Seasonal and age-related changes in energy content were determined by analyses of variance and the Student-Newman-Keuls (SNK) test (Nie et al. 1975). Differences in age at first mat-

TABLE 2.—*Water content and calorific equivalents (kcal/g dry weight) of northern pike collected from three Michigan lakes. Values are means ± SE; sample sizes are in parentheses.*

Variable	Lake	October	March	May
		Males		
Somatic % water	Murray	76.7 ± 1.1 (5)	76.0 ± 0.3 (9)	76.0 ± 0.4 (14)
	Houghton	75.1 ± 0.4 (11)	76.3 ± 0.4 (12)	75.8 ± 0.4 (7)
	Vieux Desert	75.2 ± 0.4 (13)	76.1 ± 0.2 (12)	75.8 ± 0.2 (16)
Somatic calorific equivalents	Murray	4.6 ± 0.1 (5)	4.6 ± 0.1 (5)	4.7 ± 0.1 (5)
	Houghton	4.5 ± 0.1 (5)	4.7 ± 0.0 (5)	4.7 ± 0.1 (5)
	Vieux Desert	4.4 ± 0.1 (5)	4.7 ± 0.2 (5)	4.5 ± 0.1 (11)
Gonad calorific equivalents	Murray	5.3 ± 0.1 (5)	5.7 ± 0.1 (5)	5.2 ± 0.1 (5)
	Houghton	5.4 ± 0.1 (5)	5.4 ± 0.1 (5)	5.3 ± 0.1 (5)
	Vieux Desert	5.2 ± 0.1 (5)	5.3 ± 0.1 (5)	5.4 ± 0.1 (9)
		Females		
Somatic % water	Murray	77.6 ± 0.5 (7)	76.2 ± 0.4 (7)	77.1 ± 0.4 (9)
	Houghton	76.5 ± 0.4 (9)	77.3 ± 0.6 (7)	75.9 ± 0.5 (9)
	Vieux Desert	75.7 ± 0.3 (10)	76.3 ± 0.4 (9)	75.9 ± 0.4 (9)
Somatic calorific equivalents	Murray	4.9 ± 0.1 (5)	4.5 ± 0.1 (5)	4.6 ± 0.1 (5)
	Houghton	4.7 ± 0.1 (5)	4.4 ± 0.1 (5)	4.3 ± 0.1 (5)
	Vieux Desert	4.5 ± 0.1 (5)	4.8 ± 0.0 (5)	4.5 ± 0.0 (9)
Gonad calorific equivalents	Murray	5.4 ± 0.1 (5)	5.6 ± 0.1 (5)	4.9 ± 0.0 (5)
	Houghton	5.6 ± 0.0 (5)	5.7 ± 0.0 (5)	5.1 ± 0.1 (5)
	Vieux Desert	5.4 ± 0.1 (5)	5.4 ± 0.1 (5)	5.0 ± 0.1 (9)

uration were assessed by chi-square tests (Conover 1971).

Results

Water Content and Calorific Equivalents

Somatic water contents of 176 northern pike (Table 2) did not vary with fish weight ($r = -0.04$; $P = 0.422$), sex (t-test; $P = 0.658$), lake (SNK test; $P > 0.05$), or month (SNK test; $P > 0.05$). Therefore, moisture data were pooled by sex, month, and lake in the determination of total somatic calories.

Somatic calorific equivalents did not vary among lakes for male or female northern pike (Table 2). Males had no change in somatic calorific equivalent over time, whereas females did. Therefore, an overall value was used for males to estimate total somatic calories, but a monthly mean value for data grouped by lake was used for females.

Gonad calorific equivalents varied considerably between sexes (Table 2). Testicular calorific equivalents did not vary among lakes or months, so an overall mean was used to represent total testicular energy. Ovarian calorific equivalents varied significantly among lakes and months, so individual means for each lake and month were used to estimate ovarian energy content.

Timing of Growth

The timing of somatic growth of northern pike varied little from lake to lake (Fig. 1). In general, male and female fish aged 1 to 3 had significant positive growth during summer and winter and significant energy loss during spawning in all three lakes.

Testicular growth occurred during summer in all of the lakes. Major energy losses occurred during spawning and some losses occurred over winter (Fig. 2). Ovarian growth occurred mainly over winter in all the lakes; summer growth was smaller but often significant. Energy losses occurred during spawning (Fig. 2). No latitudinal pattern emerged in the lake-specific timing of gonad growth.

Magnitude of Growth

The magnitude of energy allocation into reproductive and somatic tissue depends mainly on age at first maturation and rate of growth in individuals from each age class. The northern pike were nearly all mature at age 1 in Houghton Lake and at age 2 in Lac Vieux Desert; fish from Murray Lake did not fully mature until age 3 (Table 3). The differences between lakes for proportion of fish mature at age 1 were highly significant for males (chi-square test; $P < 0.05$) and nearly significant for females

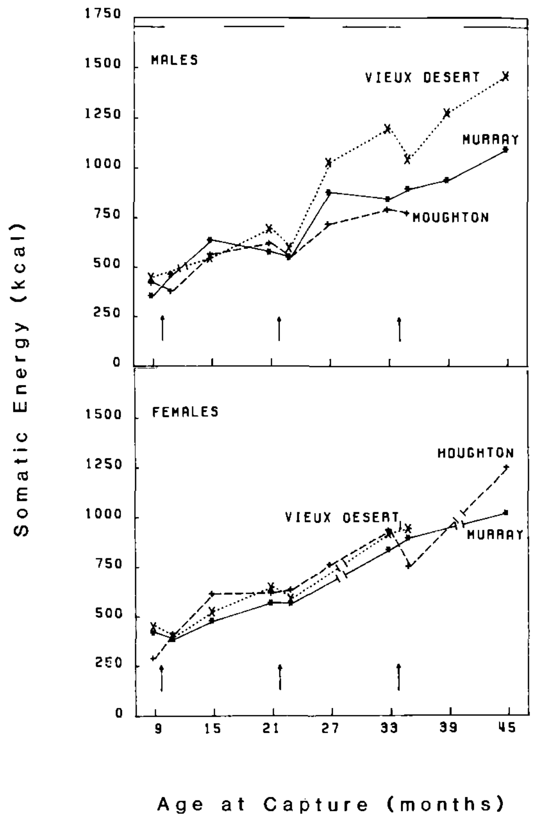

FIGURE 1.—*Seasonal changes in somatic energy content for northern pike from three Michigan lakes. Dark bars across top indicate periods of ice cover. Arrows indicate spawning periods (March–May). Blanks indicate missing data.*

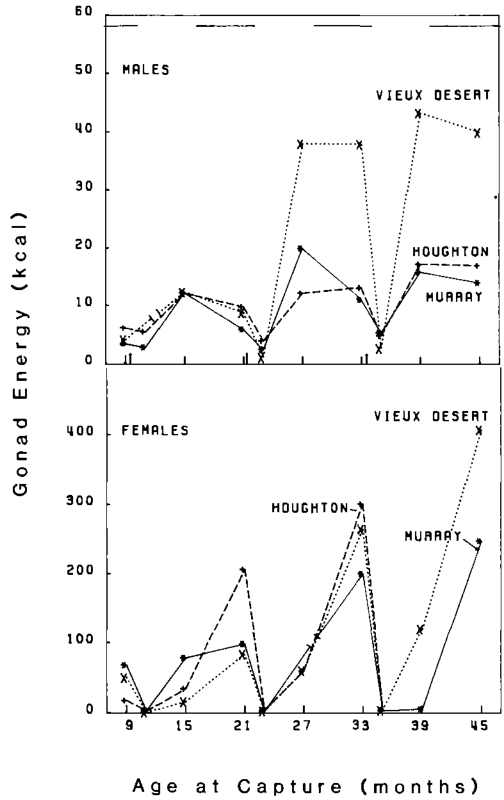

FIGURE 2.—*Seasonal changes in gonad energy content for northern pike from three Michigan lakes. Dark bars across top indicate periods of ice cover. Arrows along the upper abscissa indicate spawning periods (March–May). Blanks indicate missing data.*

($P < 0.10$). The variation in age at maturation between lakes did not follow a latitudinal or climatic cline (Table 1). However, the earliest age at maturation occurred in the lake with the highest mortality rate, whereas the latest age at maturation coincided with the lowest mortality rate.

TABLE 3.—*Percentages of collected male and female northern pike mature at age in three Michigan lakes. Sample sizes are in parentheses.*

Age	Murray Lake	Houghton Lake	Lac Vieux Desert
		Males	
1	71% (7)	100% (17)	80% (10)
2	80% (5)	100% (29)	94% (15)
3	100% (5)	100% (17)	100% (15)
		Females	
1	17% (6)	80% (5)	31% (13)
2	67% (3)	100% (15)	100% (8)
3	100% (6)	100% (8)	100% (2)

The total magnitude of energy deposition into somatic and gonad tissues summed over the first 3 years of life varied little between the three lakes, but considerably between sexes (Fig. 3). Females deposited 6–18-fold more energy in ovaries than did males in testes. Females in Houghton Lake invested somewhat more energy into ovary growth than did those in the other two lakes, and this apparently was related to their earlier age at first reproduction. Total growth of females was very similar in the three lakes.

Male northern pike differed in somatic and gonad allocations among lakes. Lac Vieux Desert males had higher totals for both tissues, due mainly to rapid production during the third year

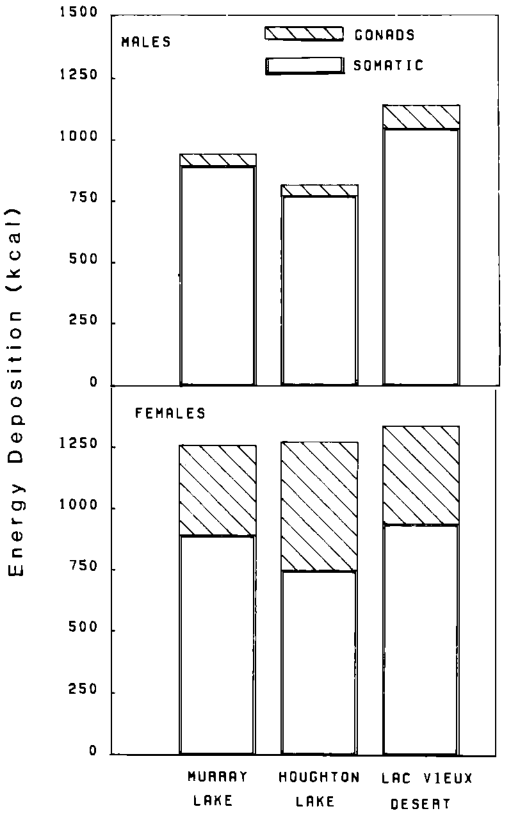

FIGURE 3.—*Total individual energy allocation over 3 years for northern pike from three Michigan lakes. Body energy = energy content at end of third year of life. Gonad energy = sum of average annual gonad energy contents for years 1–3.*

of their life. Males from the other two lakes had very similar growth allocations. Because the total gonad energy allocation of males was so small (less than 5% of the total energy deposition), changes in age at first maturation did not affect the total magnitude of growth pattern to any great degree.

Discussion

In general, the changes in the timing and magnitude of growth in northern pike were not consistent with an hypothesis that the length of the growing season directly affects the growth of fish over a minor latitudinal gradient. The growth differences discovered in the populations were generally small in magnitude and inconsistent. However, the quality of the growing season may have been a factor; these Michigan lakes are near the southern limits for the species and temperatures may have been too high for optimal growth during part of the summer. It is common for some fish to avoid high temperatures and reduce activity and growth during midsummer (Coutant 1975; Magnuson et al. 1979). The lethal temperature for northern pike is 29 C and optimal growth occurs at 19–21 C (Casselman 1978a). Because midsummer temperatures exceeded the optimal growth temperature in all of the lakes (Table 1), the summer growth season for northern pike might be more aptly described as the spring and fall, or periods when temperature is below the maximum value.

Apparently, winter growth is a common characteristic of northern pike, rather than the specific adaptation to severe Alberta winters proposed by Diana and Mackay (1979), because both males and females from all the Michigan lakes had significant somatic or gonad growth (or both) over winter. The winter contribution to the annual male somatic growth of northern pike in Lac Ste. Anne, Alberta (35%), was similar to the average male value in the three Michigan lakes (40%). The same is true for relative seasonal ovarian growth in Lac Ste. Anne (81%) and in the three study lakes (80%). However, female northern pike in Lac Ste. Anne had no winter somatic growth, whereas approximately 35% of the female somatic growth in the three study lakes occurred over winter. Thus, winter growth may be even more important to the total individual production in the southern populations. Because midsummer water temperature may often exceed the optimum for northern pike growth (Casselman 1978a) in these southern localities, it is not surprising that winter is also utilized as a major growth season.

The rate of growth for northern pike during Michigan winters agrees with laboratory studies by Diana (1982), but is more rapid than that measured by Casselman (1978a). However, these laboratory studies were done on young-of-year fish, which may differ considerably in growth from adults in the wild. It is possible that many coldwater and coolwater fish that are top carnivores may be able to grow over winter, because they are physiologically active at cold temperature and the abundance and availability of their food sources remain high at this time. However, one might predict that warmwater fish may be physiologically limited to reduced growth during winter, and that species from lower trophic levels may show reduced growth over winter due to reduced abundance of food items (Gerking 1966).

This analysis relies on two main assumptions. The first is that the annual pattern of growth is similar from year to year for northern pike. This assumption underlies both the comparisons of data from May 1980 and October 1979 to determine summer growth, and the integration of data from 1-, 2-, and 3-year-old fish to derive 3-year production estimates. Food availability, temperature regimes, and density of northern pike all could vary annually, which would affect growth. However, Diana and Mackay (1979) found no significant differences in northern pike growth over 3 years in an Alberta lake, indicating that this assumption may be reasonable for a given lake; still, the validity of this assumption has not been tested. However, the food resources could vary between lakes and might mask any climatic trends in growth (Carlander et al. 1978). The lakes all had similar mean depths, temperature regimes, and fish communities; they were chosen specifically to be similar in food and physical structure.

The second assumption is that there is no size-selective mortality in these populations, which would bias the samples. Frost and Kipling (1970) reported that northern pike less than 20 cm do not often survive their first winter, but I did not analyze any fish before March of their first winter so this factor can be ignored. Another major size-selection bias may have been added by angling. However, the Michigan size limit for northern pike is 50 cm total length, so this factor probably would not affect the fish much until they reach the age of 3. If fishing removed the largest individuals of a cohort, my growth estimates would be conservative. The problem could be especially acute in Houghton Lake, and might account for the lesser somatic growth observed there (Fig. 3). This angling problem could also affect the magnitude of differences among lakes, because fishing pressure varied widely among lakes.

Lake-specific changes in age at first maturation were very distinct, and appeared related to total mortality. There were extreme differences in the intensity of sportfishing in each of the study lakes. Murray Lake is unexploited, being a reserve on University of Michigan property; Houghton Lake is one of the most heavily fished northern pike lakes in Michigan. Thus, the difference in total mortality among the three lakes (Table 1) undoubtedly is due to increased fishing mortality. Increased mortality resulted in an earlier age at first maturation and an increased total allocation of energy to gonads in females. These results are consistent with the data of Healey (1975, 1980) for lake whitefish under a variety of exploitation pressures. The effect of variable mortality (induced by fishing) on maturation in the three Michigan populations was similar to the effects of mortality induced by climate on maturation of Atlantic salmon (Schaffer and Elson 1975).

The timing of ovarian and testicular growth in northern pike was similar in this study and in several others, testis growth occurring in late summer and ovary growth over winter (Frost and Kipling 1967; Casselman 1978a; Medford and Mackay 1978; Diana and Mackay 1979). Annual growth in length for northern pike was intermediate in these three lakes, compared to the populations analyzed by Miller and Kennedy (1948) and Toner and Lawler (1969).

The growth patterns of northern pike in this study differ considerably from several other sources. Miller and Kennedy (1948) found, over a large latitudinal zone, a positive relationship between growth rate and length of the ice-free season; their lakes had 17–40 weeks of open water, whereas the Michigan lakes were ice-free 30–35 weeks. Frost and Kipling (1967) examined annual variations in growth of northern pike from Windermere (approximately 10 weeks with water temperatures ≤4 C) and found a good positive correlation between annual growth and number of degree-days over 14 C. In the present study, no such relationship was found. Differences in data collection and aging methods may make direct comparisons among these studies difficult. An analysis of growth by one standard method over a very wide range of latitudes is necessary to evaluate further the general applicability of the results of this and the previous two studies.

This study demonstrated an apparent similarity in timing and magnitude of growth of northern pike across a small latitudinal gradient, and a lowering of age at first reproduction correlated with higher fishing pressure. The timing of growth and the body composition of northern pike in the three lakes were similar to those of fish in Lac Ste. Anne (Diana and Mackay 1979). Winter growth was common in all of the lakes. There was no relationship between total growth and length of ice-free ("growing") season.

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