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Changes in Fish Populations over an 80-Year Period: Big Pine Lake, Wisconsin

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Abstract

From 1897 to 1977, landowners recorded sport catches for Big Pine Lake, a 256 hectare lake in northern Wisconsin that has experienced light fishing pressure. The species composition of the catch remained fairly stable for 40 years, from 1897 through 1940, with muskellunge *Esox masquinongy,* walleye *Stizostedion vitreum vitreum,* and black bass (*Micropterus* spp.) all accounting for substantial fractions of the total. Northern pike *Esox lucius* were first recorded in 1946, apparently having entered after an outlet dam washed out in 1944. Subsequent increases in the proportion of northern pike coincided with declining percentages of muskellunge. By the 1950s, the relative abundance of walleye declined, ultimately almost to zero, while the percentage of bass more than doubled. This change began during the warmest decade on record. By 1977, the walleye population had rebounded, bass had declined to pre-1940 levels, northern pike were abundant, and muskellunge were relatively scarce. Long-term changes in summer temperatures and colonization by northern pike appear to have been important factors causing changes in species composition. Effects of human exploitation have been slight. Although the species composition changed dramatically over the 80 years, the only sustained change has been the substitution of northern pike for muskellunge.

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Catch data from fisheries are useful in documenting long-term changes in fish communities, in associating these changes with human activity, and in calling attention to interactions among fish species. Good examples from inland waters are records for the Great Lakes exceeding 100 years (Christie 1974) and for other large lakes with 40- to 90-year histories of commercial fishing (Schupp and Macins 1977; Smith 1977). Long records for small lakes are rare, but sport fisheries have been monitored up to 35 years in several Wisconsin lakes (Kempinger and Carline 1977; Snow 1978).

Big Pine Lake provides a new record, 80 years long, of sport catch in a lightly fished lake. This 256 hectare lake in northcentral Wisconsin is entirely surrounded by private land and has been closed to public access since 1865. A limited sport fishery, by owners and guests, has existed since the 1890s. Fishing pressure probably has been insufficient to appreciably affect the structure of the fish community, but adequate to monitor its composition. Anglers recorded their catches in a logbook kept on the premises. This record provides a basis for reconstructing the history of the fishery and, by inference, of changes in the relative abundance of game species and the reasons for these changes.

Study Site and Its History

Big Pine Lake (Fig. 1) is part of a network of lakes at the headwaters of the south fork of the Flambeau River, which drains to the Chippewa and Mississippi rivers. The lake is shallow for one of its surface area (Table 1; Fig. 1) and its fetch is sufficient to prevent summer stratification. In our measurements during the summer of 1977, temperatures varied less than 4 C from surface to bottom, even after several warm, calm days in July. Conductivity, alkalinity, and pH were nearly uniform throughout the water column. Alkalinity and conductivity are low and the water has a distinct brown color.

A mix of coolwater and warmwater fishes typical for the region inhabits the lake. The species list in 1977 included muskellunge *Esox masquinongy,* northern pike *Esox lucius,* walleye *Stizostedion vitreum vitreum,* yellow perch *Perca flavescens,* smallmouth bass *Micropterus dolomieui,* largemouth bass *Micropterus salmoides,* rock

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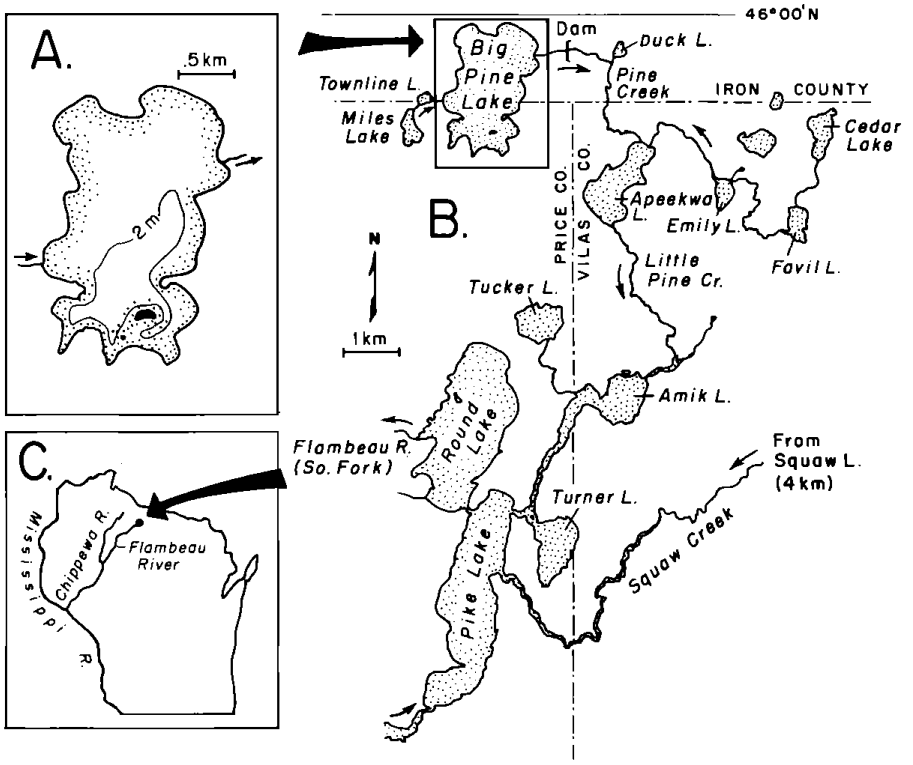

FIGURE 1.—*Map of Big Pine Lake (A) and its location in northern Wisconsin (B and C). Location of the 2-m contour is approximate.*

bass *Ambloplites rupestris,* black crappie *Pomoxis nigromaculatus,* bluegill *Lepomis macrochirus,* pumpkinseed *Lepomis gibbosus,* white sucker *Catostomus commersoni,* black bullhead *Ictalurus melas,* bluntnose minnow *Pimephales notatus,* golden shiner *Notemigonus crysoleucas,* and mottled sculpin *Cottus bairdi.*

A variety of human activities may have affected the fishes.[2] The surrounding forest was logged clear in the early 1890s, when the property was owned by a logging company. Later in the decade, the property was sold to private citizens. It since has been administered collectively by a small group of owners. There has been turnover within this group. During the early 1900s, living accommodations were erected on the larger island, and a small house and a barn for subsistence farming were built on the southeast shore. Some time between 1900 and 1917, channels large enough to accommodate a small boat were dug, linking Big Pine, Townline, and Miles lakes (Fig. 1). An earthen dam was constructed on the intermittent outlet

TABLE 1.—*Selected morphometric and summer water quality characteristics of Big Pine Lake. Data are from our 1977 survey, except as noted otherwise.*

Measure	Value
Surface area (hectares)[a]	256
Maximum fetch (km)[b]	2.5
Length of shoreline (km)[a]	7.26
Shoreline development factor[a,c]	1.28
Drainage basin area (hectares)[a]	1,684
Average depth (m)	2–3
Maximum depth (m)	11
Temperature (C)	
Maximum surface	27
Maximum bottom (7 m)	22
Dissolved oxygen (% saturation)	
Minimum bottom (7 m)	87
Secchi disc transparency (m)	1.9–3.2
Total alkalinity (mg/liter $CaCO_3$)	13
Conductivity (μmhos/cm at 25 C)	37
pH	6.9

[a] Black et al. (1963).
[b] From Fig. 1.
[c] Ratio of lake perimeter to circumference of a circle having the lake's area.

[2] The following background information was obtained from "The Island Club: 1917–1977," an unpublished 1977 history of the property by M. Lobermeier, and from personal communications with A. A. Oehmcke (who formerly worked in the area for the Wisconsin Department of Natural Resources) and property owners.

TABLE 2.—*Documented stocking history of Big Pine Lake. Records were provided by the Wisconsin Department of Natural Resources, except for the 1961 walleye stocking and the 1977 muskellunge stocking, which were reported by individuals familiar with the lake.*

Year	Species	Number stocked	Size
1961	Walleye	40,000	Fry
1964	Muskellunge	300	Fingerlings
1965	Walleye	12,370	Fingerlings
1968	Muskellunge	150	Fingerlings
1969	Muskellunge	300	Fingerlings
1974	Muskellunge	50	18 cm
1977	Muskellunge	50	28–38 cm
1979	Muskellunge	75	Fingerlings
1979	Smallmouth bass	350	13 cm

TABLE 3.—*Frequency of words used in the Big Pine Lake logbooks to describe the number of fish caught and the numerical equivalents assigned to them.*

Term	Assigned number	Number of times used: Muskellunge	Walleye	Bass
Couple	2	1		
Several	4		9	4
Few	4		1	1
A number of	5		1	
Some	5			1
Many	10	2		1
Plenty	15		2	
Innumerable	20		1	

sometime prior to 1940. The dam washed out in 1944.

Muskellunge, smallmouth bass, largemouth bass, walleye, yellow perch, rock bass, bluegill, and pumpkinseed were all present in Big Pine Lake prior to 1917. Muskellunge and smallmouth bass were valued as game fish and were more actively sought by anglers than were walleyes and largemouth bass, which were regarded more as meat. During the 1930s, the Wisconsin Department of Natural Resources used muskellunge from Big Pine Lake as spawning stock for a portable hatchery. An undocumented number of progeny were returned to the lake. Muskellunge, walleye, and smallmouth bass have been stocked since the 1960s (Table 2). We are informed that several small plantings of smallmouth and largemouth bass have gone unrecorded. Club policy strictly mandated the release of all angler-caught smallmouth bass, except for badly injured fish. Muskellunge were harvested occasionally, but the majority were returned to the lake. Northern pike first appeared in the catch in 1946 but rarely were fished intentionally. Anglers initially released northern pike but, with time, the species increasingly was regarded as a nuisance. By 1977, a significant fraction of northern pike captured was killed. Efforts to remove northern pike by netting during the spawning season were made during the 1960s and 1970s, under the auspices of the Wisconsin Department of Natural Resources.

Sources of Data

The history of the fishery was reconstructed from entries in logbooks dating back to 1897. Most of the entries listed the number of each species caught. Because smallouth and largemouth bass often were not separated, we grouped them into one category. Owners, however, agreed that smallmouth have been more plentiful than largemouth bass. Some entries also specified weights, but many only gave a range (for example, "ten muskellunge from 10 to 15 lb"). Individual weights were listed more often for muskellunge than for other species. We assumed that bass and walleyes described as "small" weighed less than 0.9 kg. Lengths were given only for unusually large fish. Few entries stated the number of angler hours, so catch per effort cannot be calculated. Alternative measures or indicators of effort are also unavailable. Entries for species other than muskellunge, northern pike, walleye, yellow perch, or bass appeared only four times (twice for rock bass and twice for bluegill) and were excluded from the analysis.

Anglers occasionally described the catch in qualitative terms, particularly for walleye. We assigned numerical equivalents to words such as "couple," "several," and "many" (Table 3). Such vague references were uncommon.

These data do not constitute a complete tally of all angler-caught fish. Records for many years were missing altogether. No data were available from 1900 through 1916. Fishermen were generally diligent about reporting their catches during the period 1917–1937. Records for the following decades were much less complete, with partial reporting in some years and none in others. The custom of recording catches eroded after 1960 and largely ceased by 1977. Entries in the logbook for most years from 1965 to 1976 were too infrequent to be assumed to represent

the actual catch. We conducted an angler survey during the summer of 1977 to supplement the logbook record. Catch report forms were provided, and anglers were asked to complete these forms during or after a day's fishing. The 1977 creel census accounted for most (94%) of the 162 fish reported between 1975 and 1977.

Discussions with persons of longstanding association with Big Pine Lake helped corroborate or refute trends implied by the data after 1937. Six individuals were interviewed, including four whose familiarity with the lake dates back prior to 1940. The two others often fished in Big Pine Lake during the 1950s and 1960s. These people were asked to recount their perceptions of how the fishery has changed, if at all. Only a few specific questions about the fishery were asked, aside from clarifications. These questions pertained to the relative abundance of smallmouth and largemouth bass, the year in which the dam washed out, the year in which northern pike first appeared, and the occurrence of undocumented stockings.

We obtained length measurements and scale samples for northern pike and incidentally captured muskellunge during the northern pike removal program in April 1978. The fyke nets used in sampling had a mesh size of 2.5-cm bar. Scales were impressed on acetate slides and their impressions examined at 39× magnification. Criteria for annuli were similar to those of Frost and Kipling (1958).

Air temperatures are from United States Weather Stations at Minocqua, 30 km away, for 1905 to 1911, and Park Falls, 31 km away, for 1912 to 1980 (NOAA 1905–1980). Mean monthly temperatures for June, July, and August were averaged to give an average summer temperature.

Results

Species Composition

An initial period of relative stability in the species composition of the sport catch in Big Pine Lake was followed by an era of considerable change (Fig. 2). The relative numbers in the catch of muskellunge, northern pike, walleye, and bass differed among the 13 5-year periods (G-test = 904; df = 36; $P < 0.001$; with muskellunge deleted: G-test = 512; df = 24; $P < 0.001$). From 1897 through the middle 1930s, muskellunge, walleye, and bass all contributed appreciably to the total catch, and relative abundances in the angler catch were similar on both sides of the gap in the catch record (1900–1916). Percentages ranged from 20 to 44% for muskellunge, 42 to 54% for walleye, and 14 to 27% for bass. Muskellunge continued at the same general level of relative abundance through the middle 1950s (23–47%) except during the early 1940s, when the sample size was very small. The relative abundances of bass and walleye, however, changed dramatically. Between 1940 and 1960, bass dominated the catch (35 to 65% of the total) and walleyes became rare (2–17%). Walleyes nearly disappeared from the fishery in the early 1960s. Yellow perch accounted for more than 1% of the reported catch only during the late 1950s and early 1960s, when walleyes made up less than 3% of the catch. Walleyes were stocked twice during the 1960s (Table 2). Since then, walleyes again have become abundant, and the percentage of bass in the catch has declined sharply. Because of the scarcity of data for the late 1960s and early 1970s, it is unclear whether these changes occurred gradually or suddenly.

Creel census data indicate that, by 1977, the relative abundances of *Esox*, *Stizostedion*, and *Micropterus* species had reverted to pre-1935 levels, but that northern pike, which first entered the fishery in the late 1940s, accounted for most of the esocid component. The replacement of muskellunge by northern pike (Fig. 2; Table 4) occurred after the dam on the outlet washed out in 1944 and allowed northern pike to enter the lake. Prior to 1945, no northern pike had been caught. The muskellunge decline began in the late 1950s and continued through 1977. Northern pike increased from 1% of the catch in the late 1940s to 34% by the early 1960s, and to 37% by 1977. During this period of northern pike abundance and muskellunge scarcity, muskellunge were stocked in six out of 20 years (Table 2), northern pike were netted and removed at spawning time, and anglers usually killed the northern pike they caught.

Major changes in the ratio of walleye to bass were foreshadowed by periods in which summers were unusually warm or unusually cold (Fig. 2; Table 5). Average air temperatures fluctuated irregularly from 1905 to 1930, with no sustained trends. The relative abundance of walleye and bass changed little during this period. The 1930s, the decade preceding the ap-

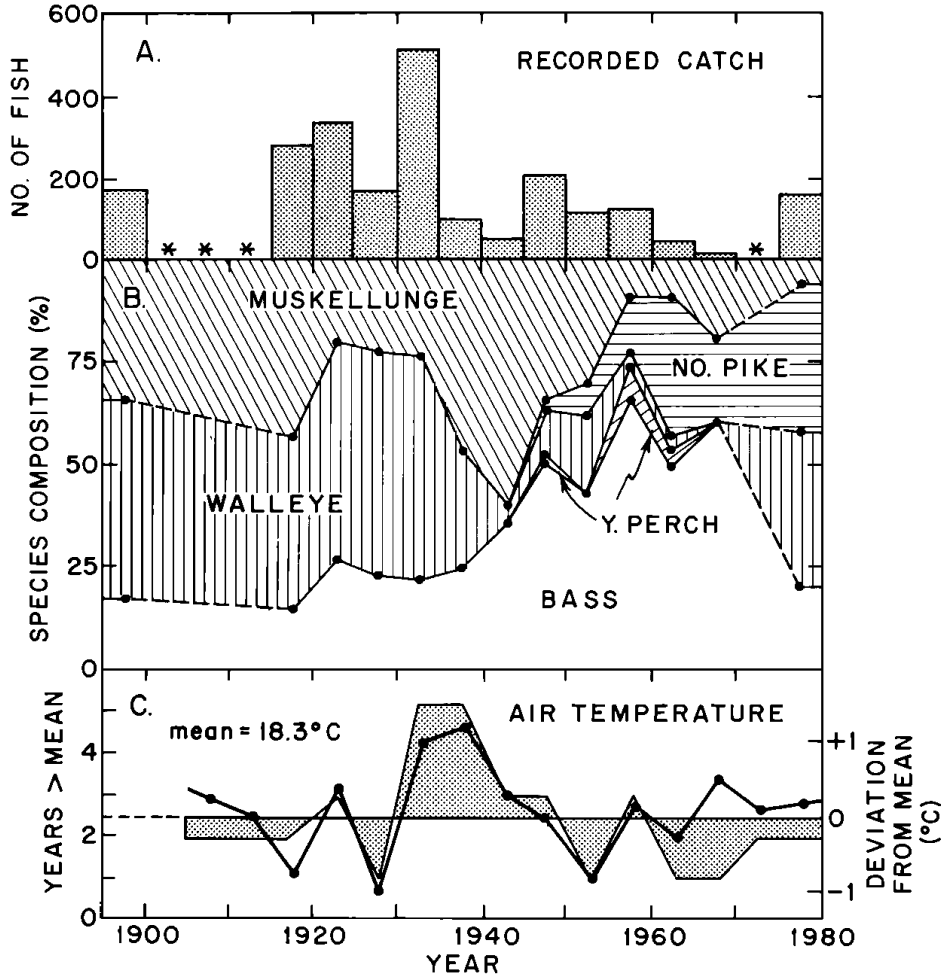

FIGURE 2.—*Species composition of the angler catch (1897–1977) in Big Pine Lake grouped by 5-year intervals beginning with 1895 (B), the total number of fish recorded for each interval (A), and the number of years out of five that the average summer (June–August) air temperature exceeded the mean for 1905–1980 (shaded area), together with the average deviation from the mean for the 5-year interval (solid line) (C). Asterisks (*) signify missing data.*

parent switch in relative abundance, were characterized by a succession of warm summers. The 1940s and 1950s had a mix of warm and cool summers, and the relative abundance of walleye in the fishery declined. A preponderance of cool summers during the 1960s and 1970s was followed by an increase in the relative abundance of walleye, and a decrease in the relative abundance of bass.

The percentage of muskellunge in the reported catch also increased during the late 1930s and early 1940s, following the sequence of warm summers. Sample sizes for these years were quite small. Changes in relative abundances of north-

TABLE 4.—*Numbers of muskellunge and northern pike recorded in the catch before and after the dam washed out of the outlet (G-test = 268; df = 1; P < 0.001).*

Time	Muskellunge	Northern pike
Before washout (1895–1944)	491	0
After washout (1945–1977)	141	105

TABLE 5.—*Numbers of walleye and bass recorded in the catch during the 20 years before and the 20 years after January 1, 1940, which is the midpoint of the warmest decade on record (G-test = 342; df = 1; P < 0.001).*

Time	Walleye	Bass
1920–1939	581	183
1940–1959	45	252

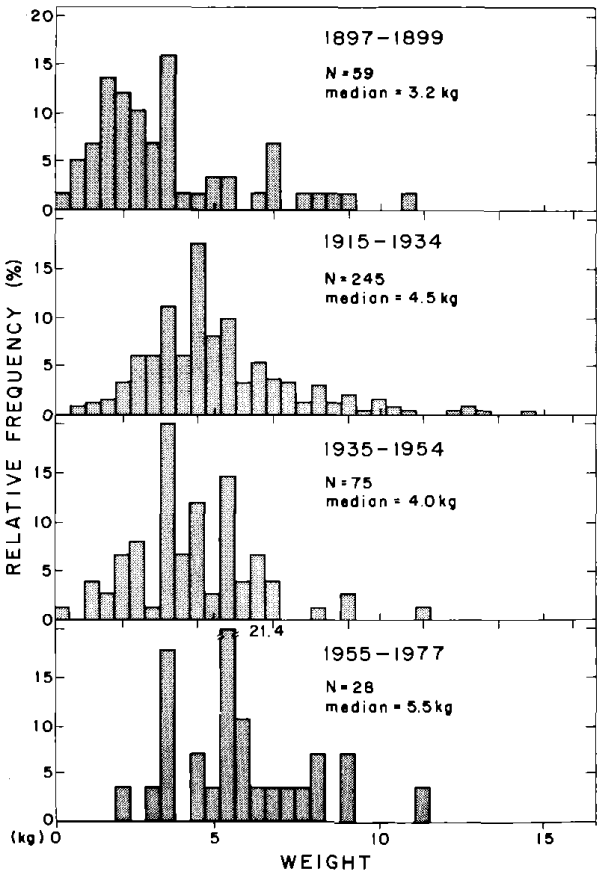

FIGURE 3.—*Weight-frequency distributions of angler-caught muskellunge grouped by years, Big Pine Lake.*

ern pike and yellow perch do not appear to be related to average summer air temperature (Fig. 2).

Size and Age Composition

Only 11 out of the 407 recorded muskellunge (2.7%) were heavier than 10 kg. The heaviest weighed 14.5 kg.

Weights of muskellunge in the angler catch increased over time (Fig. 3). Small muskellunge predominated in the catch during the late 1800s. The median weight was 3.2 kg, and 27% of those captured weighed less than 2.2 kg. Muskellunge caught in the two following recording intervals (1915–1934 and 1935–1954) were larger. Median weights were 4.5 and 4.0 kg, respectively, and roughly 5% of the catch weighed less than 2.2 kg. Weight-frequency distributions for these two periods were generally similar. In the most recent interval (1955–1977), the median increased to 5.5 kg, and small muskellunge were uncommon. No fish in the recorded catch weighed less than 2.2 kg.

Small, young muskellunge were also absent among fish captured in fyke nets during spring 1978 (Fig. 4). In northern Wisconsin, most male muskellunge probably spawn for the first time at age 4 and females at age 5 or 6 (Johnson 1971; S. Serns, Wisconsin Department of Natural Resources, personal communication, 1982), but ages 4, 5, and 7 were poorly represented in the nets. Forty-four percent of the muskellunge captured were from the 1968 and 1969 year classes, both of which had been supplemented by stocking (Table 2).

Northern pike captured in the spring 1978 fyke nets were small and young in comparison to muskellunge (Fig. 4). Most northern pike probably spawn for the first time at age 2 (Priegel and Krohn 1975), and ages 2 through 6 all were represented.

More than 60% of the bass caught by anglers exceeded 0.9 kg (Fig. 5). Proportions of bass in the three weight categories were relatively sta-

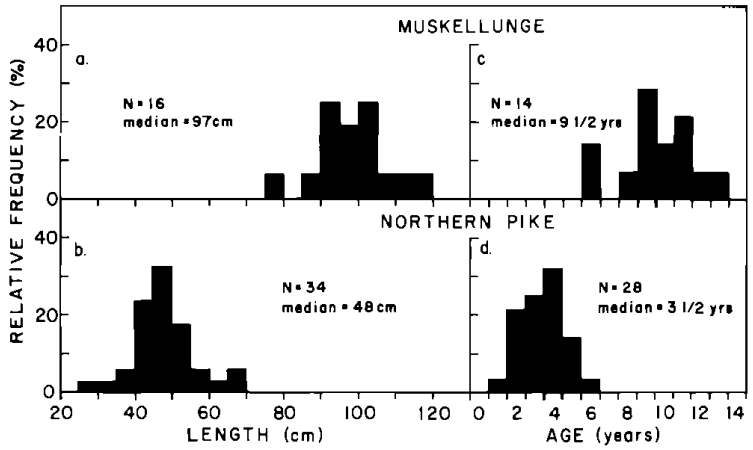

FIGURE 4.—*Length- (a, b) and age- (c, d) frequency distributions for muskellunge and northern pike captured in 2.5-cm bar mesh fyke nets in Big Pine Lake, April 1978.*

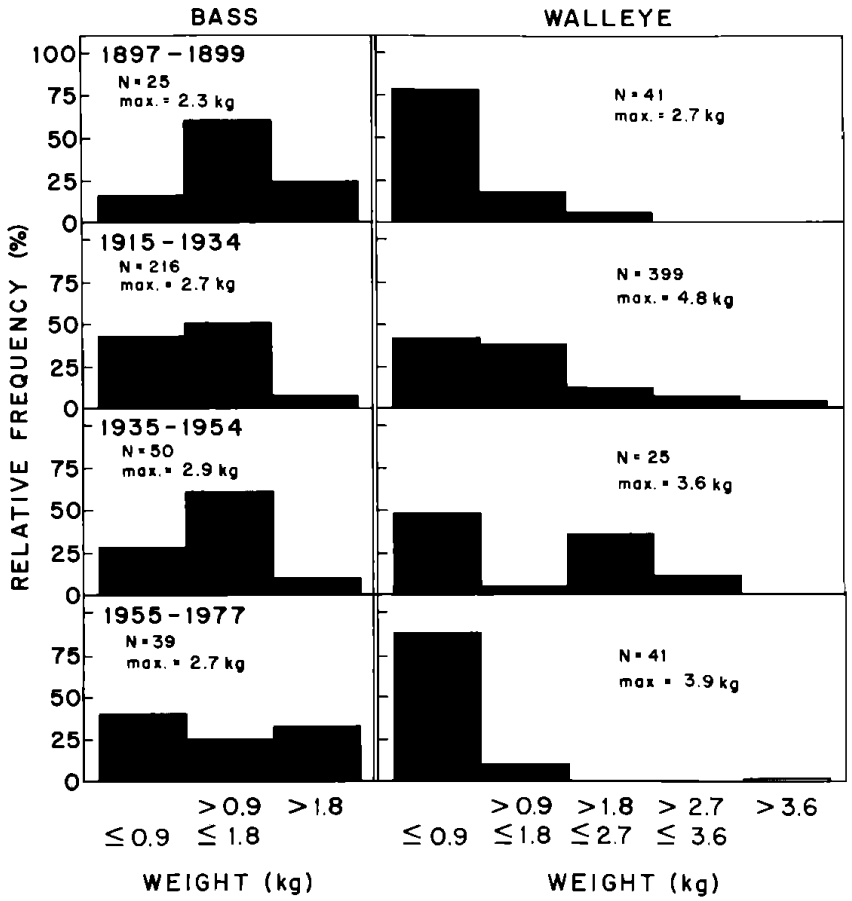

FIGURE 5.—*Weight-frequency distributions for angler-caught bass and walleyes, grouped by years, Big Pine Lake.*

ble from the 1890s to the mid-1950s. The pattern changed in recent years, to a higher percentage of large bass and a lower percentage in the intermediate size range.

Walleye size structure also varied (Fig. 5). Small fish were particularly abundant in the records for the 1890s and for the most recent period. The intervening years had a more even distribution among weight classes.

Evaluation of the Catch Record as an Indicator of Changes in Fish Populations

If we are to interpret the logbook record as a chronicle of changes in relative abundances of sport fishes in Big Pine Lake, we must first consider whether or not the data are adequate for this purpose. Two concerns are paramount. (1) Are sample sizes large enough to assume that the catch data accurately reflect fish community structure? (2) Does the logbook track changes in fishing or recording habits of anglers rather than changes in relative abundances of fishes?

We have judged that the general trends in the data are valid based on five lines of evidence. (1) Game fish were stocked at times when their proportions were low in the recorded catch. (2) Written comments of a general nature in the logbook support general, but not precise, inferences based on the catch record. (3) Responses of anglers to questions about past abundances of game fish in Big Pine Lake corroborate the logbook. (4) Inferences based on the relative number and the relative size of fish caught are consistent. (5) Catches in adjacent 5-year periods vary regularly rather than erratically.

The stocking history of Big Pine Lake indicates that owners perceived the same major changes in relative abundance implied by the logbook data, at least for the middle 1950s through the 1970s. Because there is no public access to Big Pine Lake, the Wisconsin Depart-

ment of Natural Resources does not stock the lake. Owners must contract with private fish culturists when stocking is desired. Years in which recorded stockings occurred (Table 2) closely correspond with periods of decreased relative abundance (Fig. 2). Walleyes were stocked in the 1960s but not in the 1970s, muskellunge were stocked both in the 1960s and 1970s, and bass were stocked in 1979 only.

Logbook entries included observations that we did not convert to numerical terms but are relevant. A 1938 entry commented on the "very nice smallmouth bass and pike [walleye] fishing." One 1948 account mentioned that there were "always enough pike [walleye] to eat," and another stated that a northern pike had been caught in Big Pine Lake, "the third ever." The 1958 entries included the following remark: "Quite a few fish have been caught during August. Most of them have been bass and northerns." When compared against the actual catch record, these last two observations fit nicely, but the 1938 and 1948 comments on walleye do not. Catch data indicate a sharp decline in the relative abundance of walleye during the late 1930s and early 1940s, while recorded angler impressions do not. The discrepancy can be reconciled if muskellunge dramatically increased in abundance while walleye abundance remained constant or changed only slightly; however, we have no independent evidence of a sharp increase in muskellunge and cannot determine precisely when the walleye decline began.

Interviewed anglers were consistent in their recollections that the decline in walleye had occurred by the middle 1950s. Four anglers whose familiarity with the lake dates back to the late 1940s or before, independently recalled a period of walleye scarcity that included the 1950s. Two individuals recalled the decline as beginning "after World War II," and a third placed it in the early to middle 1950s. The fourth person did not specify a date.

If recruitment failure occurred for walleye in the 1950s, the few reported during the 1950s and early 1960s, prior to the restocking, should have been larger than those from previous or later years. Recorded weights of walleyes captured between 1950 and 1963 were large and varied from 2.3 to 3.9 kg (11 fish). This does not simply reflect selective recording. Three interviewees independently commented on the absence of small walleyes during the late 1950s and 1960s.

The consistency in catch between adjacent 5-year intervals suggests that the samples represent a real property of the lake's fish community. For example (Fig. 2), muskellunge were more abundant than northern pike in all nine of the 5-year periods prior to 1960, whereas the reverse was true in the three 5-year periods with data after 1960. Also, bass were more abundant than walleyes in all six of the 5-year periods between 1940 and 1970, but had been less abundant in all six of the intervals prior to 1940. A more erratic pattern would be expected if sample sizes were inadequate to determine general trends.

An assumption that general changes in the sport fish community can be inferred on the basis of this catch record seems reasonable to us. Stocking records, angler recollections, consistency between interpretations from size and abundance data, written comments in the log, and consistency in proportions between adjacent 5-year periods all support the credibility of major trends in the catch data. Even so, the possibility that selective fishing or recording habits have contributed to the observed variation in species composition of the recorded catch cannot be discounted entirely. Concern over such artifacts centers on those 5-year intervals for which the number of fish in the reported catch was small and differences in the habits of individual anglers could easily be a factor.

Discussion

Predominance in the Big Pine Lake sport fishery shifted from coolwater fishes (walleye and muskellunge) through the first half of the record, to warmwater fishes (smallmouth and largemouth bass) during 1945 to 1970, and back to coolwater fishes (including northern pike) by 1977. Parallels between species shifts and average summer air temperatures suggest that climatic fluctuations have influenced fish community structure strongly.

A positive association between summer air temperature and reproductive success of smallmouth bass has been noted for other lakes near the northern limit of the species' range (Fry and Watt 1955; Christie and Regier 1973; Shuter et al. 1980). Higher temperatures favor growth, which in turn appears to increase survival of smallmouth bass over their first winter (Oliver

et al. 1979). Distribution of smallmouth bass is very uneven where mean July air temperature is less than 18.3 C, and the northern range is bounded by the 18 and 16.5 C isotherms (Shuter et al. 1980). The long-term (1905–1980) average July air temperature for the vicinity of Big Pine Lake is 19.5 C (NOAA 1905–1980). Smallmouth bass reproduction may have been enhanced by the succession of warm summers during the 1930s and early 1940s and lowered by frequent cool summers during the 1960s and early 1970s. The northern limit of the native range of largemouth bass is similar to that of smallmouth bass (Scott and Crossman 1973). Optimal temperatures for growth are in the 25–29 C range for age-0 smallmouth (Horning and Pearson 1973) and largemouth (Coutant and Cox 1976) bass. The two species probably were affected similarly by year-to-year variations in summer temperatures.

Changes in the relative abundance of bass were mirrored by reciprocal changes in the walleye fishery. The walleye decline was not simply a relative one during a time of plentiful bass. Walleyes nearly disappeared from the fishery by 1960. Negative correlations between the abundance of walleye and of bass have been noted for other northern lakes (Johnson and Hale 1977; Kempinger and Carline 1977), but the reasons for the association are unknown. Differences in thermal requirements may be a contributing factor.

Walleyes have a distinctly lower thermal optimum for growth—22–23 C for fingerlings, according to Smith and Koenst (1975)—than do either of the black basses. Seasonal changes in depth distribution of older walleyes indicated avoidance of temperatures above 21 C in a Minnesota Lake (Johnson 1968) and 24 C in a Tennessee reservoir (Fitz and Holbrook 1978). Most of Big Pine Lake warms above 24 C, even in a slightly cooler-than-average summer, such as 1977. This suggests that walleyes may experience thermal stress during an unusually warm summer; however, Wrenn and Forsythe (1978) found young walleyes to be tolerant of very warm thermal regimes (maximum temperature, 32–33 C). It is unclear what effects warm summers had on walleye survival and reproduction.

Summer air temperature alone cannot account for the sustained trends in relative abundance of walleye and bass in Big Pine Lake. Walleyes appear to have been more abundant than bass through 1930, even though there was a mix of warm and cool summers during the first quarter of the century. Similarly, bass remained relatively plentiful, and walleyes scarce, from the 1950s through the early 1960s, though again there was a balance of warm and cool summers.

These patterns can be explained if walleyes and bass interact in ways such that one suppresses abundance of the other. Fedoruk (1966) reported finding young smallmouth bass in walleye stomachs, and Johnson and Hale (1977) reported finding young-of-the-year and yearling walleyes in stomachs of smallmouth bass, all at a low frequency of occurrence. Cumulative predation by a large population of one species may reduce abundance of the other's young. Food-habit studies show little overlap between diets of walleyes and smallmouth bass older than 1 year (Fedoruk 1966; Johnson and Hale 1977); however, no information is available concerning food utilization by co-occurring age-0 fish. If there is competition between young-of-the-year walleye and bass, water temperature might influence the outcome. Suppression of one species by the other could be reversed by a sequence of unusually warm or cold years or by stockings of the less abundant species. The stockings of walleye in 1961 and 1965 may have been important in the reestablishment of the walleye population.

Available data seem to defy a simple explanation for the negative association between walleye and bass. Our data cannot isolate the mechanisms responsible for observed switches in Big Pine Lake. Even an 80-year record provides too little replication to allow any firm conclusions about the role of climate, but we feel that summer air temperature warrants further consideration as a mediating factor for the apparent interaction between these species.

Changes within the esocid component of the fishery over the course of this record suggest an interaction between muskellunge and northern pike, the other large piscivores in Big Pine Lake. The trend toward substitution of northern pike for muskellunge, which began in the 1950s, repeats events that occurred earlier in neighboring lakes (Oehmcke 1951) and throughout northern Wisconsin (Threinen and Oehmcke 1950; Johnson 1978). Northern pike were unknown from the area through 1936

(Elkins 1937), but, by the early 1940s, they were present in Pike, Round, Amik, Turner, and Apeekwa lakes (Fig. 1) (Oehmcke 1951 and personal communication, 1977). By the middle 1940s, northern pike were abundant in these waters, and anglers complained of deteriorating muskellunge fishing (Oehmcke 1951). The dam on the outlet stream delayed colonization of Big Pine Lake through 1944; however, by the middle 1950s, northern pike had become abundant there, and the muskellunge catch was down.

Predation by young-of-the-year northern pike on young-of-the-year muskellunge is a possible mechanism of interference (Oehmcke 1951). Northern pike hatch earlier, often occur in the same parts of lakes as young muskellunge, and are cannibalistic at sizes as small as 21 mm (Hunt and Carbine 1951). The early size advantage of northern pike would make young muskellunge especially vulnerable to northern pike predation.

Size- and age-frequency data for esocids from Big Pine Lake are consistent with the hypothesis that northern pike interfere with muskellunge recruitment. The establishment of northern pike was accompanied by a drop in the relative abundance of small muskellunge in the angler catch, and no young muskellunge were caught in the spring 1978 fyke nets. Immature muskellunge rarely are captured in spring fyke nets (Serns, personal communication, 1982), so the absence of 2- and 3-year-old fish should be expected; however, ages 4, 5, and 7 were also absent. Four- and 5-year-old northern pike, on the other hand, were relatively plentiful in the catch. Nearly half of the muskellunge in the fyke nets belonged to year classes that had been augmented by stockings. We have no information concerning the breakdown of stocked versus naturally reproduced individuals in these age groups; nonetheless, it appears that the fishery has changed from one supported entirely by natural reproduction to one dependent on periodic stockings.

The species structure of Big Pine Lake has responded to a series of disturbances and resultant periods of change. The important disturbances in our view were the arrival of northern pike and the extended sequences of warm and cool summers. Should the climatic sequences recur, we predict corresponding changes in the relative abundance of walleye and bass. The trend toward substitution of northern pike for muskellunge seems more permanent in the absence of human intervention.

Studies of unexploited fish populations repeatedly have demonstrated a high proportion of large, old fish. Most information is for populations of salmonid and coregonid fishes in Arctic lakes (Johnson 1972, 1976; Power 1978), but similar observations have been recorded for centrarchids and percids in Michigan and Wisconsin (Clady et al. 1975; Goedde and Coble 1981).

Research has shown that angling quickly can change the size structure of bass populations. When a large tract of land in northern Michigan switched from private to public ownership in 1966, fishery managers opened four lakes on the property to trophy fishing for smallmouth bass, with a minimum size limit of 46 cm (Clady et al. 1975). The number of smallmouth bass exceeding this limit dropped sharply within 1 year in three of the four lakes. A similar response was observed for a population of largemouth bass when a previously unfished Wisconsin lake was opened to public angling (Goedde and Coble 1981).

Because of the historically low fishing effort in Big Pine Lake, and the catch-and-release policy for muskellunge and smallmouth bass, we expected the fish community to have a history of large fish. This expectation is borne out by the size data for bass but not for muskellunge. More than half of the bass were heavier than 0.9 kg. This compares with a 24-year average weight of 0.33 kg for bass harvested from Escanaba Lake, a nearby lake with public access and no minimum size limits, bag limits, or closed season (Kempinger et al. 1975).

Muskellunge in Big Pine Lake have not been unusually large. The prevalence of small muskellunge in the early years of the fishery (1897–1899) and the absence of exceptionally large muskellunge throughout the years are contrary to expectation for a lake that has received so little fishing pressure. Because the scarcity of large fish persisted through the 1960s and 1970s, when muskellunge density was low, intraspecific density-dependent factors cannot be solely responsible.

The sustained high relative abundance of muskellunge in the Big Pine Lake fishery does contrast with what happened in neighboring,

more heavily fished lakes. Railroads made area lakes accessible to anglers beginning around 1880 (Nesbit 1973). By the turn of the century, muskellunge had grown scarce in many lakes, and Wisconsin judged it necessary to begin a program of artificial propagation (Nevin 1901).

We are less confident about characterizing walleye in Big Pine Lake as a lightly exploited stock. Owners concur that the walleye harvest has increased in recent years. One individual estimated that the annual harvests in 1976 and 1977 were in the hundreds. The size distribution for 1977, however, was not radically different from that for 1897–1899, a time when the population was, we believe, in the very earliest stages of even light exploitation.

Kelso and Ward (1977) reported considerable annual variability in the size and age structures of the walleye population in a culturally unstressed Manitoba lake and concluded that the cause was year-to-year variation in reproductive success. Salmonid and coregonid populations in many unexploited Arctic lakes have stable size structures in spite of variable reproductive success (Johnson 1972, 1976). Such stability is possible where species are long-lived and grow rapidly toward an asymptotic size (Power 1978). Modes in length-frequency distributions for such populations consist of several, or many, age groups, and missing year classes do not create such noticeable gaps as they do for populations composed of fewer age groups. Natural lifespans for esocids, percids, and centrarchids in Wisconsin are considerably shorter than for salmonids or coregonids in the Arctic. Variations in year-class strength probably influence size structure to a greater degree in Big Pine Lake than does exploitation. This natural variation could produce results contrary to expectation for a lightly fished community.

Associations among the relative abundances of walleye, black bass, muskellunge, and northern pike indicate that long-term climatic trends and interactions among these species have played a greater role in shaping the fishery than has angling pressure.

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