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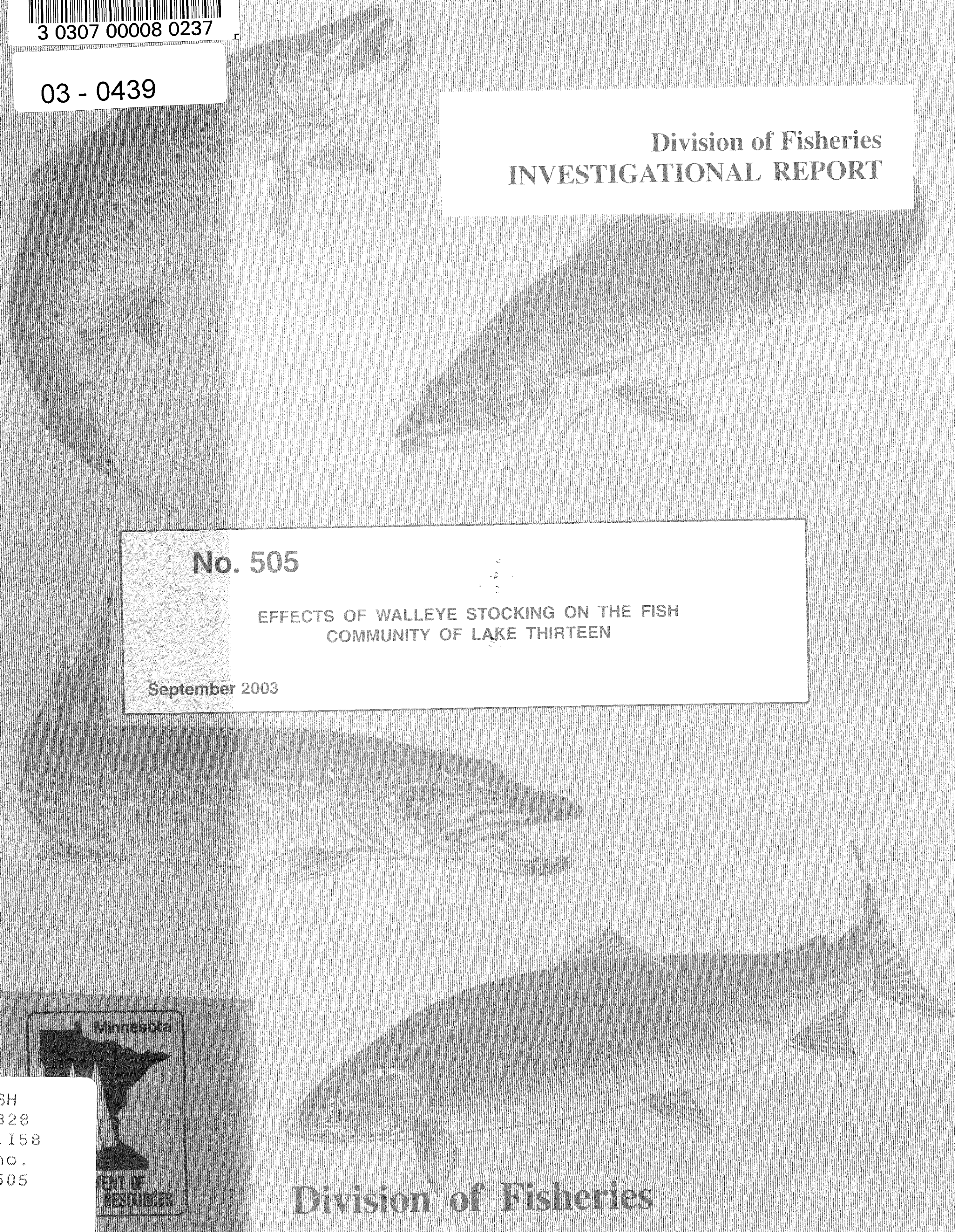

No. 505

EFFECTS OF WALLEYE STOCKING ON THE FISH COMMUNITY OF LAKE THIRTEEN

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Minnesota Department of Natural Resources
Investigational Report 505, September 2003

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EFFECTS OF WALLEYE STOCKING ON THE FISH COMMUNITY OF LAKE THIRTEEN[1]

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Abstract.–Fish community responses to discontinuing, then resuming walleye stocking were monitored in Lake Thirteen, a lake with a consistent history of fry stocking. Fish population assessments during 1986-2002 tracked changes in relative abundance, size structure, and growth rates of fish in response to discontinued walleye stocking during 1989-1996. Large changes occurred in size structure and relative abundance of walleye. The effect of discontinued stocking was to decrease the abundance of younger age classes of walleye in the lake. Yellow perch were most sensitive to changes in the walleye population. When stocking was discontinued, reduced predation on small yellow perch allowed their numbers to increase and led to reduced growth rates. When stocking was resumed, predation by stocked walleye reversed the trend, reducing yellow perch numbers and improving their growth rates. Variable recruitment was predominant among the fish species in Lake Thirteen, and limited food resources led to intraspecific competition that was intense enough to restrict fish growth rates. Density-dependent growth was evident for walleye, yellow perch, and largemouth bass. Variable recruitment, intraspecific competition for food, and interannual climate changes all helped confound our ability to interpret changes in fish community structure, and masked any effects of walleye stocking on species other than yellow perch. Although this study was intended to evaluate the influences of walleye stocking on a fish community, results are relevant to the ecological role of walleye in lakes where it is a native species, and illustrate how predator sizes can mediate structural changes in a prey population.

[1] This project was funded in part by the Federal Aid in Sport Fish Restoration (Dingell-Johnson) Program. Completion Report, Study 624, D-J Project F-26-R Minnesota.

Introduction

Walleye *Sander vitreus* stocking has historically been a major component of the fisheries management program in Minnesota. Both fry and fingerling stocking have been used to create walleye fisheries in lakes that did not seem capable of sustaining naturally reproducing walleye populations. In 1985, for example, Minnesota stocked over 511 million walleye fry and nearly 2.8 million fingerlings. More intensive review and evaluation of walleye stocking during the next decade led, in many cases, to discontinuing ineffective stocking. By 1996, the walleye stocking program had been reduced to 196 million fry and 2.2 million fingerlings. In spite of these advances, political and social pressure rolled back the rational use of walleye stocking beginning in 1999, and stocking was increased statewide with much less regard for efficiency or the ecological consequences on fish community dynamics.

The enormity of the walleye stocking program in Minnesota led to our initial questions about the effects that walleye stocking has on other fish populations within aquatic communities. Work conducted in Lake Thirteen during 1986-1996 (Pierce and Tomcko 1998) monitored fish community responses to discontinued walleye stocking in the lake. The initial work at Lake Thirteen posed some new questions that had further management implications. First, would high densities of small yellow perch observed during 1994-1996 limit the effectiveness of restocking walleye as fry? Second, would the trends toward increased numbers of small yellow perch and reduced recruitment of northern pike be reversed by restocking walleye? Third, did changes in walleye stocking have any long-term effects on other fish species in Lake Thirteen? We tried to answer these questions by monitoring fish community responses to resumption of fry stocking during 1997-2002. Studies of fish communities in small lakes with such a consistent longer-term sampling program (17-years) are rare. Therefore, this study was also used to identify potential pit-falls in interpreting data from the less frequent fish population surveys commonly conducted in Minnesota lakes.

Study Area

Lake Thirteen is surrounded by the Chippewa National Forest in Cass County, Minnesota (47° 17' N latitude, 94° 32' W longitude). It has a surface area of 222 ha, a maximum depth of 17.0 m, and total alkalinity of 117 $mg \cdot l^{-1}$ $CaCO_3$. The lake has extensive littoral area with 74% of the lake surface area shallower than 4.6 m. Shoal areas are predominantly sand, large beds of muskgrass *Chara* spp., and a fringe of bulrush *Scirpus acutus*. Other macrophytes such as pondweeds *Potamogeton* spp. are also present in low densities. Substrate in depths greater than 3-4 m consists of silt and remains of mollusk shells. Lake Thirteen had a relatively simple fish community consisting of only six large-fish species - northern pike *Esox lucius*, white sucker *Catostomus commersoni*, pumpkinseed *Lepomis gibbosus*, largemouth bass *Micropterus salmoides*, yellow perch, and walleye. Small cyprinids common in Lake Thirteen were blackchin shiner *Notropis heterodon*, blacknose shiner *Notropis heterolepis*, spottail shiner *Notropis hudsonius*, and bluntnose minnow *Pimephales notatus*. Other small-fish species sampled were central mudminnow *Umbra limi*, tadpole madtom *Noturus gyrinus*, banded killifish *Fundulus diaphanus*, brook stickleback *Culaea inconstans*, Iowa darter *Etheostoma exile*, and Johnny darter *Etheostoma nigrum*. The centrarchid population of Lake Thirteen was somewhat unique because it consisted only of pumpkinseed and largemouth bass until 2001, when bluegill *Lepomis macrochirus* were first discovered in the lake.

Historically, fish stocking was a prevalent management practice in Lake Thirteen with walleye stocking records dating back to 1945. Walleye fingerlings and fry were stocked frequently after 1950 and fry were stocked annually between 1976 and 1988, and again from 1997-2002 (approximately 500,000 fry per year). Early records also show some stocking of northern pike, largemouth bass, and black crappie, although none of these species were stocked after 1966.

Sand Lake, also located in Cass County (46° 54' N latitude, 94° 20' W longitude), was used as a reference lake for interpreting year class fluctuations and environmental influences on the fish communities during this study. Sand Lake has a surface area of 54 ha, a maximum depth of 16.5 m, and total alkalinity of 37 mg·l^{-1} $CaCO_3$. The littoral area (depths less than 4.6 m) is 40% of the surface area. Shoal areas in Sand Lake are predominantly sand with patches of pondweeds and bulrush. The fish community in Sand Lake was more complex than Lake Thirteen, with large species consisting of the six from Lake Thirteen along with yellow bullhead *Ameiurus natalis*, brown bullhead *Ameiurus nebulosus*, rock bass *Ambloplites rupestris*, bluegill, and black crappie *Pomoxis nigromaculatus*. Additional small species were golden shiner *Notemigonus crysoleucas* and mimic shiner *Notropis volucellus*. Walleye fingerlings or fry were stocked seven times between 1965 and 2002, and walleye natural reproduction has also been evident in Sand Lake.

Methods

Lake Thirteen Sampling

Fish sampling gear consisted of (1) 19-mm-bar mesh single-pot trap nets with 12.2-m leads, two throats, and a 0.9 X 1.8-m rectangular frame opening into the trap; (2) multifilament nylon gill nets that were 76.2 m long and had panels with 19, 25, 32, 38, and 51-mm bar meshes; and (3) an electrofishing boat operated along the shoreline at night with 150 V and 5-7 A pulsed DC current. In 1986, initial sampling of the fish populations in Lake Thirteen was by gill netting and electrofishing during fall (23 September-9 October). With the exception of 1993, electrofishing and trap netting were conducted annually from 1987-2002. In 1993, we used only electrofishing in an effort to determine if walleye natural reproduction was occurring. Electrofishing was conducted in early fall (24 August-20 September) with efforts of 150-420 minutes each year. Trap netting was conducted in late summer (30 July-28 August) with efforts of 10-24 overnight net sets each year. Gill netting was also conducted in late summer during 1987, 1988, 1995, 1996, 2000, and 2002 using 9 overnight gill net sets each year. Some supplemental gill netting occurred during 1991-1993 using 4-6 overnight net sets each year. Gill net sampling locations were randomly picked each year from grid locations on a lake map although nets were not fished shallower than 2 m, and they were not fished in depths with low dissolved oxygen concentrations (<5 mg/l). Fish were subsampled for total length (mm) and weight (g) measurements. Proportional stock densities (PSDs) were calculated using the criteria in Anderson and Gutreuter (1983). Confidence limits for PSDs and other proportions were calculated with the quadratic formula described by Fleiss (1981).

Scale samples were obtained from northern pike, largemouth bass, pumpkinseed, walleye, and yellow perch to determine age and growth rates. Additionally, opercles were obtained from walleye and cleithra from northern pike as additional structures for aging fish. The microcomputer program DISBCAL (Frie 1982) was used to back calculate body growth from scale measurements. A linear growth model (Weisberg and Frie 1987; Weisberg 1989) was used to model the growth of scales sampled from fish. The linear growth model partitions variation in scale growth into age effects and year (or environmental) effects. Age effects are from the size of the fish or its life history stage. Year effects are interannual differences in growth that are due to changes in the fish's environment, such as food resources or temperature. Log_e transformation of scale increments was used to improve residual plots for the model. To examine the effects of interannual temperature changes on fish growth, year effect coefficients were regressed on mean daily air temperatures compiled for June-August each year at nearby National Weather Service stations.

Sand Lake Sampling

Fish populations in Sand Lake were sampled by gill netting, trap netting, and electrofishing using procedures similar to those used in Lake Thirteen. Electrofishing occurred during early fall in most years (1987-1992, 1994-1998, 2000, 2002) using 75-105 min of effort each year. Trap netting was conducted during the same years in late summer using 6-12 overnight net sets. Gill netting occurred during late summer using 4-6 overnight net sets in 1987, 1988, 1992, 1995, 1996, 2000, 2002

Results

Walleye

Large changes occurred in the size structure of the walleye population in Lake Thirteen. The changes were a result of 1) an unusually large year class of walleye produced in 1988, 2) the discontinuation of walleye stocking between 1989-1996, and 3) the re-establishment of walleye by fry stocking beginning in 1997. The strong 1988 year class of walleye in Lake Thirteen dominated subsequent walleye catches (Figure 1) and was responsible for high gill net catch rates recorded in 1991-1992 (Figure 2). Growth of individuals from the 1988 year class affected annual mean lengths, PSDs (Figure 2), and length frequency distributions of walleye caught in gill nets (Figure 3). By 1996, the mean length of walleye caught in gill nets had increased to 517 mm (SE=6 mm), and PSD had increased to 100%. Fry stocking was apparently not successful in 1997, but good year classes were re-established in 1998, 1999, and 2001. As a consequence, gill net catch rates at the end of the study were similar to the high rates observed in 1991-1992, and mean length and PSD for walleye caught in gill nets were both reduced compared to 1995-1996.

After walleye stocking was discontinued in Lake Thirteen, only a small amount of natural reproduction was evident. Some natural reproduction was apparent for 1992 (Figure 1), but by 1996 the gill net catch consisted of 31 age 8 walleye (1988 year class) and 5 age 4 fish (1992 year class). This paucity of year classes during 1995-1996 differed from earlier years and later years of fry stocking when gill net catches consisted of a broader range of ages (Figure 1). No walleye younger than age four were encountered in any gear in 1996. Although we found no small walleye in Lake Thirteen during 1995-1996, the mean gill net catch rate of 4.0 walleye/net lift (SE=0.8) in 1996 indicated that there was still a relatively large number of older individuals present.

Density-dependent growth was evident in back calculated lengths of walleye caught in Lake Thirteen. The large 1988 year class of walleye grew slowly with an average back calculated length at age 3 of 260 mm (SE=3 mm; Table 1). Walleye captured from the 1992 year class, which did not have to compete with stocked fish and adjacent year classes, grew much faster reaching 388 mm (SE=5 mm) in 3 years. Similarly, re-establishment of walleye by stocking in 1998-1999 led to fast initial growth rates; average back calculated lengths at age 3 were 412 mm (SE=27) for the 1998 year class and 327 mm (SE=5) for the 1999 year class.

Walleye recruitment in Sand Lake provided a contrast to Lake Thirteen, with catches in 1995-1996 showing a broader spectrum of walleye sizes. Gill netted walleye during 1995-1996 ranged in length from 205 to 604 mm. The 1988 and 1992 year classes of walleye were only 5-11% of the catches during 1995-1996. Walleye recruitment was distributed among other year classes with fish from 1991, 1993-1999, and 2001 represented in electrofishing and gill net catches. As a result, mean length for walleye in gill net catches was more consistent over the study period in Sand Lake than in Lake Thirteen (Figure 2).

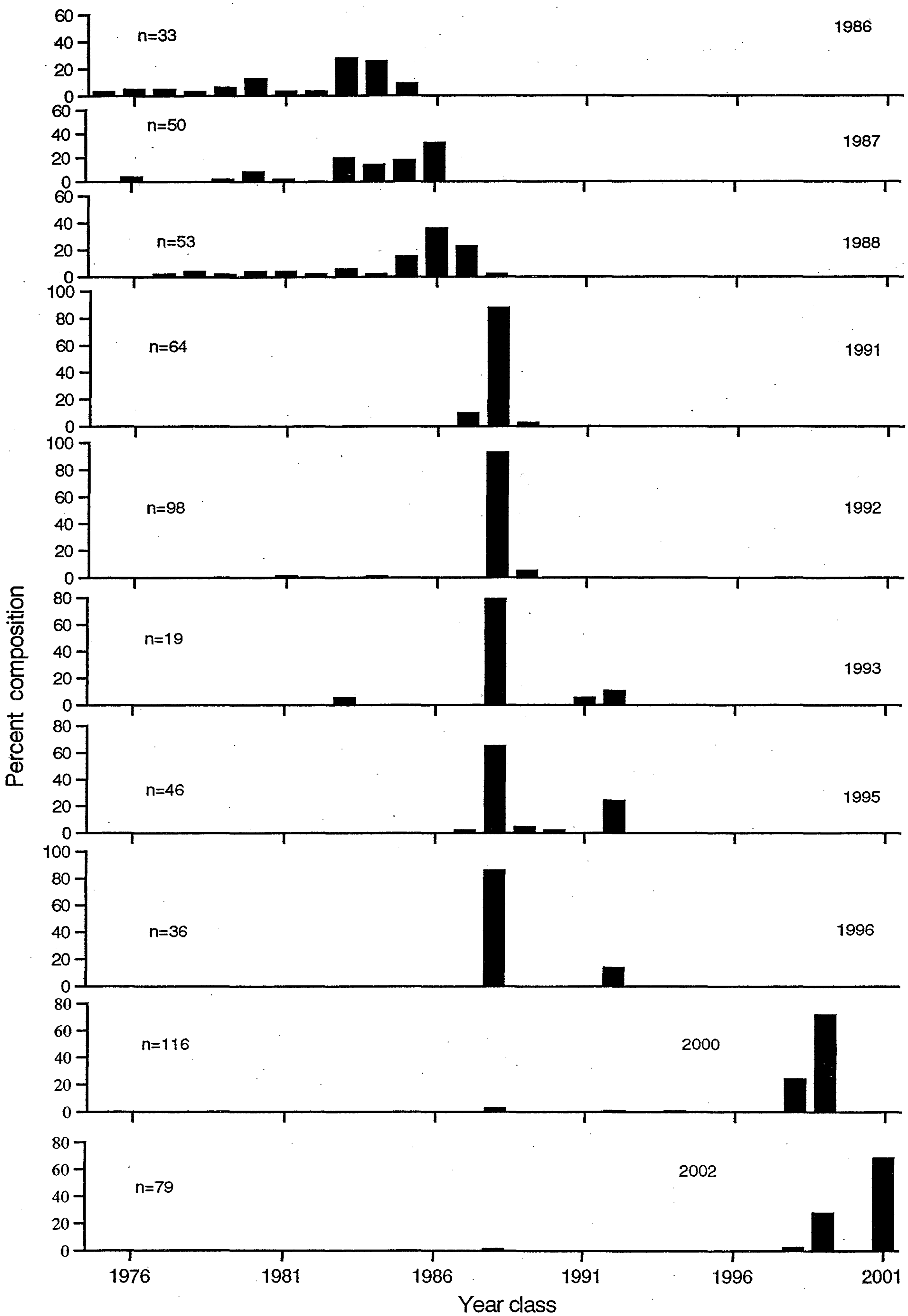


Figure 1. Percent composition of walleye year classes in gill net catches, 1986-2002.

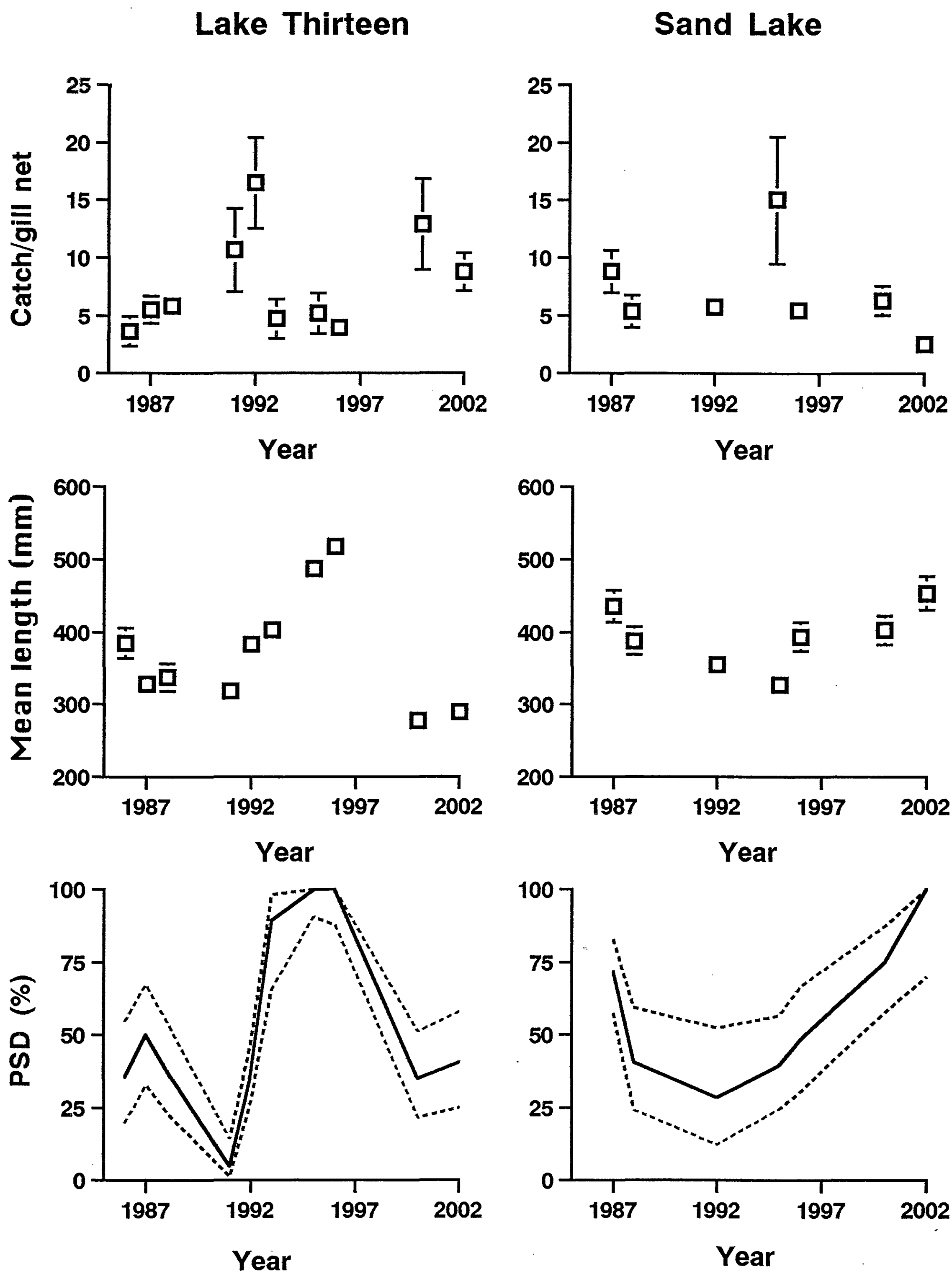


Figure 2. CPUE (±SE), mean length (±SE), and PSD (with 95% confidence limits) for walleye caught by gill netting in Lake Thirteen and Sand Lake.

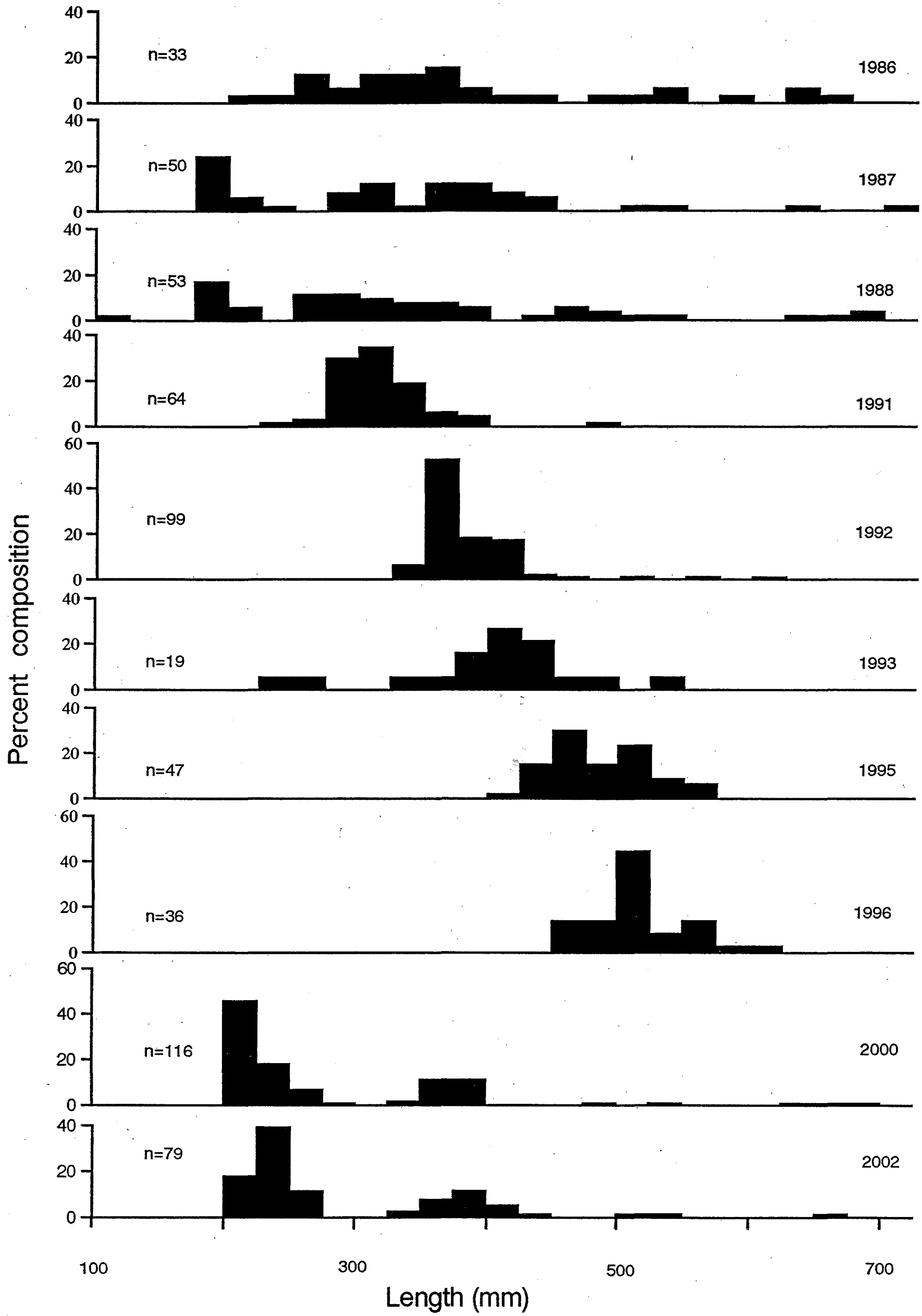


Figure 3. Length frequency distributions for walleye caught by gill netting in Lake Thirteen, 1986-1996.

Table 1. Mean back calculated length at age 3 for walleye year classes sampled in Lake Thirteen.

Year class	Year sampled	Mean back calculated length at age 3 (mm)	SE
1983	1986	285	5
1984	1987	286	5
1985	1988	293	6
1988	1991	260	3
1992	1995	388	5
1998	2002	412	27
1999	2002	327	5

Yellow Perch

The yellow perch population in Lake Thirteen was initially typified by abundant large fish and a broad range of age classes. Mean lengths in gill net catches during 1986-1988 were 199-224 mm and PSDs were 48-87% (Figure 4). During the same time, mean lengths in electrofishing catches were 166-213 mm and PSDs were 21-79% (Figure 5). Catches for both gears consisted of 7-10 age classes of yellow perch (Figures 6-7). The strong 1986 year class, which followed a weak 1985 year class, caused low mean lengths and PSDs during sampling in 1988 compared to 1986-1987.

During the study, large changes were observed in the yellow perch population that coincided with changes in the walleye population. Electrofishing catches, which tended to select for smaller yellow perch than gill net catches, showed increasing numbers of small fish after walleye stocking was discontinued, and catch rates of small yellow perch peaked just prior to resumption of walleye stocking (Figure 5). Numbers of small yellow perch were reduced again following resumption of walleye stocking. Shifts in size distributions of yellow perch sampled by electrofishing also corresponded to years with the highest relative abundances of walleye. Years with the smallest average size of yellow perch in electrofishing catches (1992, 2002) were years with high catch rates for small walleye.

Gill net catches, on the other hand, showed a long-term decline in abundance of large yellow perch. By the last three years of the study, gill net catch rates had declined to means of 4-16 fish/net from initial catch rates of 42-52 fish/net, and mean lengths had declined to 168-170 mm (Figure 4). Only four age classes were represented in catches during the last two years of gill netting. Most importantly, gill net catches showed trends of declining proportions of large yellow perch. PSD in gill net catches declined to 6-13% during the last 2 years of netting (Figure 4).

Growth rates for yellow perch were strongly density-dependent and not related to summer temperatures. Regression of annual growth coefficients from the linear model of scale growth with electrofishing catch rates for yellow perch in each year showed a significant negative relationship (R^2=0.58; P=0.001; df=1,13; F=17.93). Slowest growth years were 1996-1997 and best growth years were 1988-1989 (Figure 8). Variability in growth was also illustrated in back calculated lengths. Mean back calculated lengths at age 3 ranged from 104 to 159 mm for each year class (Table 2). Regression of mean daily temperatures during the summer with annual growth coefficients from the linear scale growth model showed no apparent relationship (R^2=0.05; P=0.336; df=1,20; F=0.97).

The yellow perch population in Sand Lake was quite different than in Lake Thirteen. Generally, the population in Sand Lake was typified by low numbers of small yellow perch and even fewer large individuals. Gill net catch rates in 1987-2002 were only 0.8-5.3 yellow perch/net (Figure 4). In all the years of gill netting, only 60 yellow perch larger than 150 mm were ever caught. Large

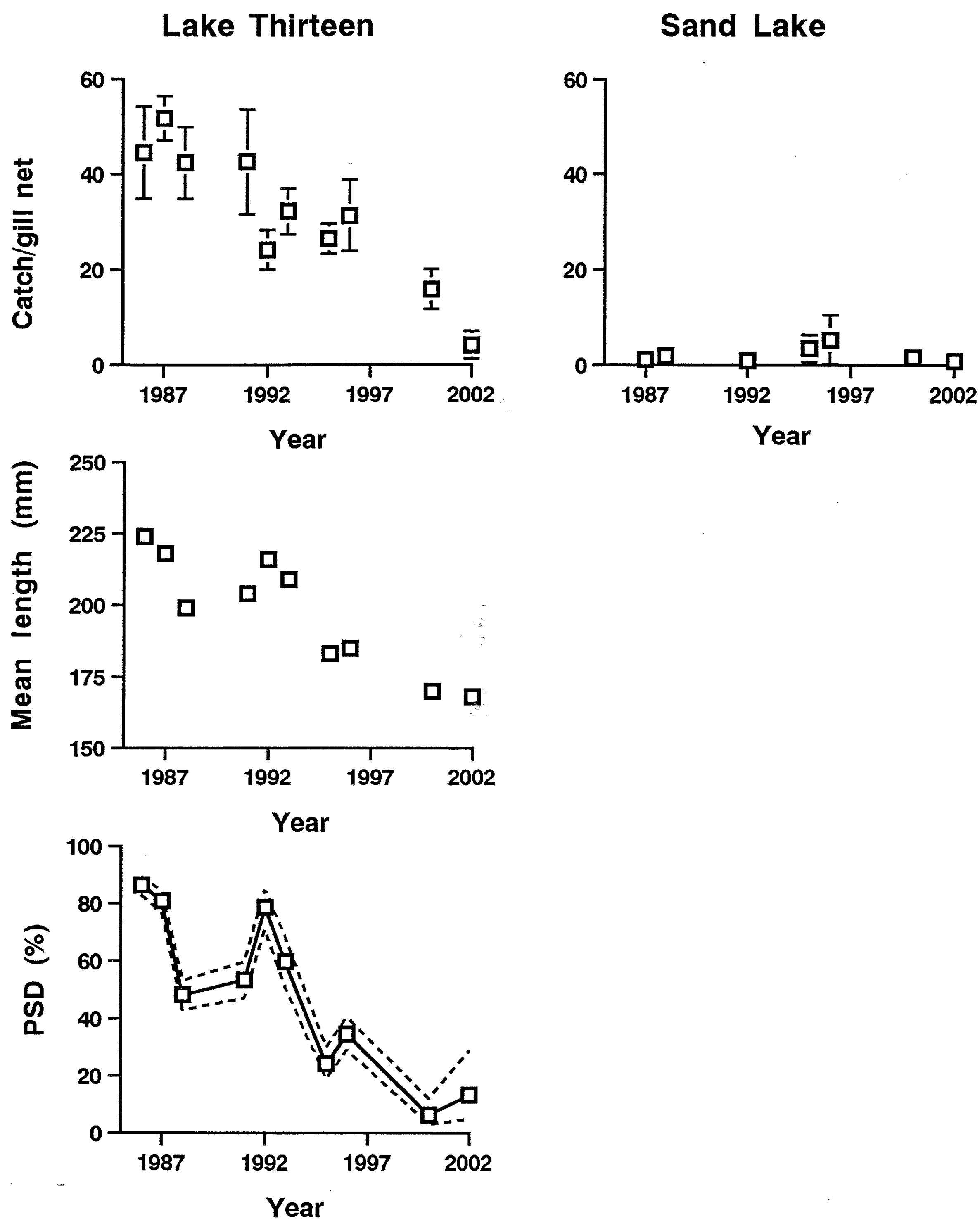


Figure 4. CPUE (±SE), mean length (±SE), and PSD (with 95% confidence limits) for yellow perch caught in gill nets in Lake Thirteen or Sand Lake.

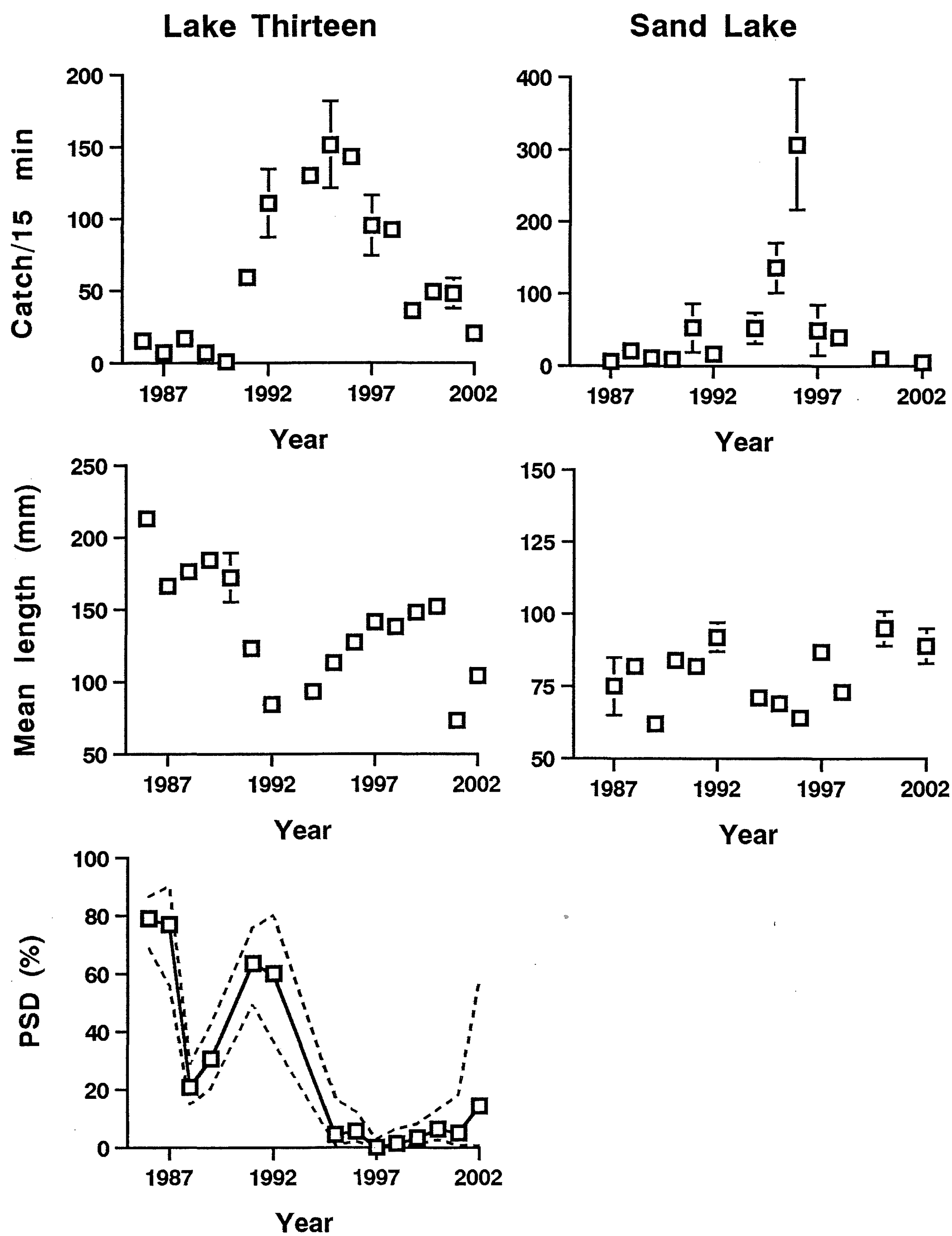


Figure 5. CPUE (±SE), mean length (±SE), and PSD (with 95% confidence limits) for yellow perch caught by electrofishing in Lake Thirteen and Sand Lake.

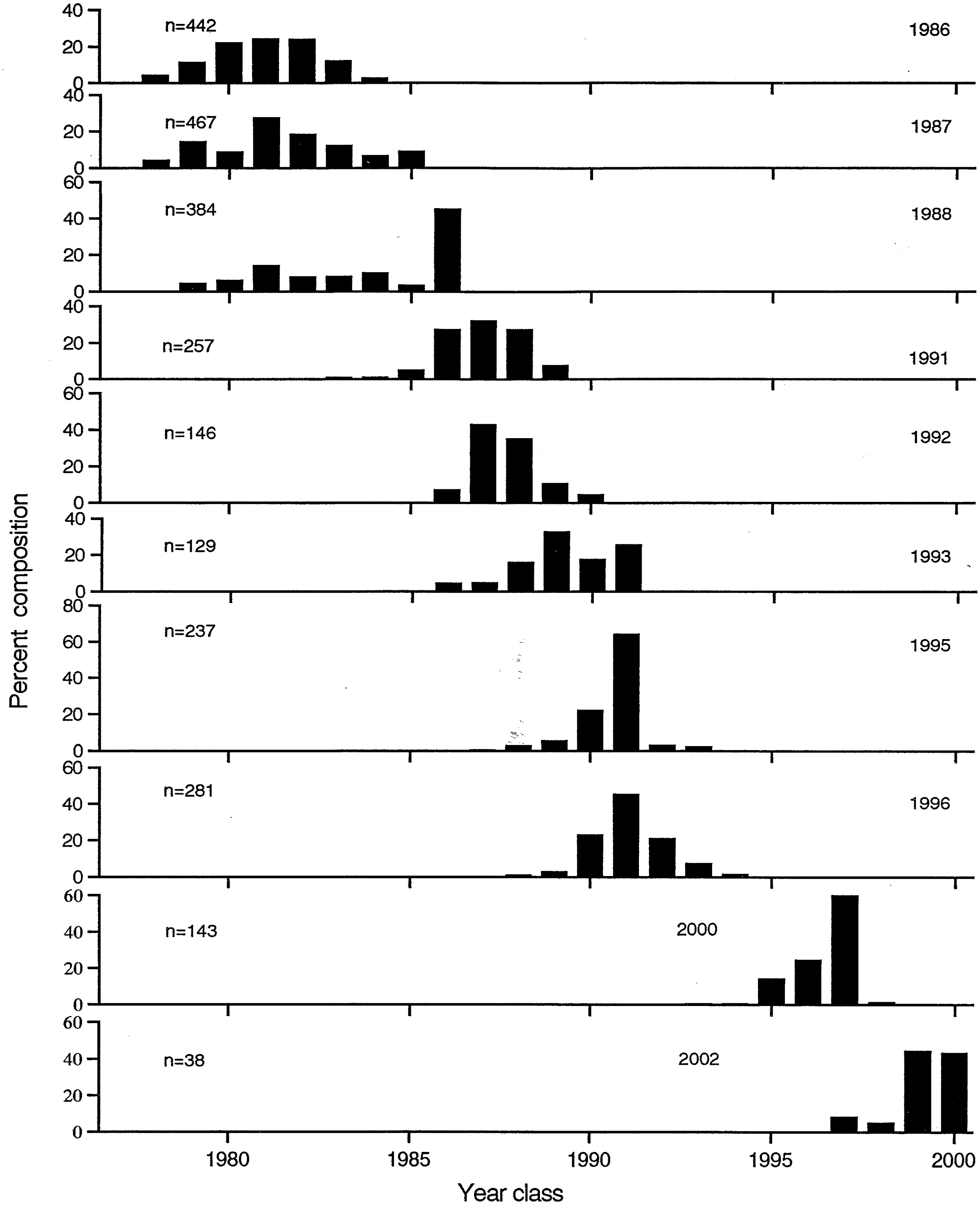


Figure 6. Percent composition of yellow perch year classes in gill net catches, 1986-2002.

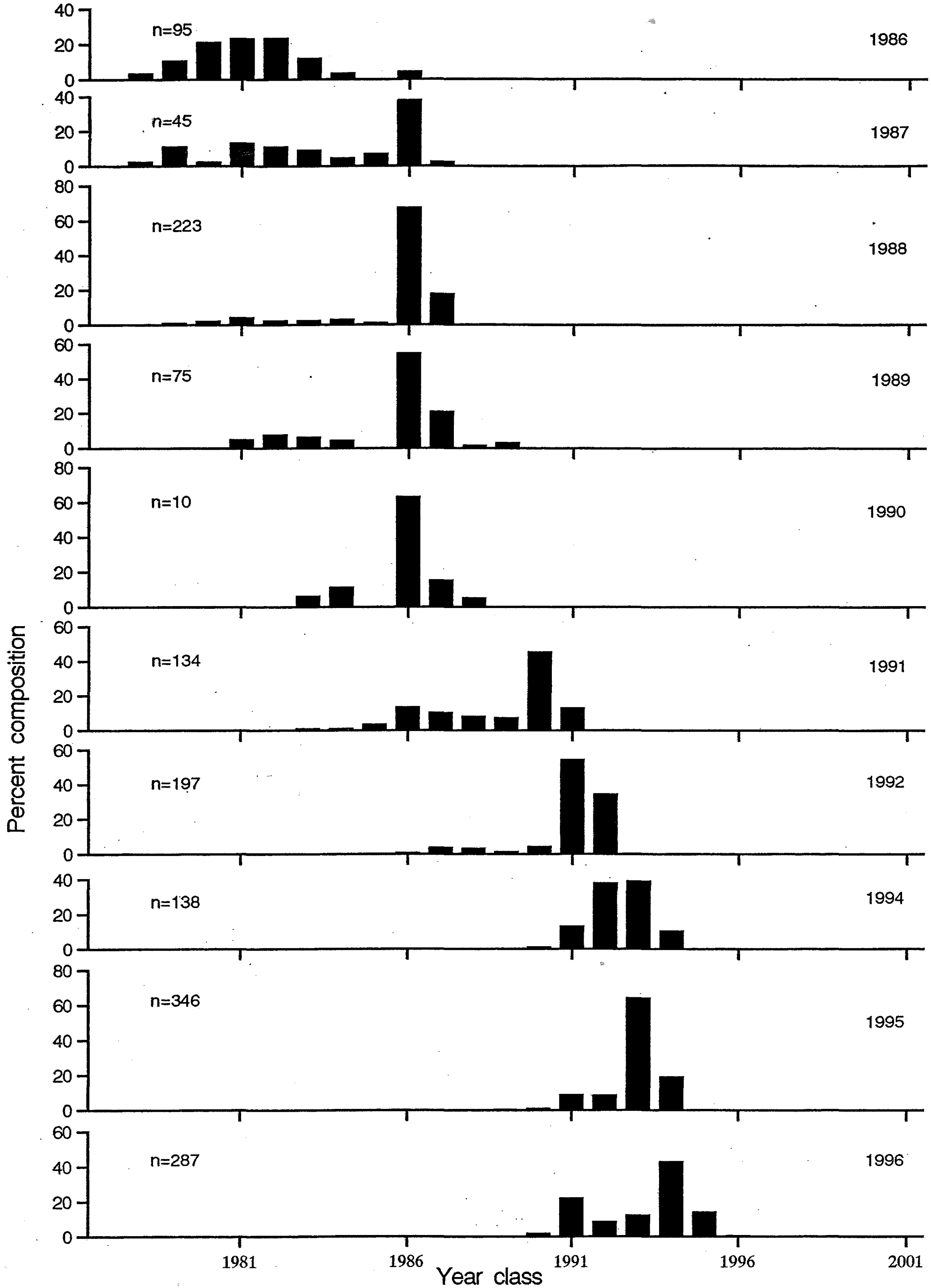
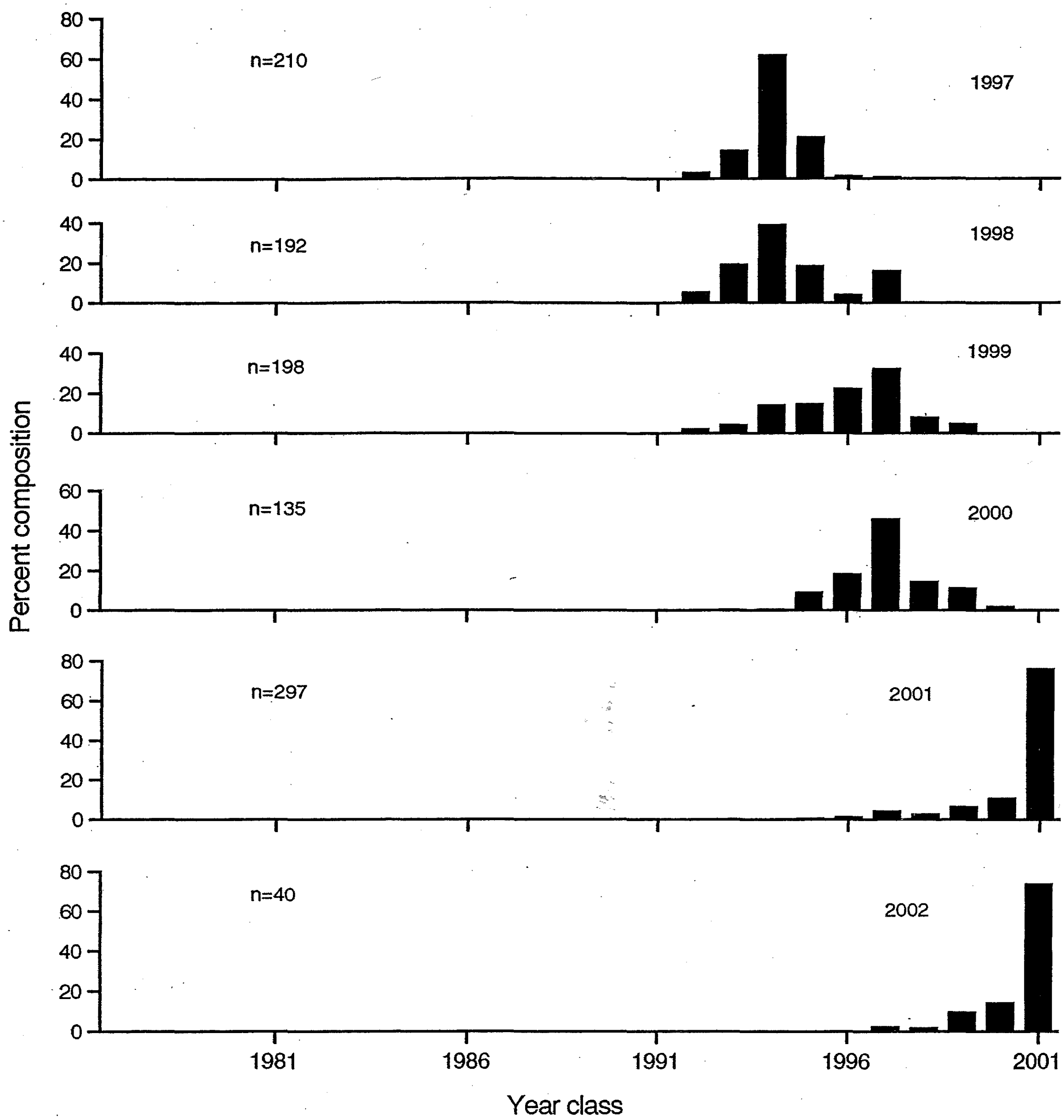


Figure 7. Percent composition of yellow perch year classes in electrofishing catches, 1986-2002.



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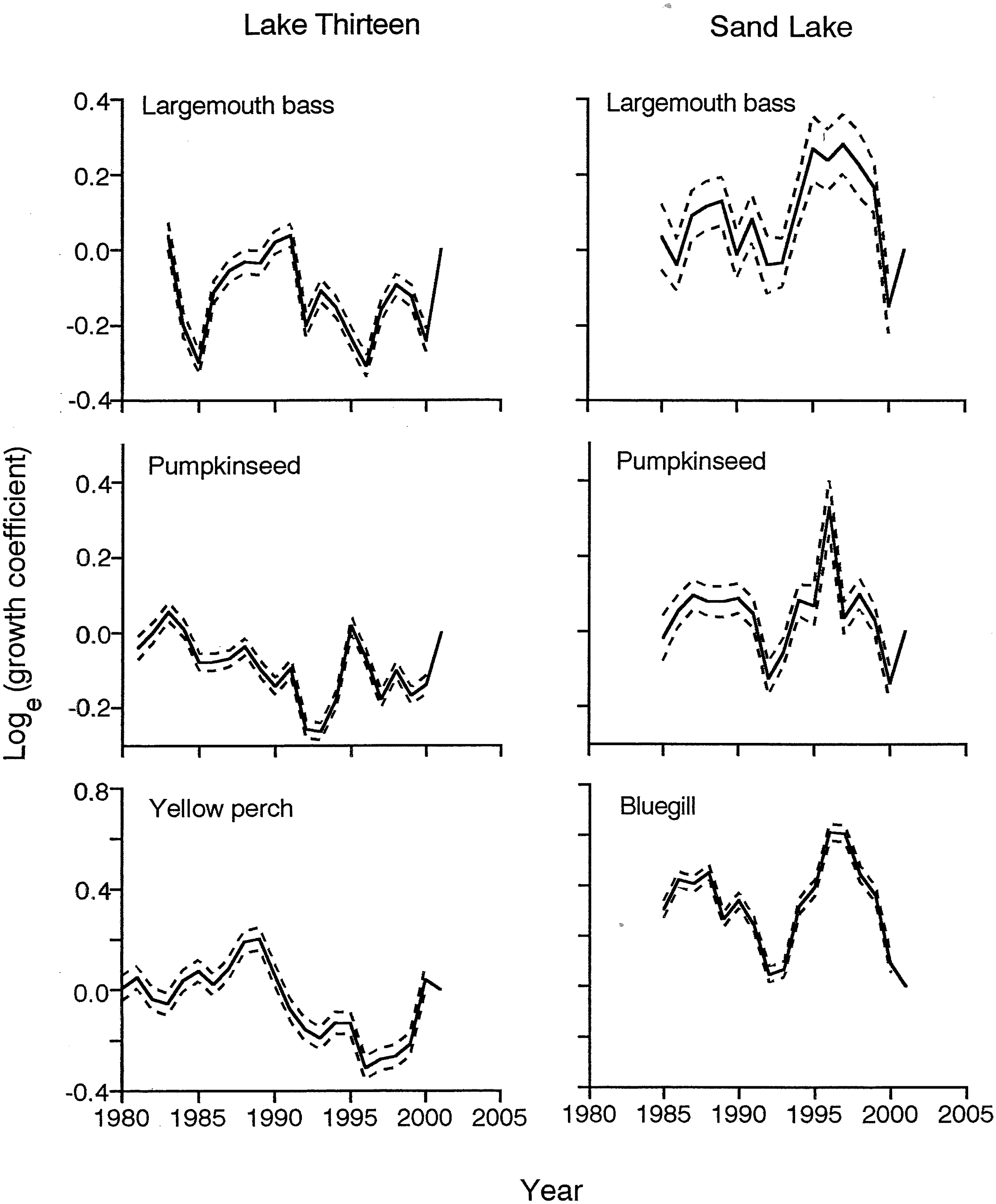


Figure 8. Growth coefficients (±SE) describing year (environmental) effects on growth of fish scales, as estimated using the linear growth model. Scale annuli measurements were from various species in Lake Thirteen and Sand Lake.

Table 2. Mean back calculated length at age 3 for yellow perch year classes sampled in Lake Thirteen.

Year class	Year sampled	Mean back calculated length at age 3 (mm)	SE
1983	1986	139	3
1984	1987	147	7
1985	1988	147	3
1986	1989	137	3
1987	1990	154	3
1988	1991	150	3
1989	1992	147	6
1990	1993	159	4
1991	1994	111	4
1992	1995	104	2
1993	1996	119	4
1994	1997	126	2
1995	1998	114	2
1996	1999	125	4
1997	2000	119	2
1998	2001	139	10
1999	2002	133	4

numbers of small (<70 mm) yellow perch were found in electrofishing catches only during 1995-1996 (Figure 5).

Northern Pike

The northern pike population in Lake Thirteen was characterized by variable recruitment. Because of poor recruitment between 1992-1997, the northern pike population in Lake Thirteen underwent changes similar to those of the walleye population. Mean length and PSD for northern pike caught in gill nets peaked in 1995-1996 (Figure 9). Length frequency distributions for northern pike showed no fish smaller than 450 mm between 1992-1996 (Figure 10). A strong 1985 year class influenced lengths of northern pike in gill net catches during 1986-1988, and strong 1989-1990 year classes influenced lengths through 1996. The high gill net catch rate in 1991 was mainly due to fish from 1989-1990 year classes, and a high catch rate in 2000 was attributed to a strong 1998 year class (Figure 11).

Northern pike year class strength was apparently not related to water levels, and not affected by predation from small yellow perch in Lake Thirteen. Spring water level during a good year for northern pike recruitment (1990) was similar to the spring water level during a poor year for recruitment (1992). In both years, the lake level was 1.8 m below a benchmark. Although good year classes were produced in 1998-1999 when water levels were high (1.4-1.5 m below benchmark), good year classes were also produced in 1989-1990 when water levels were low (1.8-1.9 m below benchmark). Even though northern pike recruitment varied in ways similar to the walleye population, no relationship was evident between relative abundance of small yellow perch (as measured by electrofishing catch rates) and gill net catch rates for northern pike, even when yellow perch catches were lagged by two years to allow for recruitment of northern pike year classes into the gill nets (R^2=0.12; P=0.46; df=1,5; F=0.65).

Growth of northern pike was relatively fast in Lake Thirteen. Average back calculated lengths at age 3 were 522-542 mm (SE=8-19 mm) during 1986-1988 and 1995-1996, and were 553-555 mm (SE=9-12 mm) during 2000 and 2002 (Table 3).

Recruitment of northern pike occurred more consistently in Sand Lake than at Lake Thirteen, with fish aged from most year classes. As a result, mean lengths and PSDs for northern pike caught by gill netting were more consistent over the study period (Figure 9). Yet, gill net catch rates during 1995-1996 were higher than in Lake Thirteen and were attributed to recruitment of the 1993 and 1994 year classes. Growth was also slower in Sand Lake. Mean back calculated lengths at age 3 were 456-465 mm (samples from 1987-1988, 1995-1996, 2000, and 2002).

Largemouth bass

The largemouth bass population in Lake Thirteen also showed evidence of variable recruitment. Weak year classes were

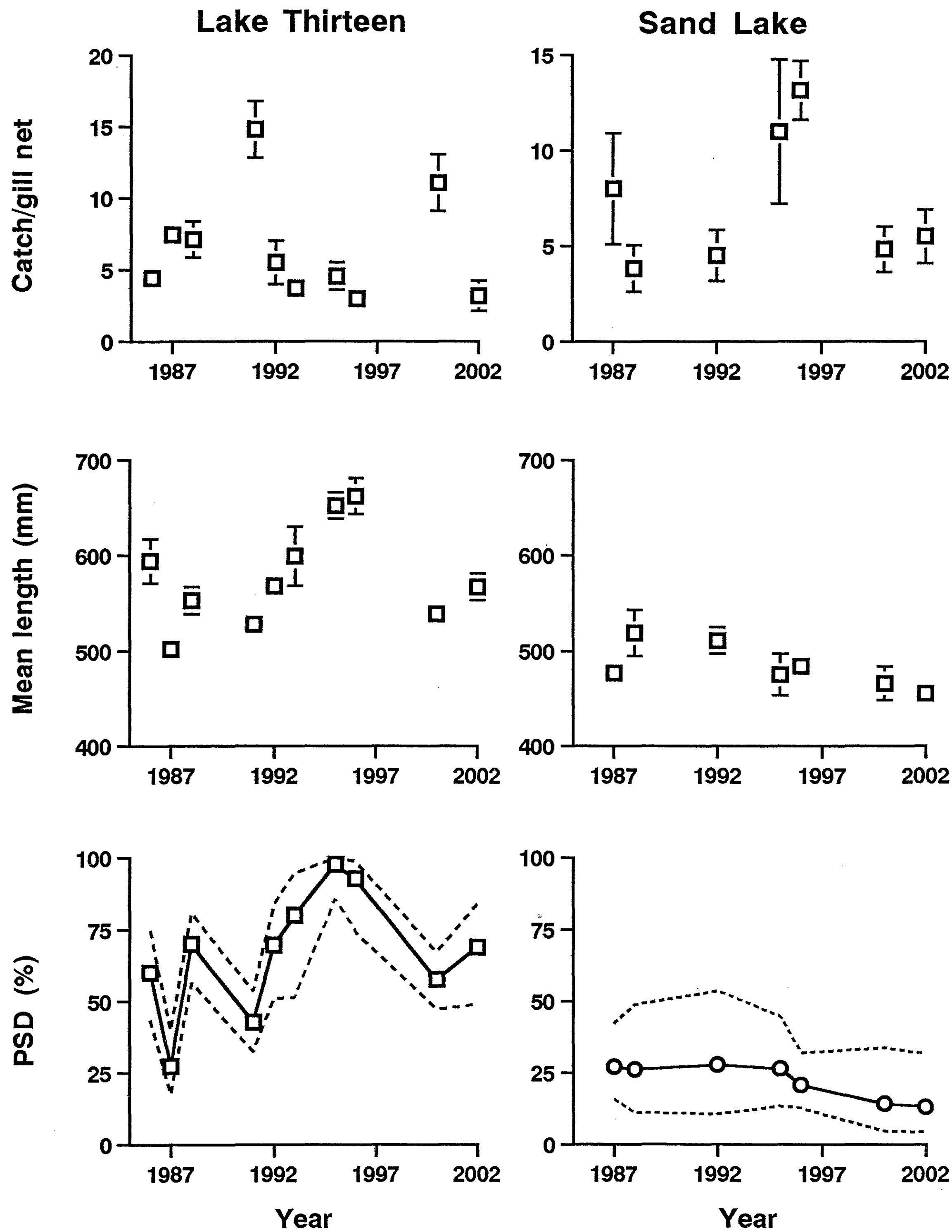


Figure 9. CPUE (±SE), mean length (±SE), and PSD (with 95% confidence limits) for northern pike caught by gill netting in Lake Thirteen and Sand Lake.

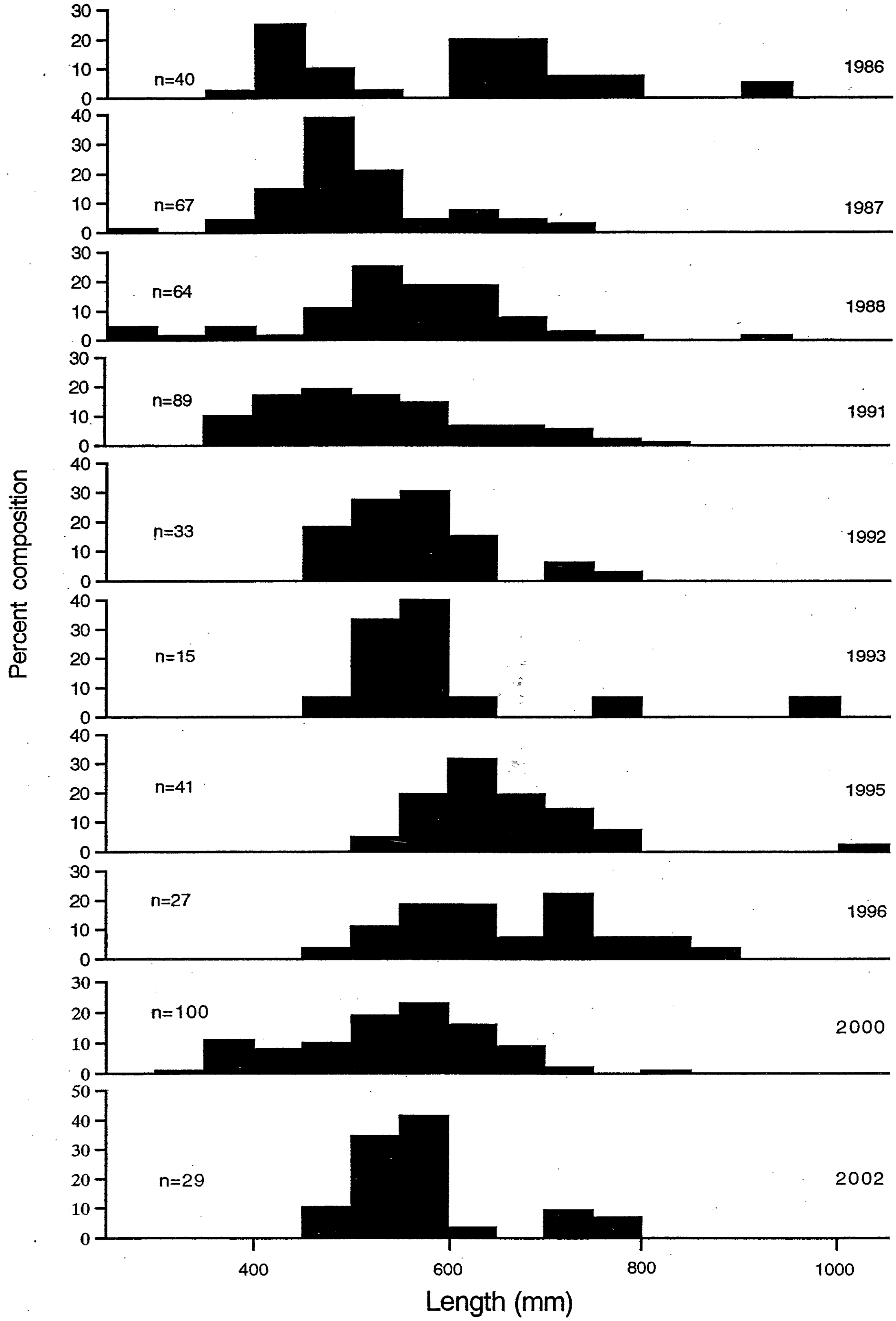


Figure 10. Length frequency distributions for northern pike caught by gill netting, 1986-2002.

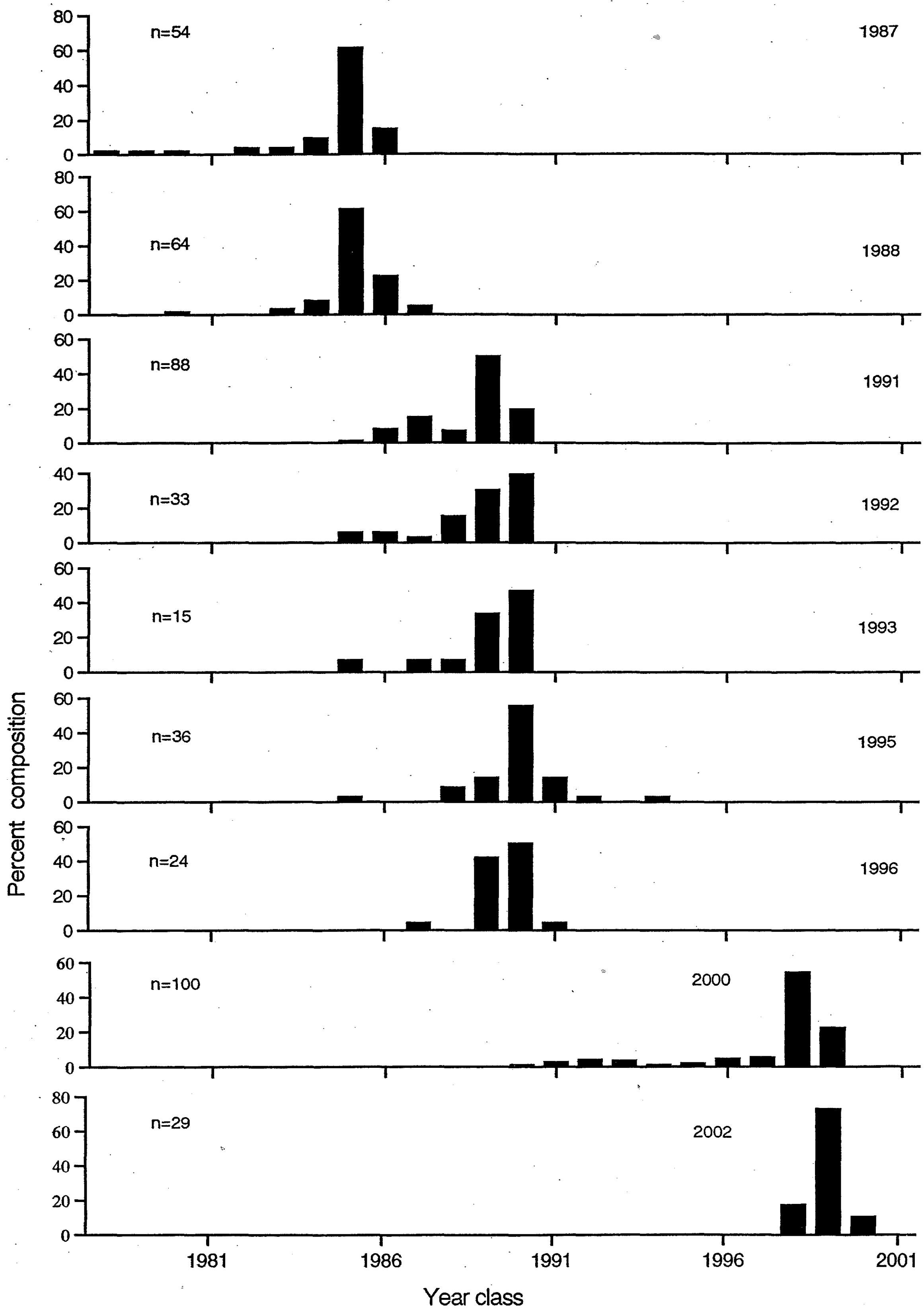


Figure 11. Percent composition of northern pike year classes in gill net catches, 1987-2002.

Table 3. Mean back calculated length at age 3 for northern pike sampled in Lake Thirteen. Due to relatively low sample sizes, mean length at age 3 was estimated using all available year classes sampled in each year.

Year sampled	Mean back calculated length at age 3 (mm)	SE
1986	542	13
1987	528	19
1988	522	8
1991	560	10
1992	517	11
1995	527	8
1996	526	13
2000	553	9
2002	555	12

apparent in electrofishing catches from 1985, 1992, and 1995-1996. The two coldest summers (1985 and 1992) corresponded to two of the weakest year classes. A particularly strong year class was evident in 1994 (Figure 12), and as a result, large numbers of small largemouth bass were caught by electrofishing after 1994. Electrofishing catch rates during 1995-1996 were much greater than other years, and the smallest mean lengths of largemouth bass were recorded in 1995-1996 (Figure 13). PSDs from electrofishing catches were also variable during the study, but never greater than 40%.

In addition to variable recruitment, largemouth bass showed variable growth rates that we related to summer temperatures and largemouth bass relative density, but not to walleye abundance. The linear growth model estimated that poor growth occurred in 1985 and 1992 in Lake Thirteen, and relatively good growth occurred in 1981 and 1991 (Figure 8). Annual growth coefficients from the linear growth model appeared to be related to air temperatures during June, July, and August. Regression with means of the June-August temperatures for each year explained 29% of the variation in annual growth coefficients derived from the linear growth model (P=0.017; df=1,17; F=6.99). The relationship between growth coefficients and largemouth bass catch rates in electrofishing gear for each year explained 27% of variation in growth coefficients (P=0.041; df=1,14; F=5.08). Density-dependent growth was demonstrated in the very strong 1994 year class of largemouth bass. Mean back calculated length at age 3 for the 1994 year class (sampled in 1997) was 186 mm (SE=2 mm), compared to mean back calculated lengths of 201-265 mm (SE=2-9 mm each year) at age 3 for all of the other year classes during 1983-1999 (Table 4). A multiple regression, with catch rates and mean June-August temperatures as independent variables, accounted for much of the differences in annual growth coefficients (R^2=0.62; P=0.0017; df=2,13; F=10.77).

In Sand Lake, the greatest catch rates for largemouth bass also occurred during 1995-1996. Electrofishing catches averaged 13.8-14.2 bass/15 min in 1995-1996 compared to 0.6-9.2 bass/15 min in other years (Figure 13). Mean lengths of electrofished largemouth bass in Sand Lake were relatively small throughout the study, ranging from 109 to 154 mm in years when total sample sizes were greater than 10 fish. Fish ages 0-1 dominated the catches in 1995-1996. Sample sizes for age and growth analyses in Sand Lake were small, but it appeared that largemouth bass growth rates were similar to Lake Thirteen. Average back calculated lengths at age 3 were 202-285 mm each year. Regression of yearly growth coefficients from the linear growth model showed relatively weak relationships with mean daily temperatures during June through August (R^2=0.17; P=0.099; df=1,15; F=3.08) and electrofishing catch rates (R^2=0.19; P=0.095; df=1,14; F=3.20).

Pumpkinseed

As with the other species, the pumpkinseed population in Lake Thirteen was

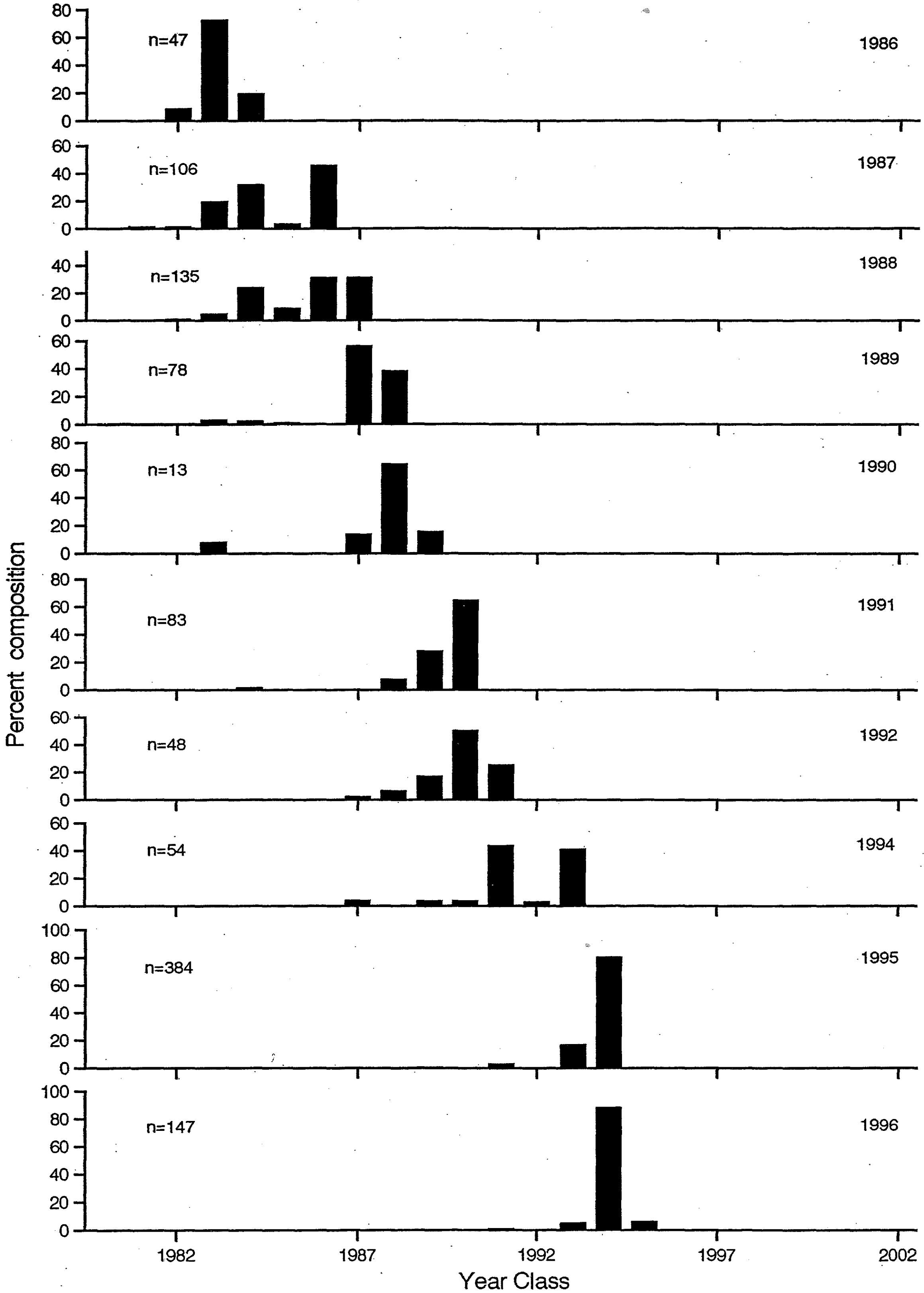
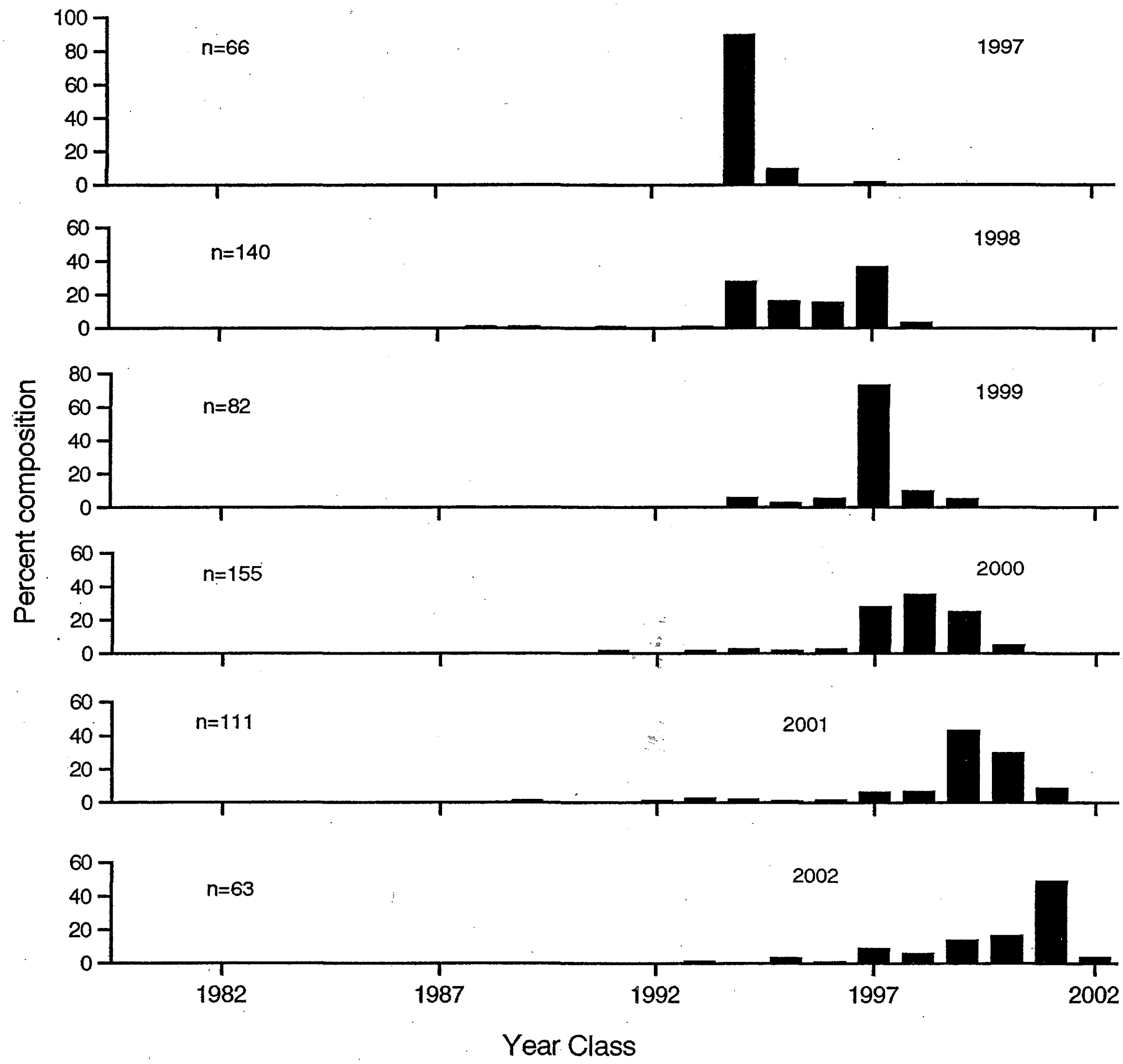


Figure 12. Percent composition of largemouth bass year classes in electrofishing catches, 1986-2002.



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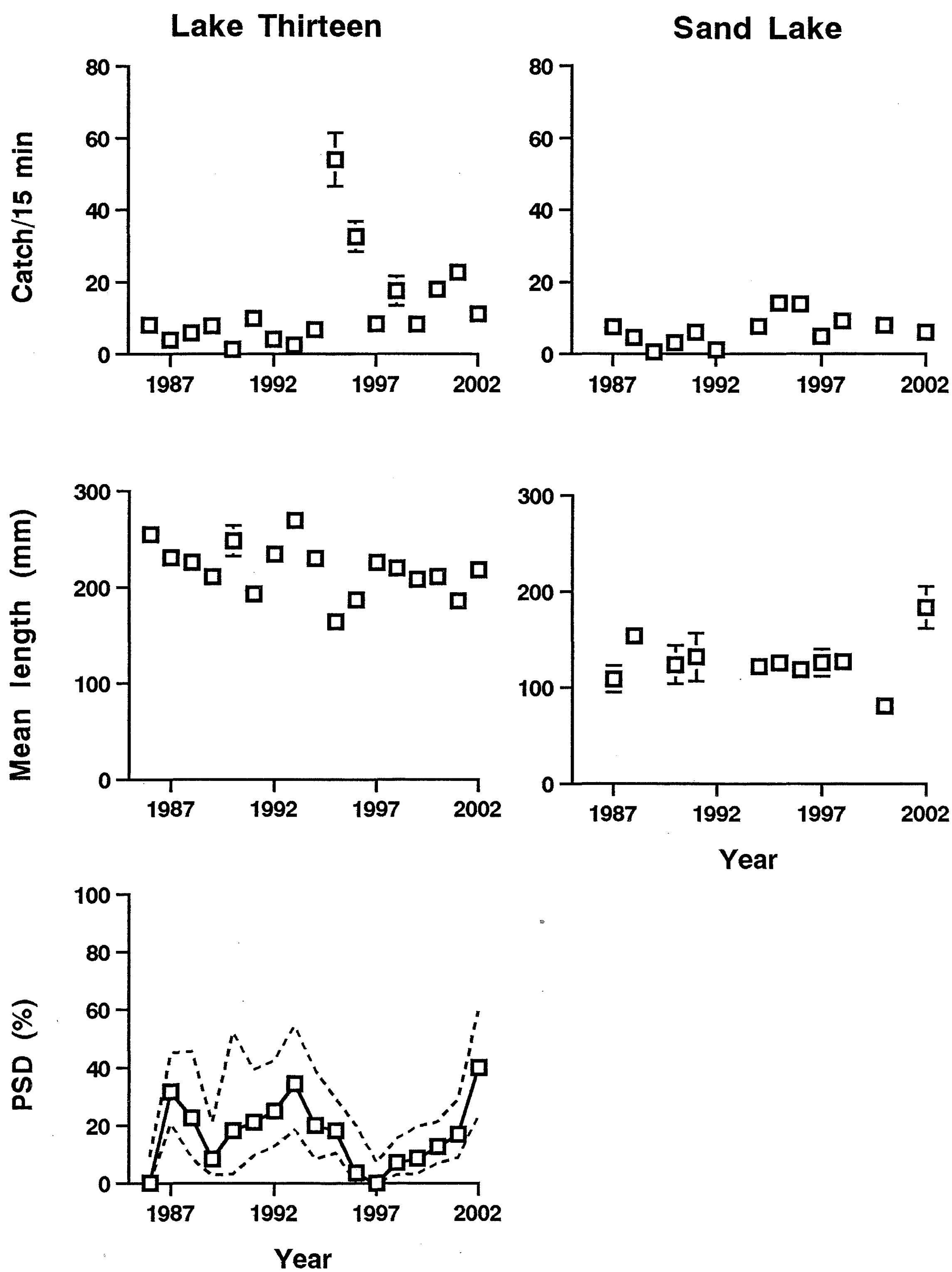

Figure 13. CPUE (±SE), mean length (±SE), and PSD (with 95% confidence limits) for largemouth bass caught by electrofishing in Lake Thirteen and Sand Lake.

Table 4. Mean back calculated length at age 3 for largemouth bass year classes sampled in Lake Thirteen.

Year class	Year sampled	Mean back calculated length at age 3 (mm)	SE
1983	1986	208	2
1984	1987	210	4
1985	1988	216	5
1986	1989	-	-
1987	1990	237	8
1988	1991	238	5
1989	1992	265	4
1990	1993	244	5
1991	1994	212	4
1992	1995	-	-
1993	1996	243	6
1994	1997	186	2
1995	1998	207	3
1996	1999	216	9
1997	2000	217	2
1998	2001	201	6
1999	2002	213	4

characterized by variable recruitment. In both electrofishing and trap net catches, strong year classes were evident during 1986-1987 and again during 1990-1991 (Figures 14-15). Weak year classes were evident in catches from both gears during 1985 and 1992-1993, which were the three coldest summers recorded at nearby Cass Lake. The variability in year class strength was reflected in differences we saw in catch rates and mean lengths of pumpkinseed caught by electrofishing and trap netting (Figure 16). The 1991 year class contributed substantially to high catch rates found during 1995-1997.

Growth of pumpkinseed in Lake Thirteen was slow, and was apparently influenced by summer temperatures and largemouth bass abundance. Mean back calculated lengths at age 3 were 70-94 mm for each year class (Table 5). Annual growth coefficients from the linear growth model (Figure 8) were positively correlated with the mean daily air temperature calculated for June-August each year (r=0.486; P=0.026), and also with largemouth bass electrofishing catch rates (r=0.611; P=0.012). Multiple regression indicated that a combination of summer temperatures and largemouth bass catch rates could explain 83% of the variation in annual pumpkinseed growth coefficients (P<0.001; df=3,13; F=30.73).

Pumpkinseed were a much less important part of the fish community in Sand Lake than in Lake Thirteen. Catch rates in Sand Lake were typically low, with very few fish caught through 1991. With the exception of 1998, catch rates were less than 10 fish/15 min electrofishing transect (Figure 16). Too few pumpkinseed were obtained to monitor trends in year class strength, mean length, or PSD. Although sample sizes were small, pumpkinseed growth rates were apparently faster in Sand Lake than in Lake Thirteen. Mean back calculated lengths at age 3 ranged from 89 to 142 mm each year. In Sand Lake, a multiple regression model of mean daily temperatures (June-August each year) and largemouth bass catch rates was unable to explain variation in annual growth coefficients from the linear growth model (R^2=0.31; P=0.183; df=2,9; F=2.07).

Bluegill

Bluegill was an important fish species found in Sand Lake that was not found in Lake Thirteen until 2001. In 2001, 37 bluegill were caught in trap nets and electrofishing gear in Lake Thirteen. The bluegill ranged in size from 106-160 mm, and were represented by only two age classes (84% were from the 1998 year class and 16% were from the 1999 year class). In 2002, 25 bluegill were sampled in Lake Thirteen with fish represented from year classes 1998, 1999, and 2001.

Catch rates for bluegill in Sand Lake were variable and were not consistent between capture gears. Bluegill catch rates in trap nets were 6.1-69.9 fish per net in each year and electrofishing catch rates were 38.7 to 276.3 fish/15 min (Figure 17). Years with high electrofishing catch rates did not necessarily correspond to years of high trap net

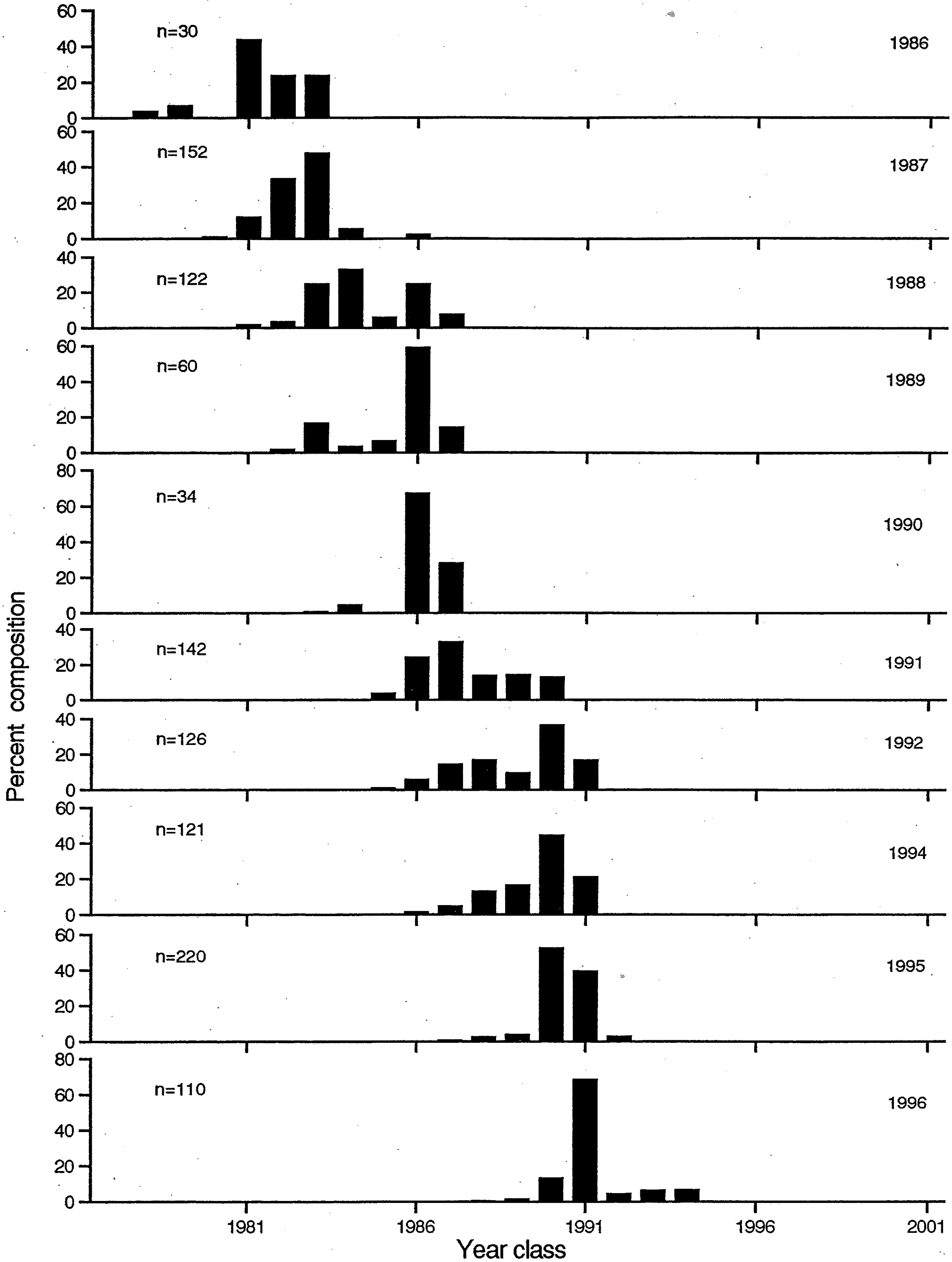

Figure 14. Percent composition of pumpkinseed year classes in electrofishing catches, 1986-2002.

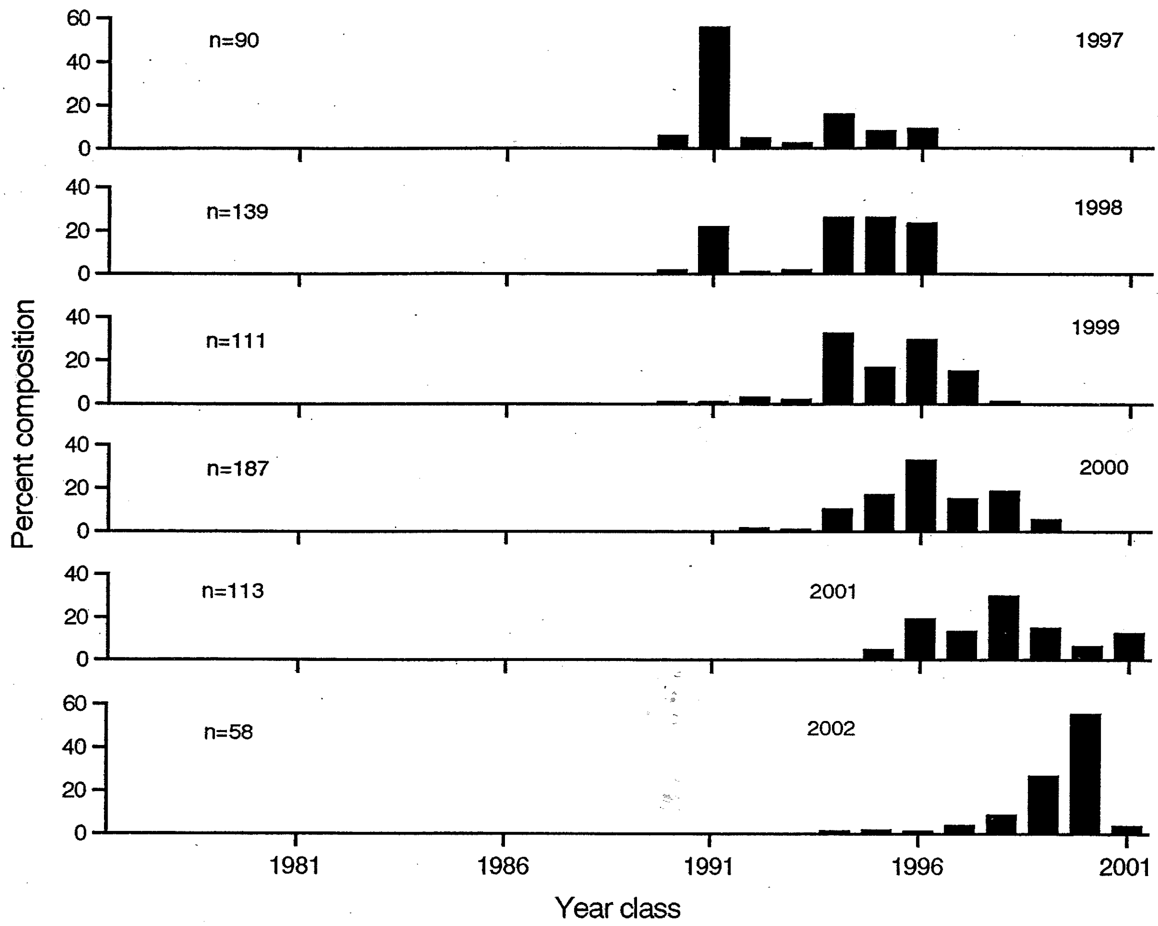

Figure 14 (continued).

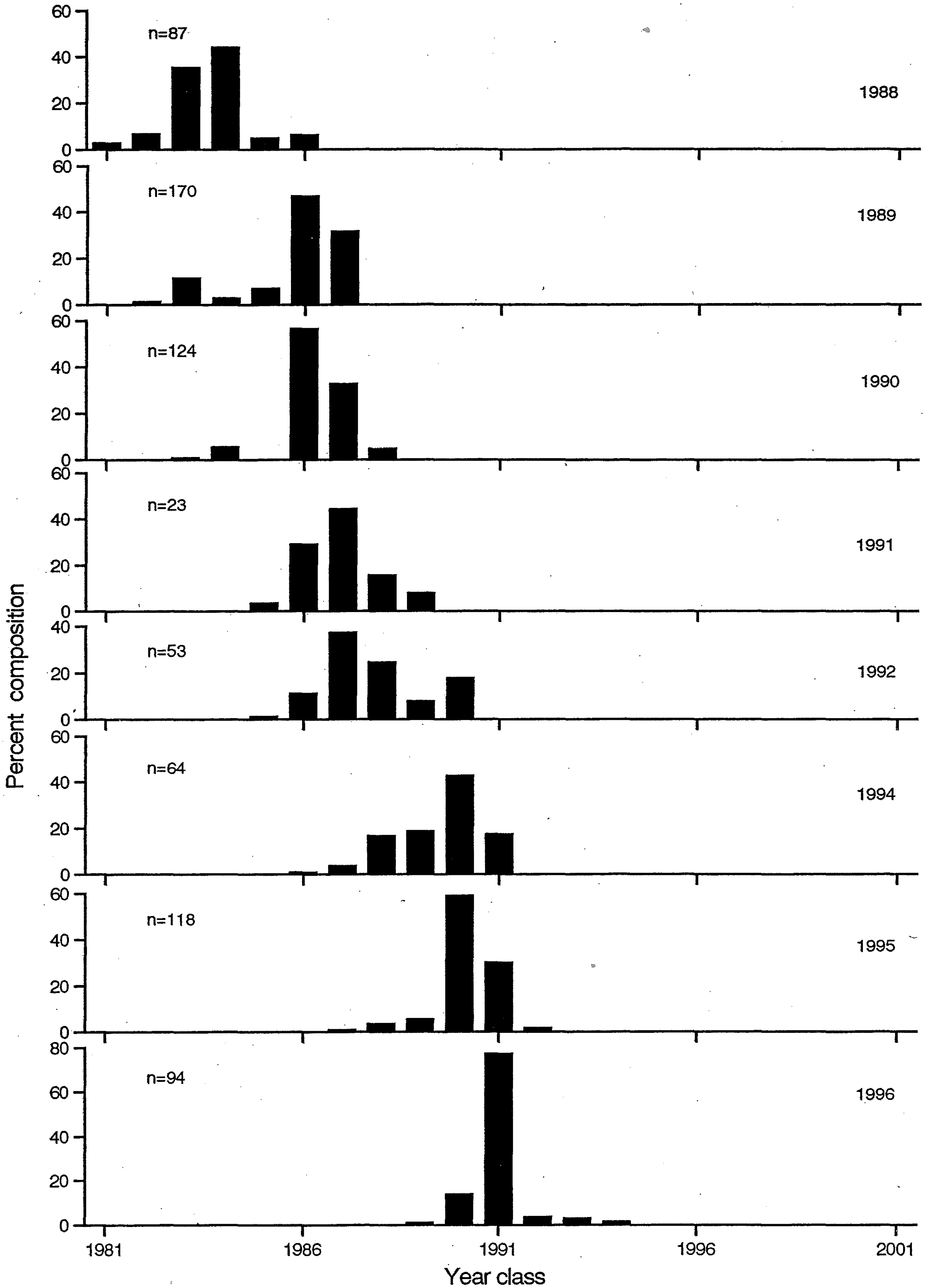

Figure 15. Percent composition of pumpkinseed year classes in trap net catches, 1988-2002.

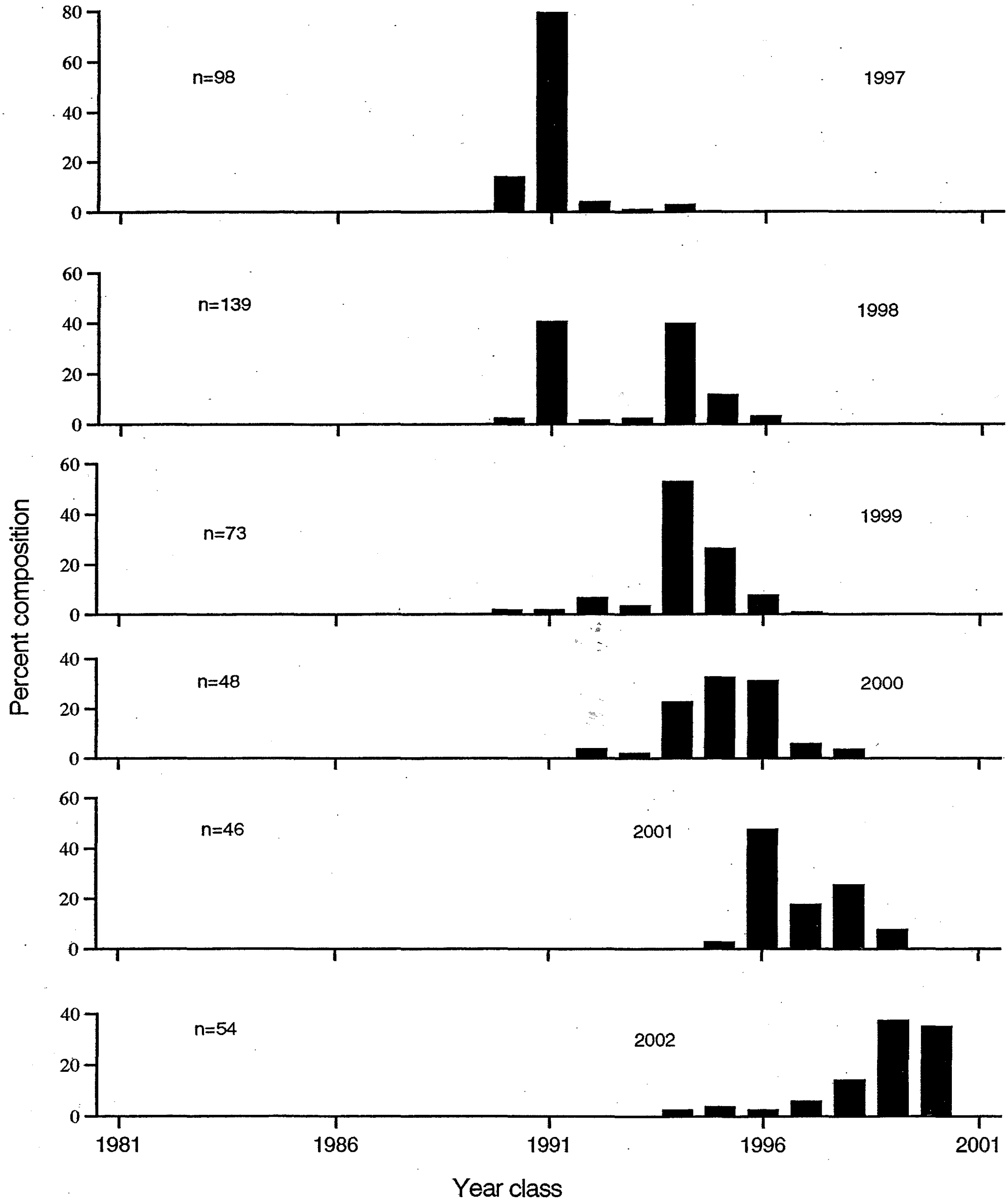

Figure 15 (continued).

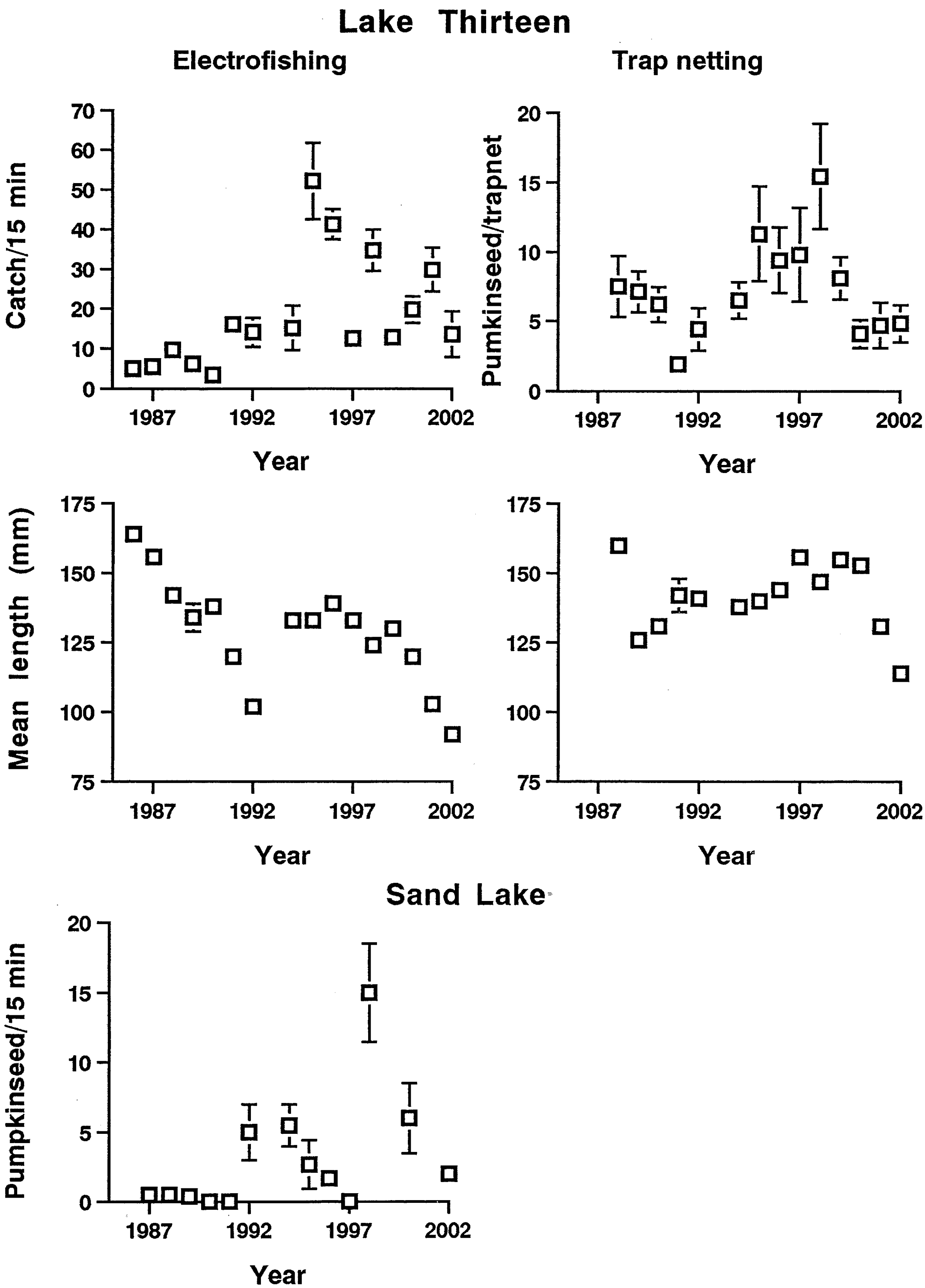

Figure 16. Electrofishing or trap net CPUE (±SE) and mean length (±SE) for pumpkinseed caught in Lake Thirteen, and electrofishing CPUE in Sand Lake.

Table 5. Mean back calculated length at age 3 for pumpkinseed year classes sampled in Lake Thirteen.

Year class	Year sampled	Mean back calculated length at age 3 (mm)	SE
1984	1987	71	4
1985	1988	92	4
1986	1989	94	2
1987	1990	83	2
1988	1991	76	2
1989	1992	80	2
1990	1993	-	-
1991	1994	70	1
1992	1995	73	-
1993	1996	88	2
1994	1997	89	2
1995	1998	85	2
1996	1999	79	2
1997	2000	78	2
1998	2001	76	2
1999	2002	85	5

catch rates. No apparent trend was evident in catch rates for either gear.

Bluegill in electrofishing catches in Sand Lake were characterized by small average size and low PSD throughout the study (Figure 17). Mean length of bluegill caught by trap netting was $\leq$150 mm each year, but proportions of large bluegill varied substantially during the study. PSDs for electrofishing catches were 0-32% each year, and PSDs for trap net catches were 9-67% each year.

Bluegill growth in Sand Lake was slow throughout the study. Mean back-calculated lengths at age 3 were 74-113 mm each year. The linear growth model showed some variation in growth rate among years (Figure 8), and growth was slowest during two of the coldest summers (1992-1993). Over the duration of the study, however, the relationship between average summer temperatures and annual growth coefficients was not clear (R^2=0.05; P=0.395; df=1,15; F=0.77). Instead, growth seemed to be related to relative abundance of both bluegill and largemouth bass. Multiple regression indicated that bluegill and largemouth bass catch rates in electrofishing gear could explain 66% of the variation in annual growth coefficients (P=0.008; df=2,9; F=8.57).

Discussion

In addition to specifically evaluating the influences of walleye stocking on a fish community, results from this study are also relevant to the ecological role of walleye in lakes where it is a native species. In particular, walleye predation played a large role in structuring the yellow perch population in Lake Thirteen. The role of walleye predation was demonstrated through changes in stocking. When walleye stocking was discontinued, reduced predation on small yellow perch allowed numbers of small yellow perch to increase, and led to reduced growth rates of yellow perch. When stocking was resumed, predation by stocked walleye reversed the trend by reducing yellow perch numbers and improving their growth rates.

Predation by northern pike may also have contributed to changes in the yellow perch population. Because of variable recruitment, changes in the northern pike population paralleled changes in the walleye population in several respects. Sizes of northern pike and walleye were greatest in 1995-1996. Furthermore, strong year classes of northern pike caused high gill net catch rates in 1991 and 2000, which were also years of high relative abundance of walleye. The diet of northern pike in Lake Thirteen also consisted largely of yellow perch (Pierce and Tomcko 1998).

Predator-prey relationships between walleye, northern pike, and yellow perch have been well documented elsewhere. In Oneida Lake, New York, predation by walleye was the principal cause of mortality for young yellow perch (Nielsen 1980). Numbers of young perch eaten by walleye during summer and fall approximated the total number estimated to be available in June (Forney

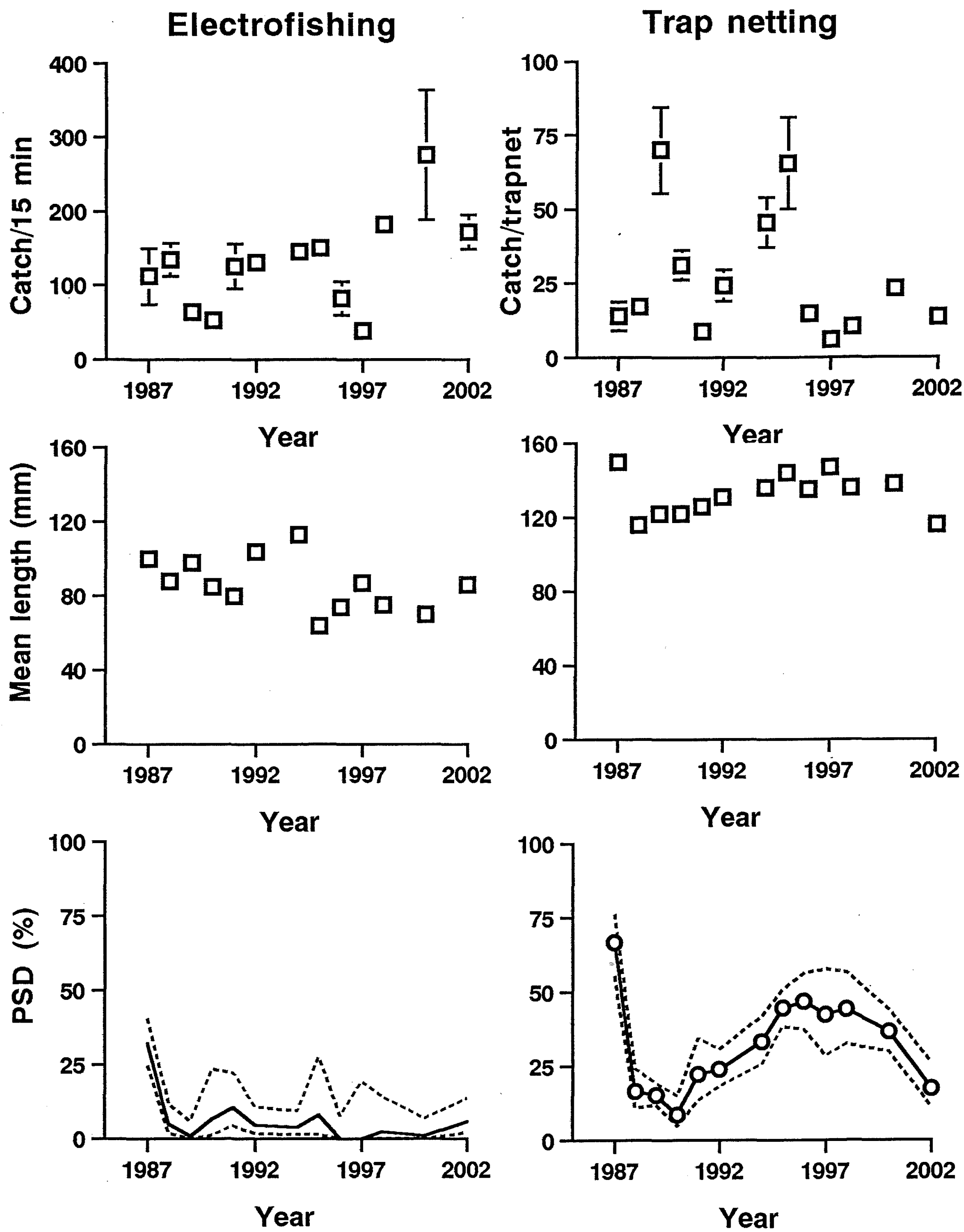

Figure 17. CPUE (±SE), mean length (±SE), and PSD (with 95% confidence limits) for bluegill caught by electrofishing and trap netting in Sand Lake.

1977; Forney 1980; Mills et al. 1987). As a result, walleye production in Oneida Lake was roughly proportional to production by young yellow perch (Forney 1980). In a small Michigan lake, dominant year classes of stocked walleye led to excessive predation on yellow perch (Schneider 1983). Other authors have suggested that yellow perch is a keystone species in transferring energy to higher trophic levels (Anderson and Schupp 1986; Mills et al. 1987). In Minnesota, yellow perch have been described as an important prey for northern pike and largemouth bass, as well as for walleye (Maloney and Johnson 1957; Seaburg and Moyle 1964; Reed and Parsons 1996), and yellow perch populations are susceptible to changes in abundance of these other predators. For instance, stocking northern pike into Horseshoe Lake, Minnesota, reduced recruitment and population densities of yellow perch (Anderson and Schupp 1986).

Reasons for the long-term decline in numbers and sizes of yellow perch in gill net catches in Lake Thirteen were not completely clear. Predation by the large sizes of walleye and northern pike that remained in the lake by 1995-1996 was originally considered to have reduced numbers of large yellow perch (Pierce and Tomcko 1998). Yet, relative abundance of large yellow perch was not restored by the end of the study. The decline in sizes of yellow perch at the end of the study was due, to some extent, to reduced growth rates during the period of high yellow perch densities (1992-1998). In addition, the study was probably not long enough to replace older age classes of yellow perch.

Variable recruitment was a predominant theme among the fish species we studied in Lake Thirteen. Weak and strong year classes of the naturally reproducing populations of northern pike, yellow perch, largemouth bass and pumpkinseed had pronounced effects on catch rates in the various gears, and also had large influences on the age and size structures of our samples. Variation in northern pike recruitment was not explained by either changes in water level or predation on larval northern pike. Spawning habitat for northern pike in Lake Thirteen seems to be limited to only a few small areas that may be vulnerable to water level fluctuation. Nevertheless, no connection was drawn between weak or strong year classes and water level. One of the possible explanations for reduced northern pike recruitment during 1992-1997 was predation by yellow perch (Pierce and Tomcko 1998). In at least one case, yellow perch have been shown to be important predators of larval northern pike (Hunt and Carbine 1951). In Lake Thirteen, however, no significant correlation was found between northern pike catch rates and abundance of yellow perch (lagged to account for northern pike vulnerability to the experimental gill nets).

Summer water temperatures affected both recruitment and growth of centrarchid species in Lake Thirteen. The cold summers of 1985, 1992, and 1993 had pronounced effects on recruitment and growth of largemouth bass and pumpkinseed. Northern Minnesota is near the northern edge of native distributions for centrarchids (Becker 1983), so these species may be particularly sensitive to cool summer temperatures. The eruption of Mount Pinatubo (Phillipines, June 1991) caused especially cool temperatures during the summer of 1992 that disrupted growth and recruitment of centrarchids in Lake Thirteen. In fact, notable climate signals from the volcanic eruption were found in lake thermal structure (King et al. 1997) and growth and recruitment of fish throughout the north-central portion of North America (King et al. 1999; Schneider and Lockwood 2002; Schupp 2002). More generally, temperature as an ecological resource has been linked to performance of freshwater fish. King et al. (1999) found that smallmouth bass *Micropterus dolomieui* grew better with increased availability of warm epilimnetic water during the summer in Lake Opeongo, Ontario. They also found that certain thermal stratification characteristics affected growth of yellow perch. Power and van den Heuvel (1999) linked growth of age-0 yellow perch to temperature in three Alberta lakes. Yields of walleye, northern pike, lake trout *Salvelinus namaycush*, and lake whitefish *Coregonus clupeaformis* have been strongly correlated with measures of thermal habitat space integrated over time during the summer growing season in large north-temperate lakes (Christie and Regier 1988).

Limited food resources led to intraspecific competition that was intense enough to restrict fish growth rates in Lake Thirteen. Density-dependent growth was evident for walleye, yellow perch, and largemouth bass. Given the wide range of diets for these species (Pierce and Tomcko 1998), these results suggest that a variety of food resources were limiting in Lake Thirteen. The importance of density-dependence in fish growth rates was recognized in Minnesota lakes as early as 1940. Eddy and Carlander (1940) concluded that the scattered examples of density-dependent growth at that time were so striking that they felt population density was more important than lake fertility and length of the growing season in causing differences in growth rates among lakes. In western Lake Erie, high predatory demand and reduced growth of walleye occurred when there were large walleye year classes (Hartman and Margraf 1992). Hanson and Leggett (1985) manipulated densities of yellow perch and pumpkinseed in littoral enclosures, and concluded that both intra- and interspecific competition for food was significant at natural densities. Persson et al. (1996) found that Eurasian perch *Perca fluviatilis* were less abundant and grew faster in small Swedish lakes with northern pike compared to lakes without northern pike. Presence of northern pike resulted in decreased intraspecific competition among the Eurasian perch. In a review of fish community ecology, Evans et al. (1987) concluded that food is a limiting factor in most fish communities.

Sand Lake, as a reference site, was not very useful for evaluating interactions between walleye, yellow perch, and other species. Relative abundance and size structure of yellow perch and pumpkinseed populations were found to be different enough that parallel comparisons with Lake Thirteen were not relevant. Moreover, the large-fish community of Lake Thirteen was so unique that other lakes with similar species compositions were not available.

Management Implications

A high-density yellow perch population, and predation by yellow perch on walleye fry, did not limit the usefulness of stocking walleye as fry. Fry stocking re-established a walleye population in Lake Thirteen in the face of high numbers of small yellow perch. Therefore, a high-density yellow perch population should not preclude the use of fry for walleye stocking.

Results from this study support arguments for using predation in "top-down" management of fish populations. In Lake Thirteen, predation by stocked walleye was able to regulate the yellow perch population. An abundance of top-level predators reduced numbers of small yellow perch and increased their growth rates. Walleye predation has also been shown to affect another prey species. Walleye predation caused increased growth and improved size structure of bluegill in Michigan lakes where walleye were stocked as a predator to bluegill populations (Schneider and Lockwood 2002). Similarly, addition of piscivorous Eurasian perch to sections of a small lake in Finland reduced recruitment of young-of-the-year crucian carp *Crassius carassius* by 90%, and increased crucian carp growth rates (Tonn et al. 1992). After reviewing studies of fish community structure, Colby et al. (1987), Evans et al. (1987), and Jackson et al. (2001) all concluded that predation is a dominant factor for structuring fish communities.

Top-down management may not always have desirable effects, however, and the effects of top-down management may not necessarily be spread throughout the panfish community. Community interactions may be complex enough that it is difficult to predict outcomes. In the case of Horseshoe Lake

(Anderson and Schupp 1986), northern pike stocking had deleterious effects on yellow perch size structure and recruitment. In the case of Lake Thirteen, walleye stocking had positive effects on growth rates of yellow perch, but the effects of walleye stocking were dampened through the rest of the food web as walleye stocking had no obvious influence on other species in the fish community. Field studies of predator diets in a Minnesota lake (Reed and Parsons 1996) and bioenergetics modeling of walleye predation dynamics elsewhere (Lyons and Magnuson 1987) has suggested that yellow perch populations can serve as a buffer to predation on other small littoral-zone fishes in lakes.

The prevalence of density-dependent growth among fish species in Lake Thirteen also has implications for managing fisheries in freshwater lakes. Density-dependence in growth must be a consideration for any management aimed at changing sizes and growth rates of fish. Heavy stocking, or other management aimed at producing large numbers of fish, can lead to poorer growth rates. Growth rates of young-of-the-year walleye stocked into rearing ponds have been affected by walleye density (Fox and Flowers 1990). In some cases where minimum length limits have increased densities of small fish, the result has been slower growth rates for species such as largemouth bass (Farabee 1974), northern pike (Kempinger and Carline 1978), and walleye (Serns 1978). Furthermore, the relationship between density and growth may be strongly curvilinear (Pierce et al. 2003), so that small changes in density could lead to large changes in growth rates.

Variable recruitment, intraspecific competition for food, and interannual climate changes all confound our ability to analyze and interpret changes in fish community structure resulting from fishery management activities. Typical netting surveys on the smaller lakes in Minnesota are conducted at intervals of five years or longer. Such surveys, without a sufficiently long time series of information, would have missed interrelationships among temperature, recruitment, fish densities, and growth rates that were evident in the more intensive sampling regime used in Lake Thirteen. The stochastic nature of fish communities makes it difficult to interpret results of stocking, new regulations, or other management changes unless the changes dramatically alter fish population dynamics.

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