

EFFECTS OF DISCONTINUING WALLEYE STOCKING ON FISH POPULATIONS IN LAKE THIRTEEN¹

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Abstract.— Fish community responses to discontinuing walleye *Stizostedion vitreum* stocking were monitored during 1986-1996 in Lake Thirteen, a 222 ha north-central Minnesota lake. Responses were compared to natural population fluctuations in a 54 ha reference lake (Sand Lake). The effect of discontinued walleye stocking, along with an apparent lack of northern pike *Esox lucius* recruitment, was to decrease the relative abundance of younger age predators in Lake Thirteen. Yellow perch *Perca flavescens* was the species most sensitive to changes in the predator populations. Increases in relative abundance of small yellow perch coincided with reductions in numbers of small walleye and northern pike. Conversely, decreases in relative abundance of large yellow perch corresponded with an increasing prominence of a strong 1988 year class of walleye as they grew to large sizes. Shifts in diets of various species were observed in Lake Thirteen, but other changes to the fish community were not readily evident. Competitive effects of walleye stocking on the largemouth bass *Micropterus salmoides* were not documented even though food and habitat use for the two species overlapped considerably. Climatic conditions, coupled with variable year class strength, had relatively large effects on the fish populations in both lakes.

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Introduction

Walleye *Stizostedion vitreum* 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 over the past decade has led, in many cases, to discontinuing ineffective stocking. By 1996, the stocking program had been reduced to 196 million fry and 2.2 million fingerlings. The enormity of the stocking program and recent attempts to make stocking more efficient has led to questions about the effects of walleye stocking on other fish populations within aquatic communities.

The influences that a given fish species has within an aquatic community depends on the other species present (Richardson and Threlkeld 1993). Complexity in the interactions among species arises from different life stages feeding at different trophic levels and from the problem that predation must be considered in relation to competition (Northcote 1988). The variety of resources used by a species and their efficiency in using them define the interactions (Werner 1977). Predation can affect the size structure of prey populations (Tonn et al. 1992) and even the threat of predation can affect rates of reproduction and growth in prey fish species (Frazer and Gilliam 1992).

Addition or removal of a species in a lake can provide some indications of the role of the species within an ecosystem (examples in Johnson 1977; Carpenter et al. 1987; Colby et al. 1987). Such whole ecosystem experiments to study fish community interactions, although they do not lend themselves to replication, remove problems of scale associated with laboratory or enclosure studies (DeMelo et al. 1992). Paired-system experiments with one reference and one experimental system are useful for large scale manipulations even

though classical statistics cannot be used to evaluate the manipulations (Carpenter 1989).

In this study, we tracked fish community responses to the discontinuation of walleye stocking in Lake Thirteen, a small north-central Minnesota lake that had a consistent history of walleye stocking. Fish populations were sampled from 1986-1996 with walleye fry stocking curtailed after 1988. Community responses in Lake Thirteen were then compared to natural fluctuations of fish populations in a reference lake (Sand Lake). 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.

Study Area

Lake Thirteen is surrounded by the Chippewa National Forest in Cass County, Minnesota (47° 17' N latitude, 94° 32' W longitude). It is a landlocked lake with a surface area of 222 ha, a maximum depth of 17.0 m, and total alkalinity of 117 mg⁻¹ CaCO₃. The lake has extensive littoral area with 74% of the lake surface area shallower than 4.6 m. Shoal areas are predominantly sand with large beds of muskgrass (*Chara* sp.), and a fringe of bulrush (*Scirpus acutus*). Other macrophytes such as pondweed (*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 *Perca flavescens*, and walleye). The centrarchid population of Lake Thirteen was somewhat unique because it consisted only of pumpkinseed and largemouth bass. 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*.

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 (roughly 500,000 fry per year). Early stocking 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 an experimental 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 CaCO₃. The littoral area (depths less than 4.6 m) was 40% of the surface area. Shoal areas in Sand Lake are predominantly sand with patches of pondweed (*Potamogeton* spp.) and bulrush (*Scirpus acutus*). 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 *Lepomis macrochirus*, and black crappie *Pomoxis nigromaculatus*. Additional small species were golden shiner *Notemigonus crysoleucas* and mimic shiner *Notropis volucellus*. Walleye fingerlings or fry were stocked six times between 1965 and 1986. Walleye natural reproduction has been evident in Sand Lake.

Methods

Lake Thirteen

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 rectangu-

lar frame opening into the trap; (2) multifilament nylon gill nets that were 76.2 m long and had 15.2 m 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. Initial sampling of the fish populations in Lake Thirteen was by gill netting and electrofishing during late fall (23 September-9 October) in 1986. With the exception of 1993, electrofishing and trap netting were conducted annually from 1987-1996. In 1993, we used only electrofishing in an effort to determine if walleye natural reproduction was occurring. Electrofishing was conducted in early fall (27 August-20 September) with efforts of 150-420 minutes each year. Trap netting was conducted in late summer (6-28 August) with efforts of 10-24 overnight net sets each year. Gill netting was conducted in late summer during 1987-1988, and again during 1995-1996, using efforts of 9 overnight gill net sets each year. Some supplemental gill netting occurred during 1991-1993 using efforts of 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, opercles, or cleithra were obtained from northern pike, largemouth bass, pumpkinseed, walleye, and yellow perch to determine age and growth rates. The micro-computer program DISBCAL (Frie 1982) was used to backcalculate body growth from scale measurements. Additionally, a linear growth model (Weisberg 1987, 1989) was used to model the growth on 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 or food resources. Log_e transformation of scale increments was used for northern pike because residual plots indicated the transformation was needed. Effects of temperature on growth rates were determined by regression of year effects from the linear growth model with means of the June, July, and August daily air temperatures for each year. Mean daily air temperatures (Table 1) were obtained from a weather station at Cass Lake, located nine km northwest of Lake Thirteen (data from the state climatologist).

Stomach contents of northern pike, white sucker, pumpkinseed, largemouth bass, yellow perch, and walleye from Lake Thirteen were sampled in 1987-1988 and again in 1995-1996. Additional stomach sampling of walleye occurred during the initial netting in 1986. Largemouth bass were caught mostly by angling during May-July and stomach contents were removed with the aid of a stomach pump (Seaburg 1957). A hemostat was used to assist in removal of crayfish from pumped stomachs. Other fish species caught primarily during gill netting and trap netting had their stomach contents removed by dissection. Large food items were identified in the field and other stomach contents were preserved in formalin for later identification and enumeration in the laboratory.

Largemouth bass and walleye use of various habitats in Lake Thirteen was documented from gill net, trap net, and electrofishing catches. Depths fished by each 15 m panel of gill net were recorded and compared to fish catches for each panel.

Voluntary creel surveys were conducted in Lake Thirteen during 1987-1988 and 1995-1996. An unmanned creel check station with a sign containing information and a ruler for measuring fish was constructed at the only public access to Lake Thirteen. Anglers were requested to voluntarily supply the following information on a trip report card: 1) date; 2) principal species sought; 3) number of hours of angling effort expended; 4) distance traveled to Lake Thirteen; and 5) numbers and lengths of each species caught. Cards which were judged to be deliberately fraudulent were not used in tabulating results. Instantaneous counts of boats and anglers were obtained during periods when other field work was being conducted on the lake (mid-May through early September). Instantaneous counts were averaged for each day, then summarized for the entire summer fishing season by calculating an overall season mean for the daily averages of anglers per count. Although the season means included no weekend fishing efforts, they still provided a consistent (though not randomized) method for comparing recreational fishing effort between 1987-1988 and 1995-1996.

Table 1. Mean daily air temperatures for June through August each year measured at Cass Lake and Deep Portage weather stations, Cass County, Minnesota.

Year	Mean daily air temperature (°C)	
	Cass Lake	Deep Portage
1983	19.8	-
1984	18.7	-
1985	16.0	16.1
1986	18.2	17.5
1987	19.4	19.7
1988	20.9	20.3
1989	19.2	19.3
1990	18.8	18.7
1991	19.7	19.8
1992	15.9	16.2
1993	17.2	16.8
1994	17.9	18.1

Sand Lake

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 nearly annually (1987-1996 except 1993) during early fall using 75-105 min of effort each year. During 1988-1996 (except 1993), some spring electrofishing (23 April-31 May) was used to sample rock bass (75-90 min effort each year). Trap netting was also conducted each year (except 1993) during late summer using 6-12 overnight net sets. Gill netting occurred during late summer using 4-6 overnight net sets in 1987-1988, 1992, and again in 1995-1996. In Sand Lake, age and growth rates were determined for rock bass, bluegill, and black crappie, in addition to the five species aged from Lake Thirteen. Average air temperatures for each month (Table 1) were obtained from a weather station at Deep Portage, located three km west of Sand Lake (data from state climatologist).

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, and 2) the discontinuation of walleye stocking after 1988. 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%.

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 eight walleye (1988 year class) and 5 age four fish (1992 year class). This paucity of year classes at the end of the study differed from earlier 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 at the end of the study, the mean gill net catch rate of 4.0 walleye/net lift (SE=0.8) in 1996 showed that there was still a relatively large number of old individuals present.

Walleye recruitment in Sand Lake provided a contrast to Lake Thirteen, with fish catches at the end of the study 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, 1994, 1995, and 1996 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).

Density-dependent growth of walleye was evident in back-calculated lengths of fish caught in 1996 from Lake Thirteen. The large 1988 year class of walleye grew slowly with an average backcalculated length at age three of 254 mm (SE=5 mm). Walleye captured from the 1992 year class, which did not have to compete with stocked fish and adjacent year classes, grew much faster reaching 386 mm (SE=3 mm) in three years.

At the end of the study, walleye showed decreased use of shallow near-shore habitats in Lake Thirteen compared to early years when fry stocking was occurring. Only one individual walleye was caught in 24 electrofishing transects that encompassed the entire shoreline of the lake during 1995-1996. Walleye were more commonly caught along shorelines during 1987-1988, when they were found at 20 of 27 electrofishing transects. Walleye were found in all other areas of the lake sampled by gill netting during both 1987-1988 and 1995-1996.

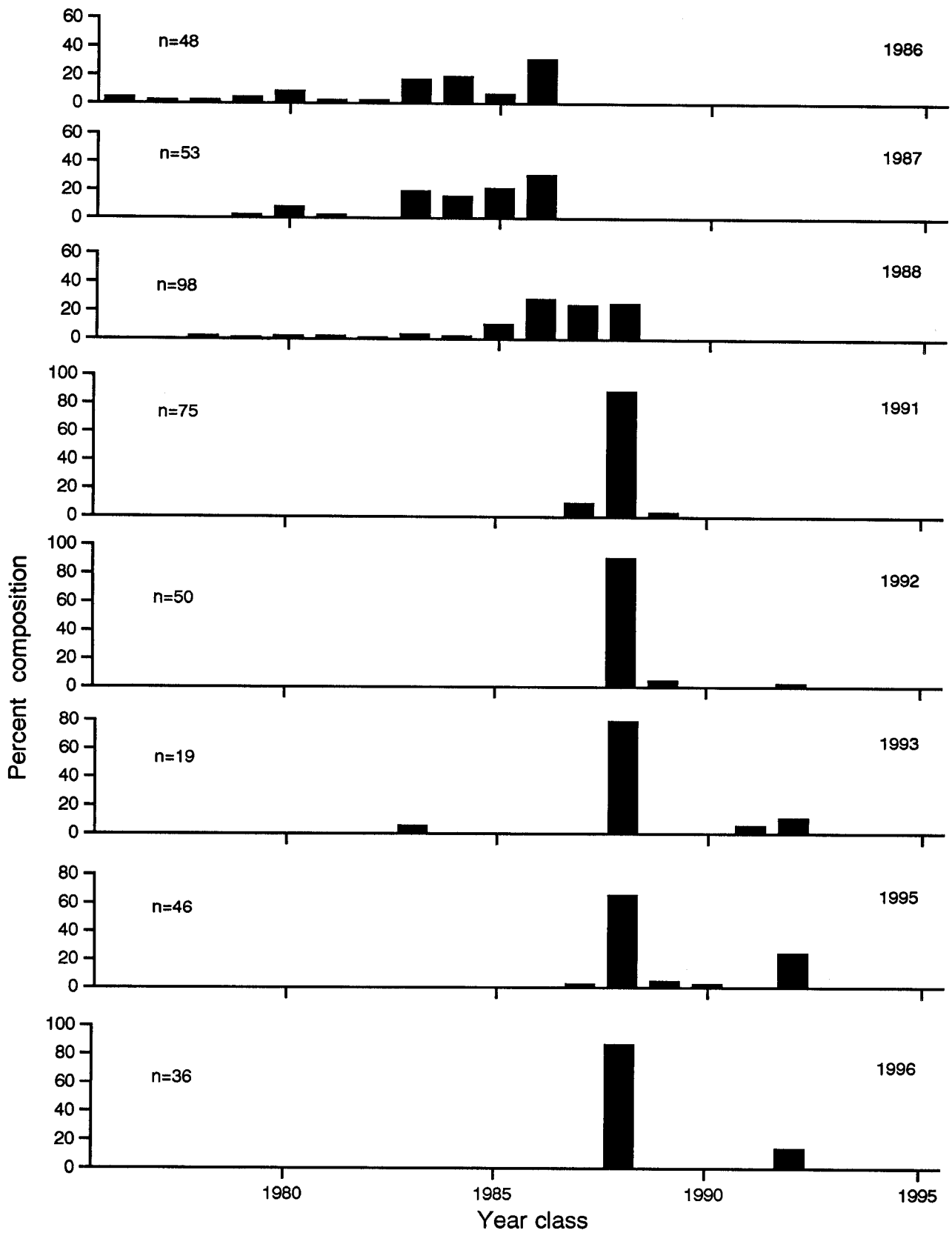


Figure 1. Percent composition of walleye year classes in gill net catches from Lake Thirteen, 1986-1996.

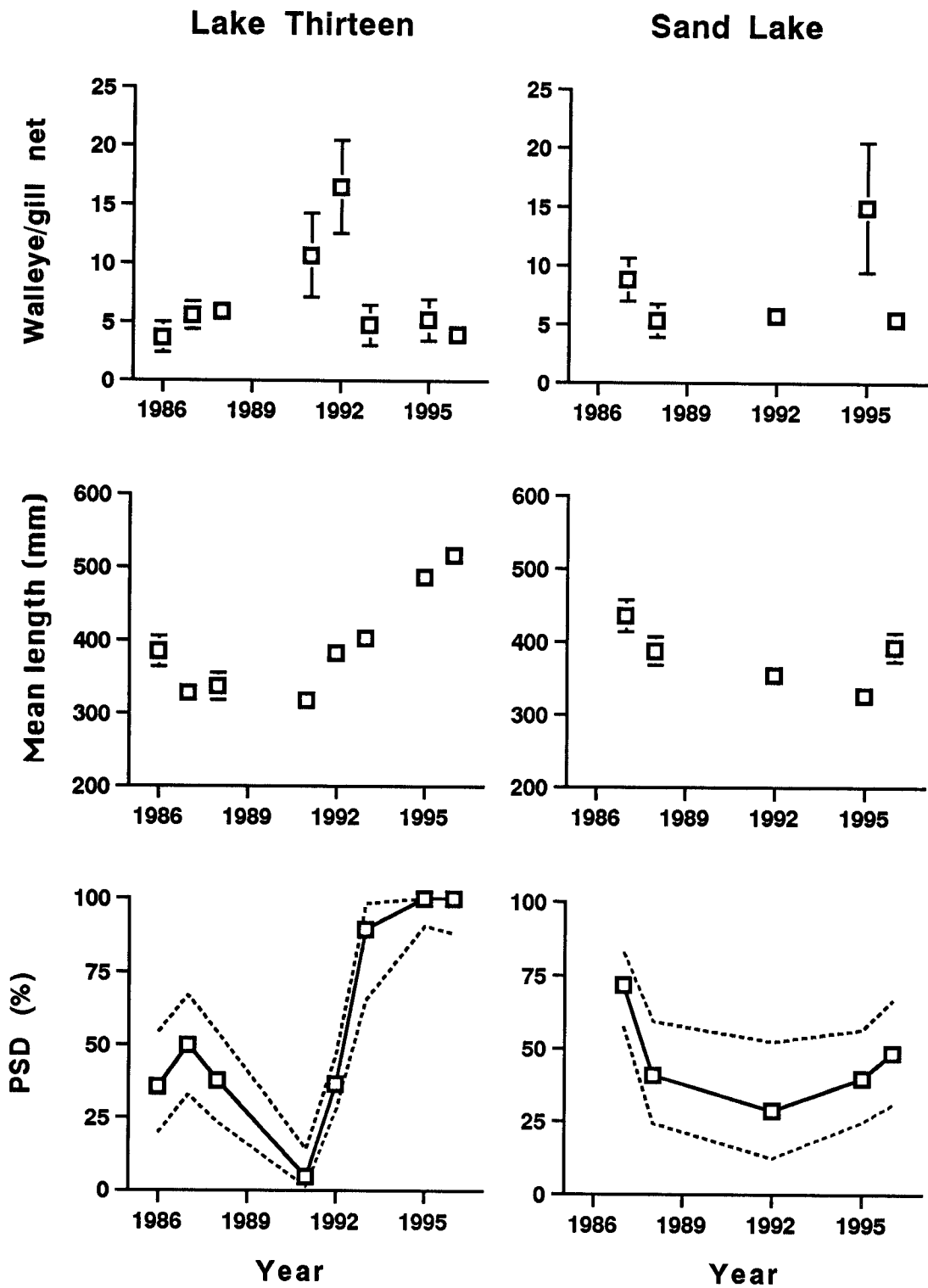


Figure 2. CPUE (\pm SE), mean length (\pm SE), and PSD (with 95% confidence limits) for walleye caught by gill netting in Lake Thirteen and Sand Lake.

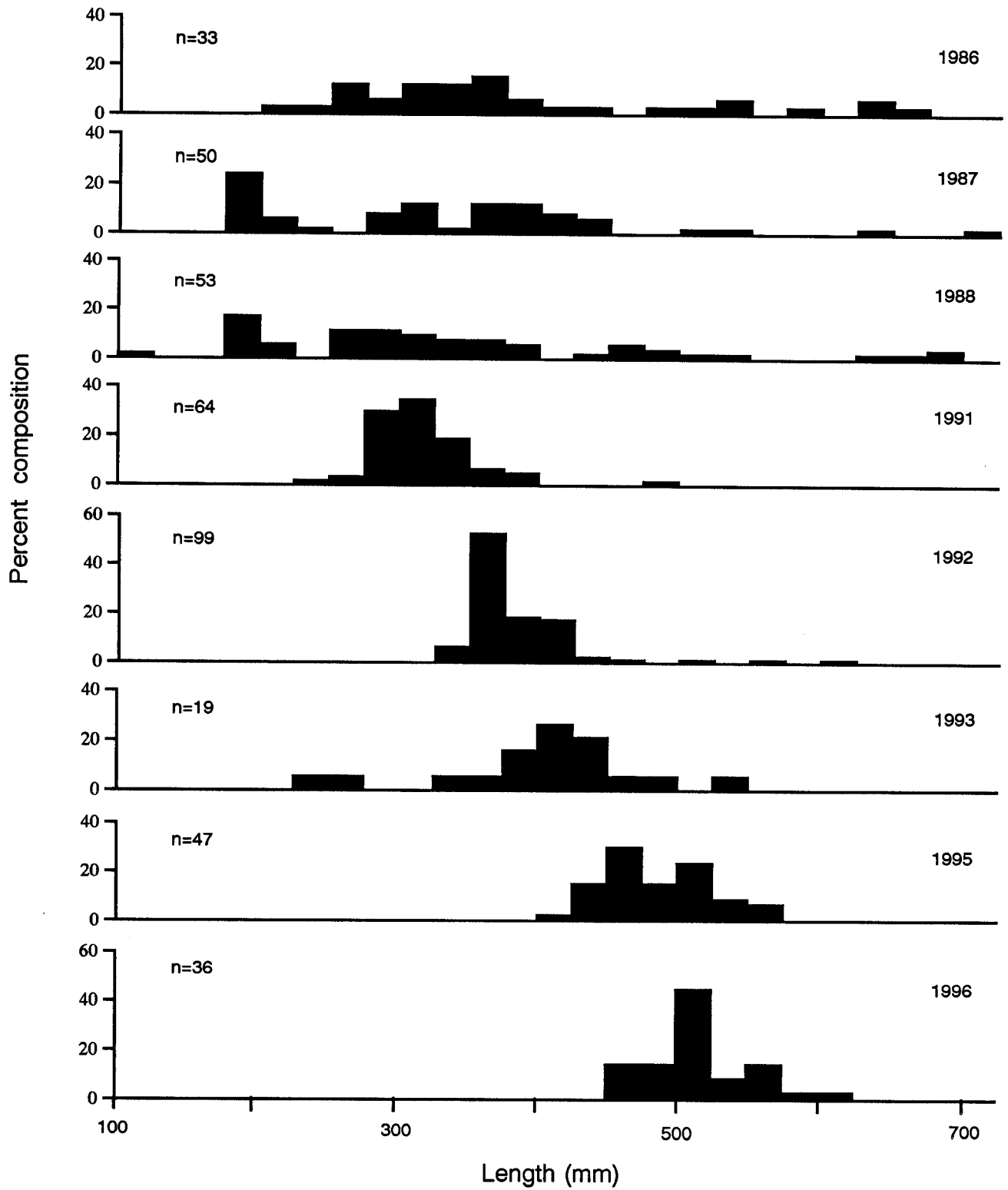


Figure 3. Length frequency distributions for walleye caught by gill netting in Lake Thirteen, 1986-1996.

Gill net panels sampled walleye at randomized locations in all depths ranging from 2 to 8 m. Nets were not set in deeper water because dissolved oxygen concentrations were less than 5 mg·l⁻¹ at depths greater than 7-10 m each year.

A shift in the diet of walleye in Lake Thirteen was found between early and late years of the study. During 1995-1996, all walleye stomachs in which we found food items contained fish (Table 2) and 95% (19/20) of identifiable fish remains were yellow perch. The walleye showed more variety in their food habits during the earlier years of fry stocking, with aquatic insects found in 70%, fish in 55%, and nematodes and zooplankton in 11-14% of stomachs containing food items during 1986-1988. Sizes of walleye sampled for stomach contents during 1995-1996 were 410-602 mm total length, compared to 188-685 mm during 1986-1988.

Northern Pike

Because of poor recruitment after 1990, the northern pike population in Lake Thirteen underwent changes similar to those of the walleye population. We found increasing mean length and PSD for northern pike caught in gill nets toward the end of the study because few fish were encountered from year classes subsequent to 1990 (Figures 4-5). Length frequency distributions for northern pike showed no fish smaller than 450 mm after 1991 (Figure 6). 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 for later years. The high gill net catch rate in 1991 was mainly due to fish from 1989-1990 year classes (Figure 5).

Northern pike year class strength was not related to spring water levels in Lake Thirteen. Spring water level during a good

Table 2. Percentages of stomachs from walleye, northern pike, largemouth bass, yellow perch, pumpkinseed, and white sucker that contained various categories of food. Only stomach samples containing at least one food item were included. Stomach sampling was conducted in Lake Thirteen during 1986-1988 and again during 1995-1996.

Predator and Years sampled	Percent of (full) stomachs containing a food item							
	Fish	Pelecypoda	Gastropoda	Decapoda	Amphipoda	Nematoda	Insecta	Other zooplankton
Walleye								
1986-88	55.1	0	0	1.0	2.0	11.2	70.4	14.3
1995-96	100.0	0	0	0	0	0	3.6	0
Northern pike								
1986-88	84.7	0	1.4	16.7	1.4	1.4	9.7	0
1995-96	100.0	0	0	3.3	0	0	0	0
Largemouth bass								
1986-88	53.4	0	1.4	43.8	4.8	2.1	49.3	5.5
1995-96	71.7	0	1.6	23.0	3.2	1.6	54.5	2.7
Yellow perch								
1986-88	6.7	3.3	13.3	30.0	40.0	0	63.3	13.3
1995-96	19.6	0	3.9	54.9	2.0	0	25.5	0
Pumpkinseed								
1986-88	6.5	16.1	38.7	0	9.7	12.9	93.5	3.2
1995-96	0	0	66.7	0	0	0	48.9	0
White sucker								
1986-88	11.1	45.5	0	0	0	0	100.0	0
1995-96	0	17.4	21.7	0	4.3	0	58.7	4.3

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. Late April through early May benchmark readings during the study ranged from 1.6 to 1.9 m.

Growth of northern pike was relatively fast in Lake Thirteen and did not seem to be affected by interannual differences in the lake environment. Average back-calculated lengths at age three were 522-528 mm (samples from years 1987-1988 and 1995-1996). Estimates of year effects from the linear growth model showed that northern pike had little interannual variation in their growth rates (Figure 7).

The food of northern pike in Lake Thirteen was predominantly fish, though some other food items were also found in northern pike stomachs. Yellow perch were the most commonly identified fish prey, being found in 53%-86% of northern pike stomachs containing identifiable fish remains. Pumpkinseed were found in 10%-16%, largemouth bass in 5%-12%, walleye in 0%-12%, and other fish in <5% of stomachs with identifiable fish prey. Differences in use of crayfish and aquatic insects among years (Table 2) may have been related to changes in northern pike size distributions. Crayfish were found in 3%-17% and aquatic insects (Diptera and Ephemeroptera) in 0%-10% of northern pike stomachs containing food items.

In Sand Lake, recruitment of northern pike occurred more consistently 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 4). Gill net catch rates during 1995-1996 were higher than in Lake Thirteen and were attributed to recruitment of 1993-1994 year classes of northern pike. Northern pike in Sand Lake have also shown little interannual variation in growth rates, as indicated by linear growth modeling, although 1992 was apparently a poor year for northern pike growth in Sand Lake (Figure 7). Mean back-calculated lengths at age three were 456-464 mm (samples from years 1987-1988 and 1995-1996).

Largemouth bass

The largemouth bass population in Lake Thirteen showed evidence of variable recruitment. Weak year classes were apparent in 1985 and 1992, whereas a strong year class was evident in 1994 (Figure 8). 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 9). PSD's from electrofishing catches were also variable during the study, but never greater than 35%.

In addition to variable recruitment, largemouth bass showed variable growth rates that we related to summer temperatures and 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 7). Annual growth coefficients from the linear growth model appeared to be related to temperatures during June, July, and August. Regression with a mean of the June, July, and August temperatures for each year explained 57% of the variation in annual growth coefficients derived from the linear growth model ($P < 0.01$). Mean back-calculated lengths for largemouth bass at age three ranged from 208-255 mm each year (samples from years 1986-1996).

Largemouth bass were found in all habitats in Lake Thirteen. Largemouth bass made extensive use of shallow shoal areas; they were caught in every electrofishing transect during 1987-1988 and 1995-1996. They were also caught at all depths that had sufficient dissolved oxygen for fish. Gill net panels sampled largemouth bass at randomized locations in all depths ranging from 2 to 8 m.

We found evidence for a shift in food habits of the largemouth bass in Lake Thirteen between early (1987-1988) and late (1995-1996) periods of the study. Largemouth bass showed increased use of fish and decreased use of crayfish. Fish were found in 53% of early and 72% of stomachs containing food items during the late sampling period (Table 2).

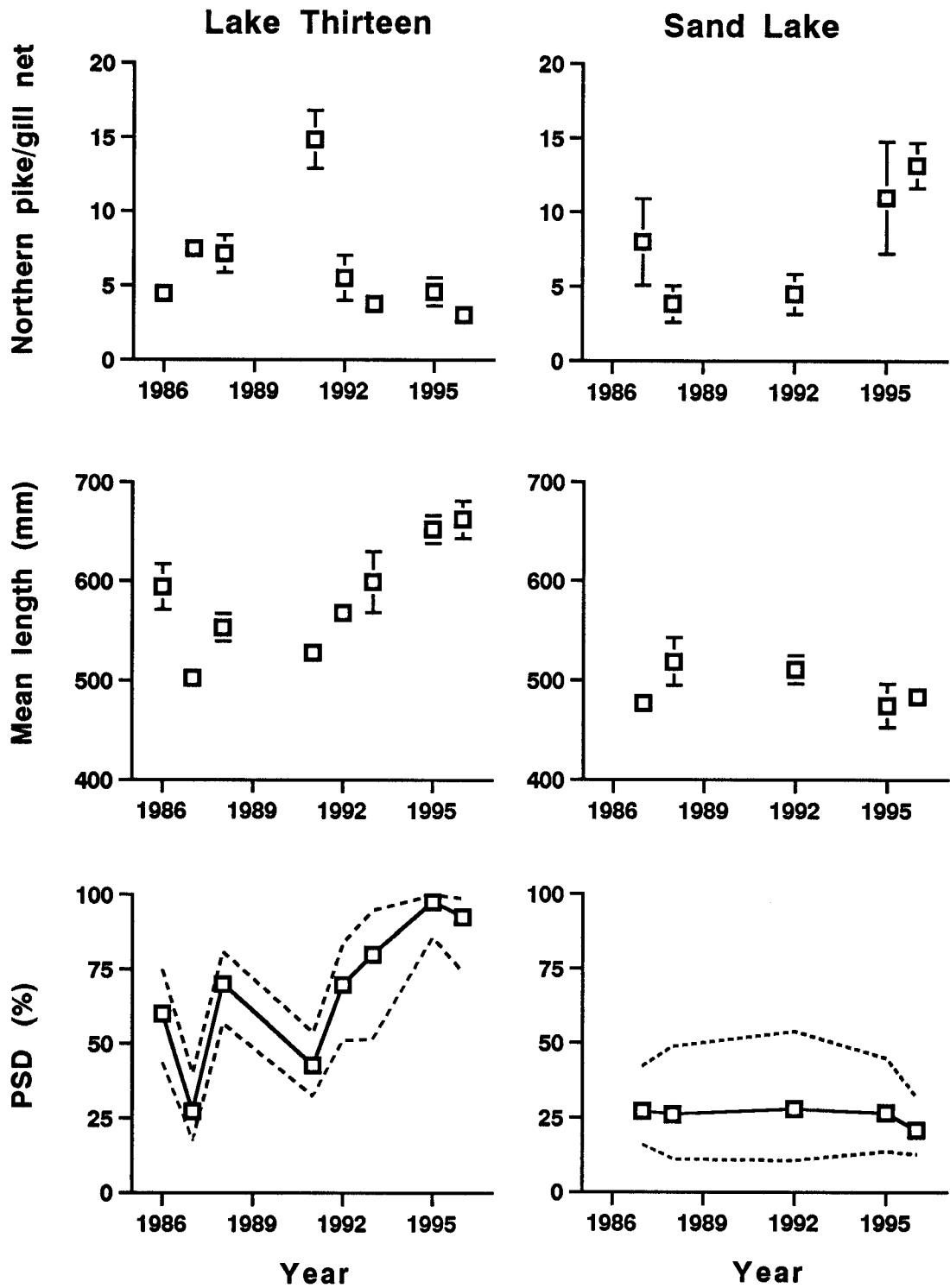


Figure 4. CPUE (\pm SE), mean length (\pm SE), and PSD (with 95% confidence limits) for northern pike caught by gill netting in Lake Thirteen and Sand Lake.

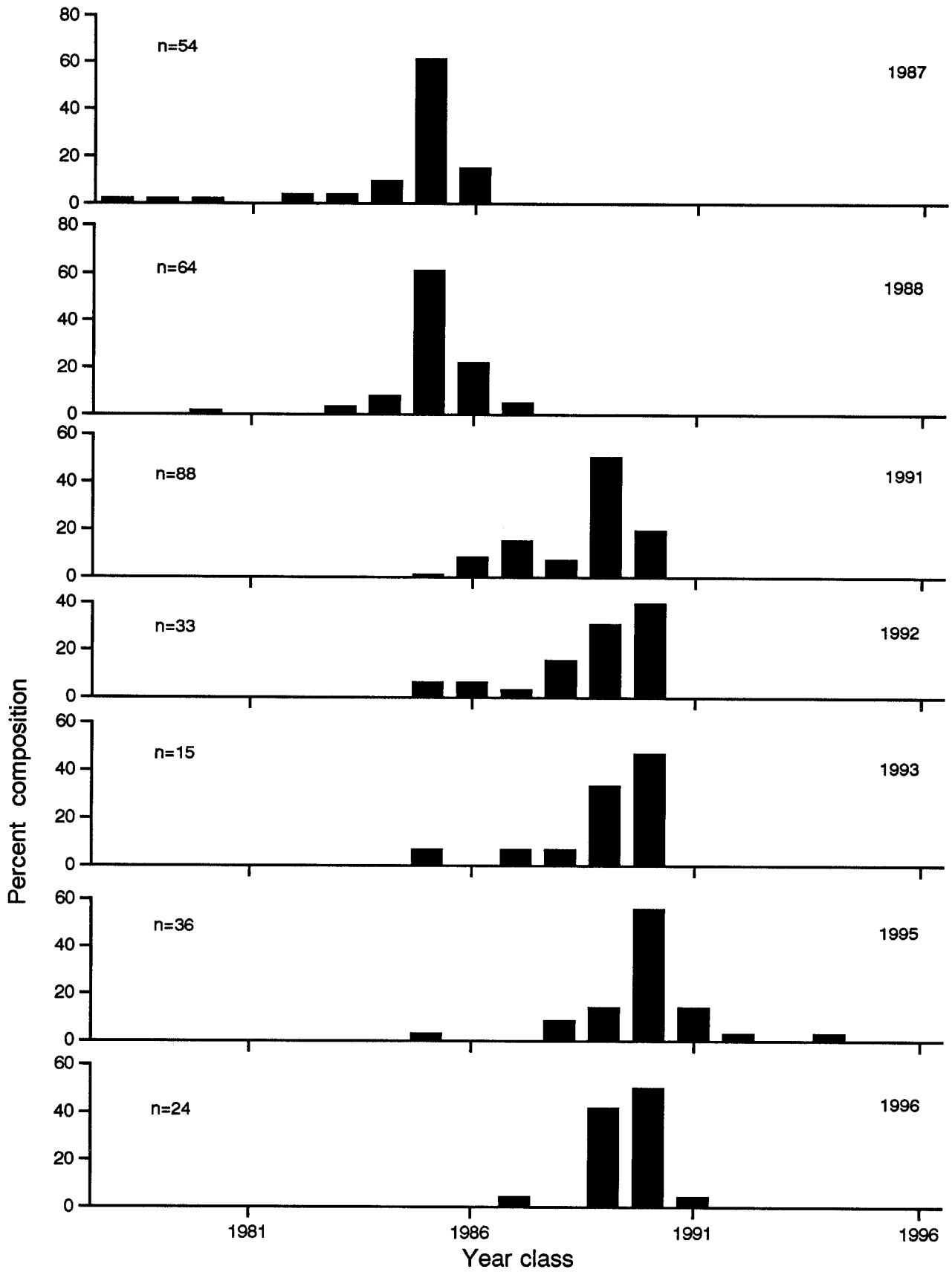


Figure 5. Percent composition of northern pike year classes in gill net catches from Lake Thirteen, 1987-1996.

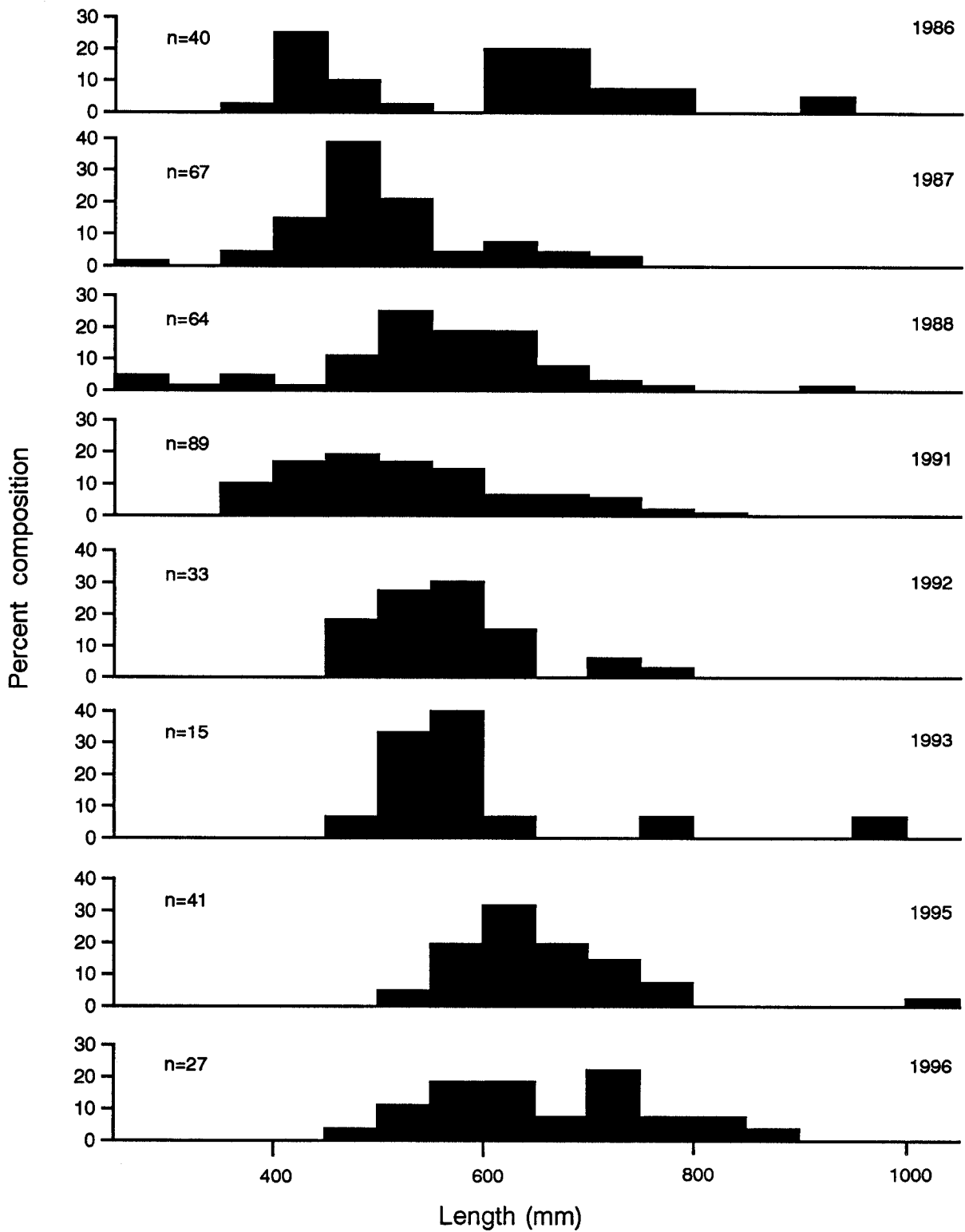


Figure 6. Length frequency distributions for northern pike caught by gill netting in Lake Thirteen, 1986-1996.

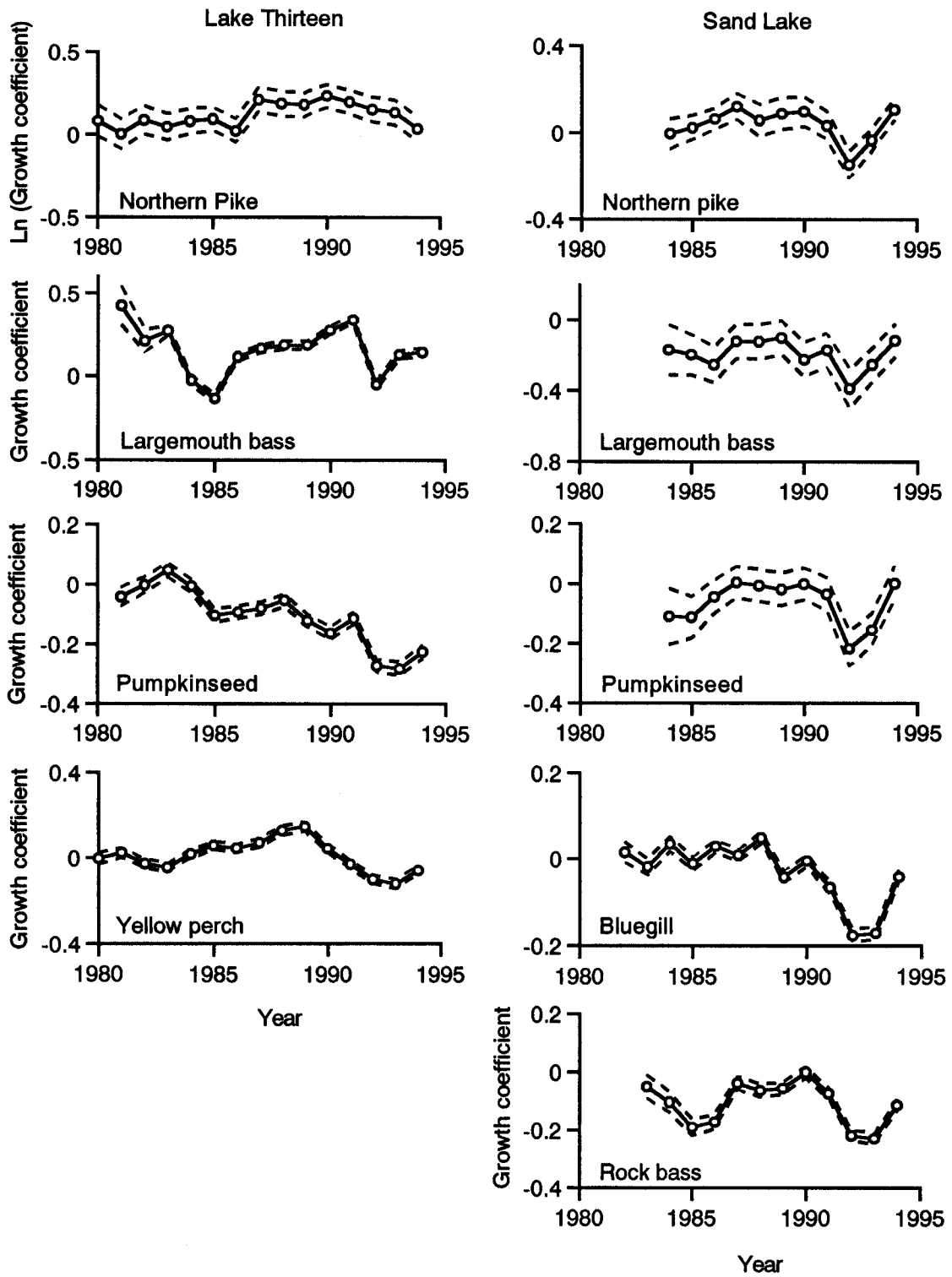


Figure 7. Growth coefficients (\pm SE) describing year (environmental) effects on growth of fish scales, as estimated using the linear growth model. Scale annuli measurements were from various fish species in Lake Thirteen and Sand Lake.

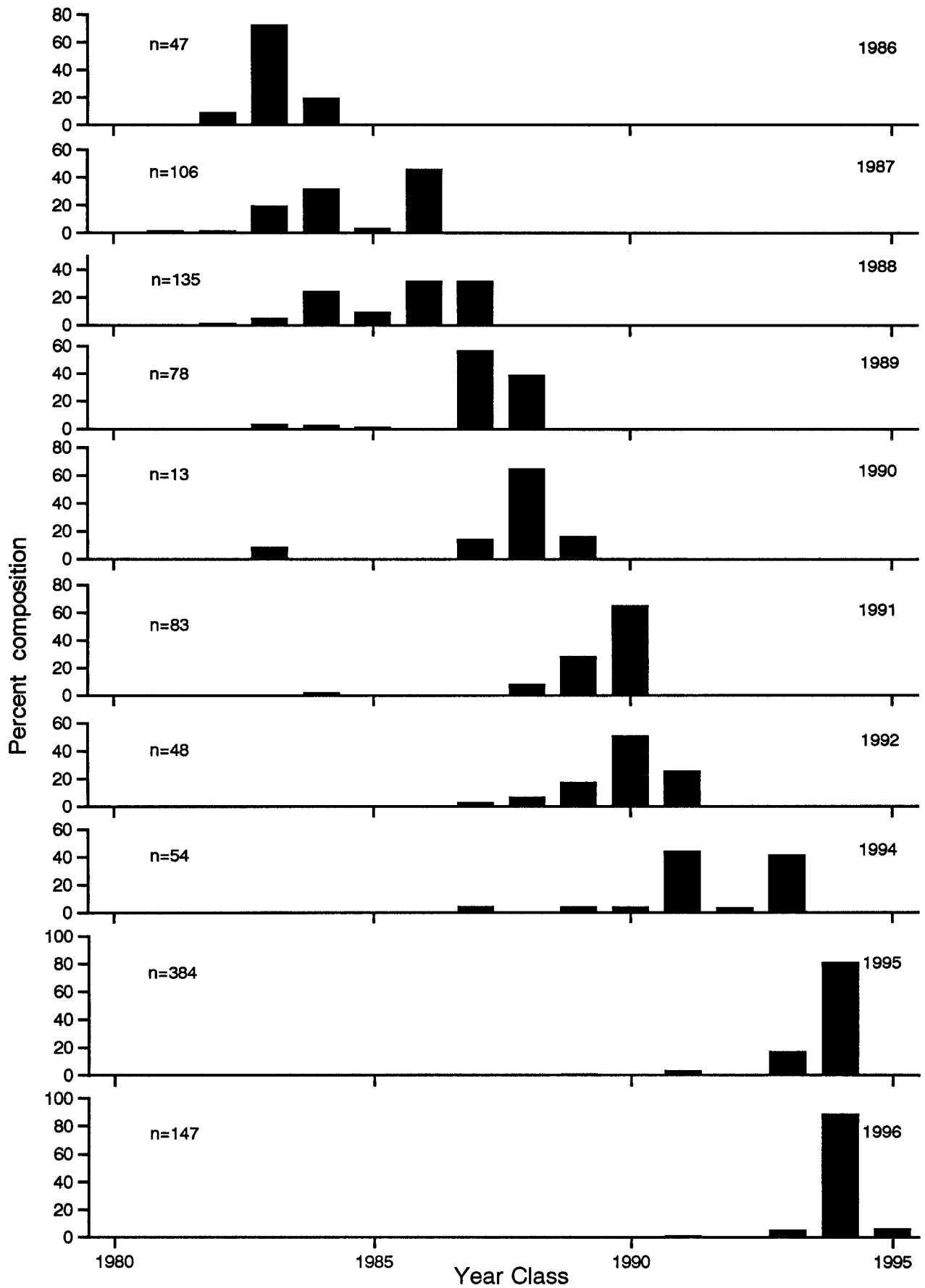


Figure 8. Percent composition of largemouth bass year classes in electrofishing catches from Lake Thirteen, 1986-1996.

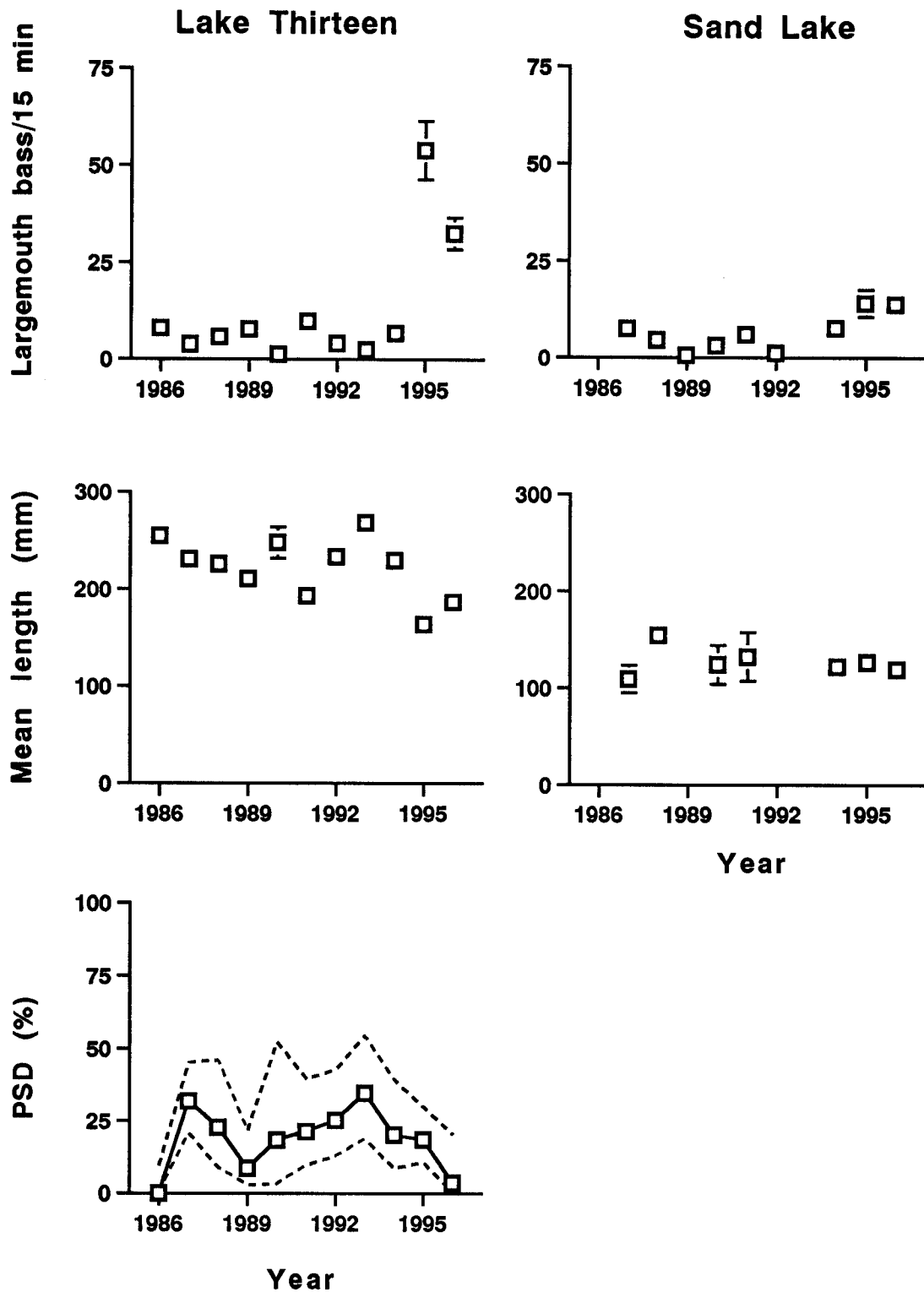


Figure 9. CPUE (\pm SE), mean length (\pm SE), and PSD (with 95% confidence limits) for largemouth bass caught by electrofishing in Lake Thirteen and Sand Lake.

Yellow perch were 48% of identifiable fish in largemouth bass stomachs in 1987-1988 and 71% of identifiable prey fish in 1995-1996. Other fish eaten were brook stickleback, small cyprinids, banded killifish, Johnny darter, and pumpkinseed. Crayfish were found in 44% of early, but only 23% of stomachs containing food items during the late sampling period. Largemouth bass ate a variety of food items, but aquatic insects (especially Ephemeroptera, Odonata, and Diptera) were important food items for largemouth bass along with fish and crayfish.

In Sand Lake, the greatest catch rates for largemouth bass also occurred during the last two years of the study. Electrofishing catches averaged 13.8-14.2 bass per 15 min in 1995-1996 compared to 0.6-7.7 bass per 15 min in other years (Figure 9). 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. Regression of yearly growth coefficients from the linear scale growth model also showed a significant relationship with mean daily temperatures during June through August ($R^2=0.52$; $P=0.02$). 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 backcalculated lengths at age three were 202-272 mm each year.

Yellow Perch

The yellow perch population in Lake Thirteen was initially typified by large numbers of big 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%. During the same time, mean lengths in electrofishing catches were 166-213 mm and PSDs were 21-79%. Catches for both gears consisted of 7-10 age classes of yellow perch (Figures 10-11). 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 beginning in 1991 (Figures 12-13). Mean lengths in electrofishing catches were 113-127 mm, and PSDs were only 5-6% during the last two years of the study (Figure 14). Gill net catches, on the other hand, showed decreasing numbers of large yellow perch. By the last two years of the study, gill net catch rates had declined to means of 27-31 fish/net, mean lengths had declined to 183-185 mm, and PSDs had declined to 24-35% (Figure 15). The number of age classes represented in the catches during the last two years ranged from 5 to 7. Most importantly, both electrofishing and gill net catches showed trends of declining proportions of large (>200 mm) yellow perch in length frequency distributions (Figures 12-13).

The relationship between summer temperatures and growth rates was not as clear for yellow perch as it was for largemouth bass. Regression of mean daily temperatures during the summer with annual growth coefficients from the linear scale growth model showed a weaker relationship ($R^2=0.23$; $P=0.07$; years=1980-1994). Slowest growth years were 1992-1993 and best growth years were 1988-1989 (Figure 7). Variability in growth was also illustrated in back-calculated lengths. Mean back-calculated lengths at age three ranged from 109 to 168 mm each year, although the smallest mean back-calculated lengths at age three were for the last three years of the study. Large year classes (e.g. 1991) appeared to grow slowest, but it was not clear how much their growth was affected by concurrent changes in water temperature or walleye abundance.

At the end of the study, yellow perch showed some apparent shifts in food habits compared to years of walleye stocking. Aquatic insect larvae, amphipods, and crayfish were predominant in stomachs in 1987-1988 (Table 2). In sampling during 1995-1996, yellow perch showed increased use of fish and

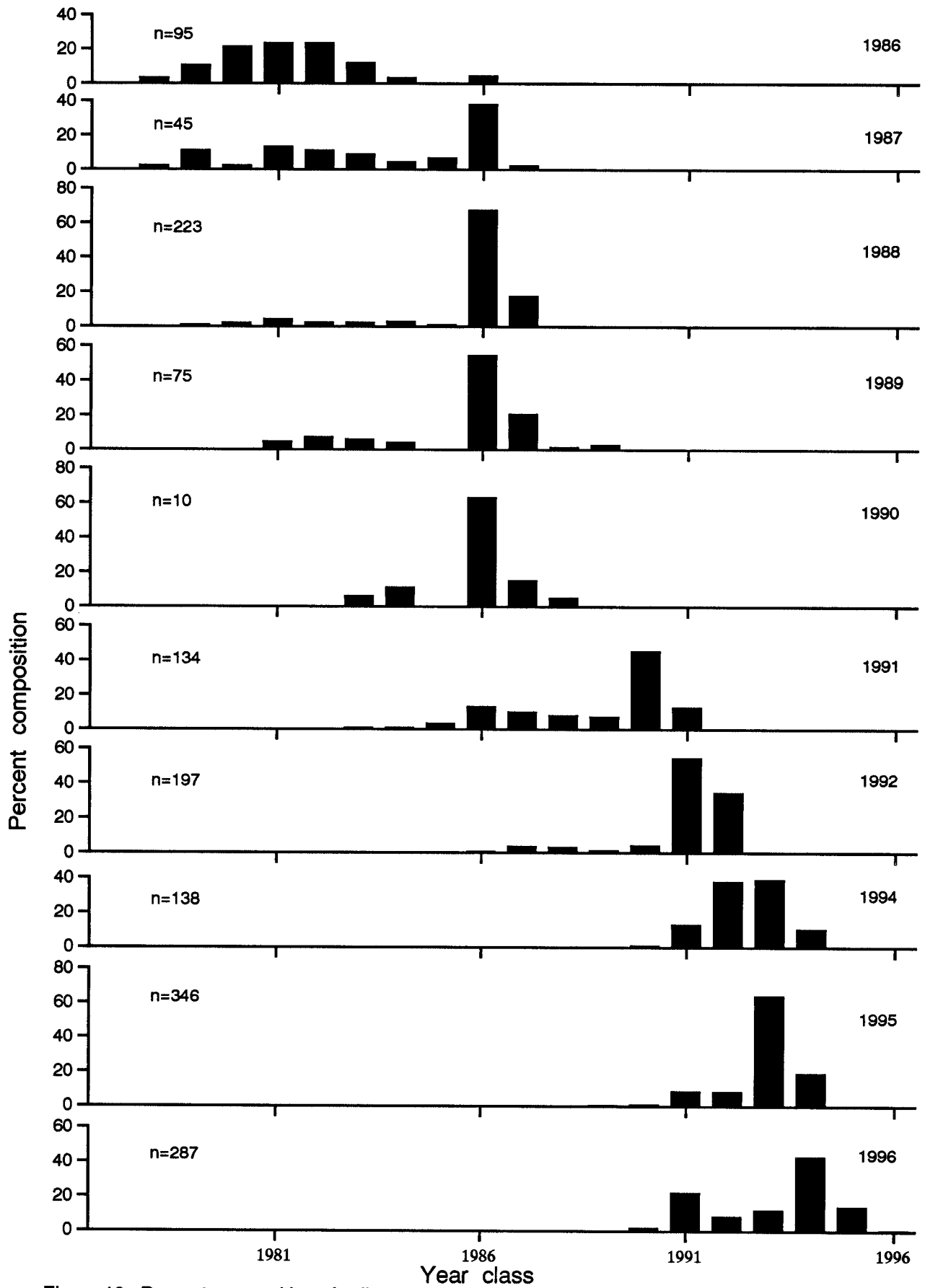


Figure 10. Percent composition of yellow perch year classes caught by electrofishing in Lake Thirteen, 1986-1996.

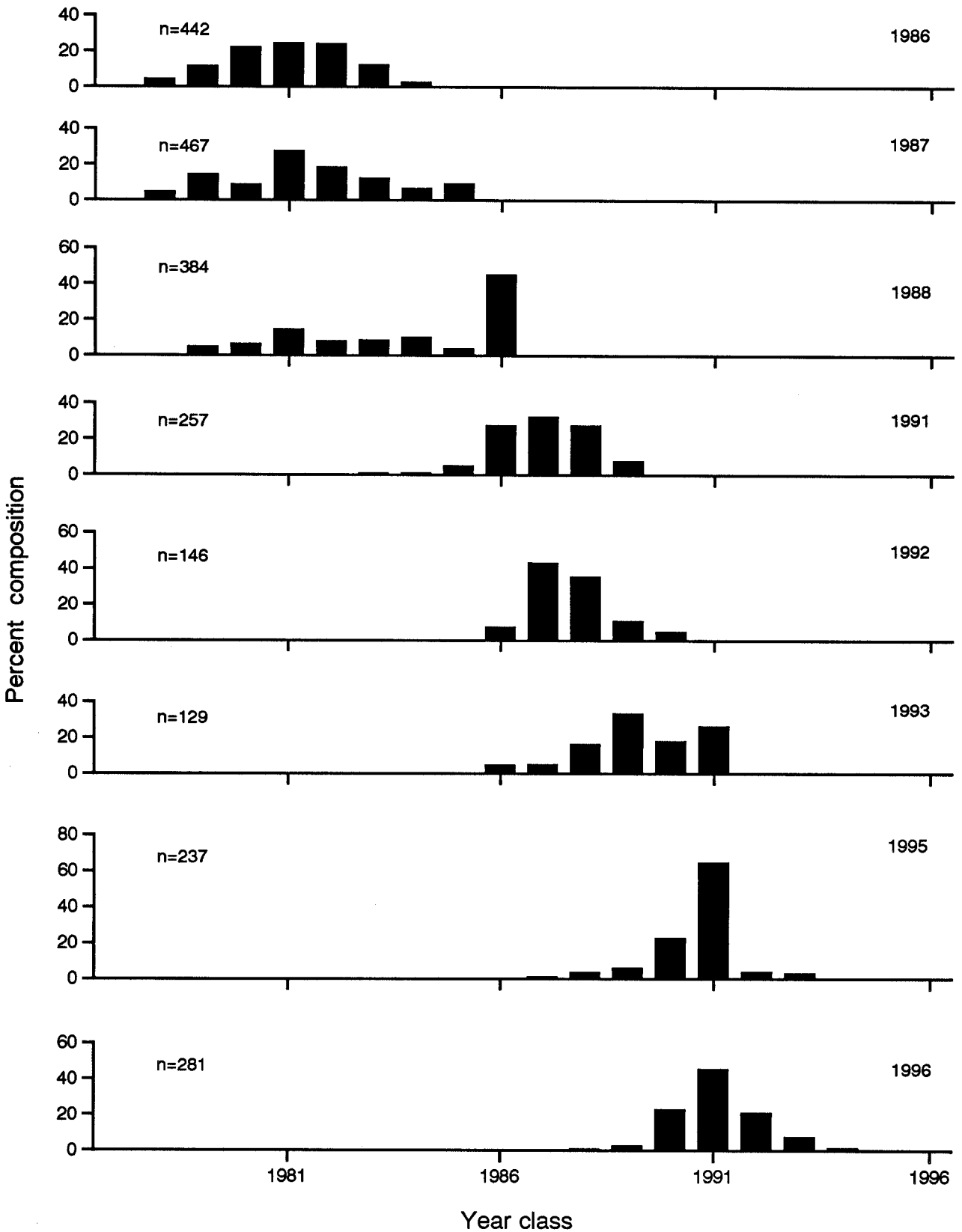


Figure 11. Percent composition of yellow perch year classes in gill net catches from Lake Thirteen, 1986-1996.

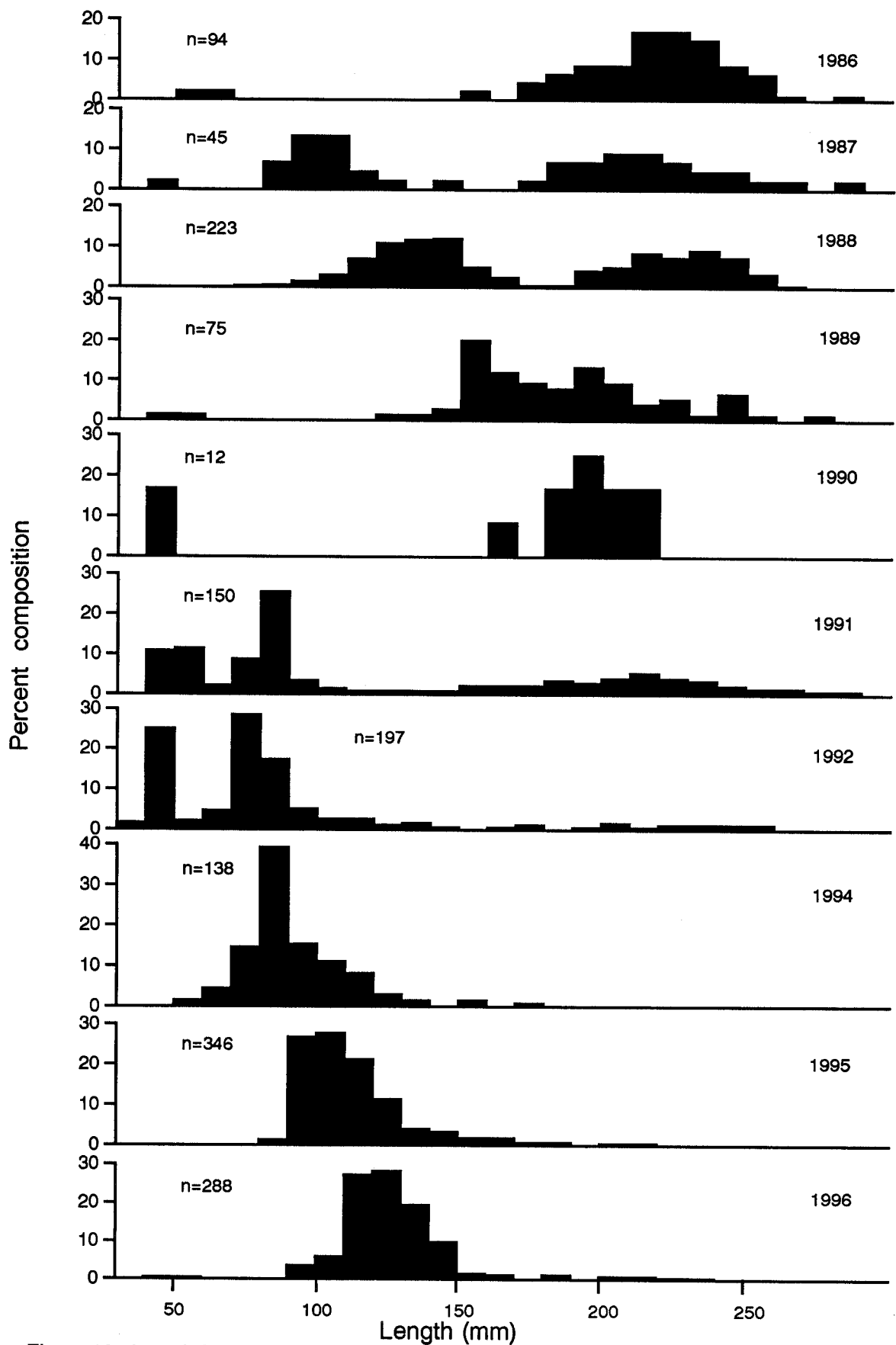


Figure 12. Length frequency distributions for yellow perch caught by electrofishing in Lake Thirteen, 1986-1996.

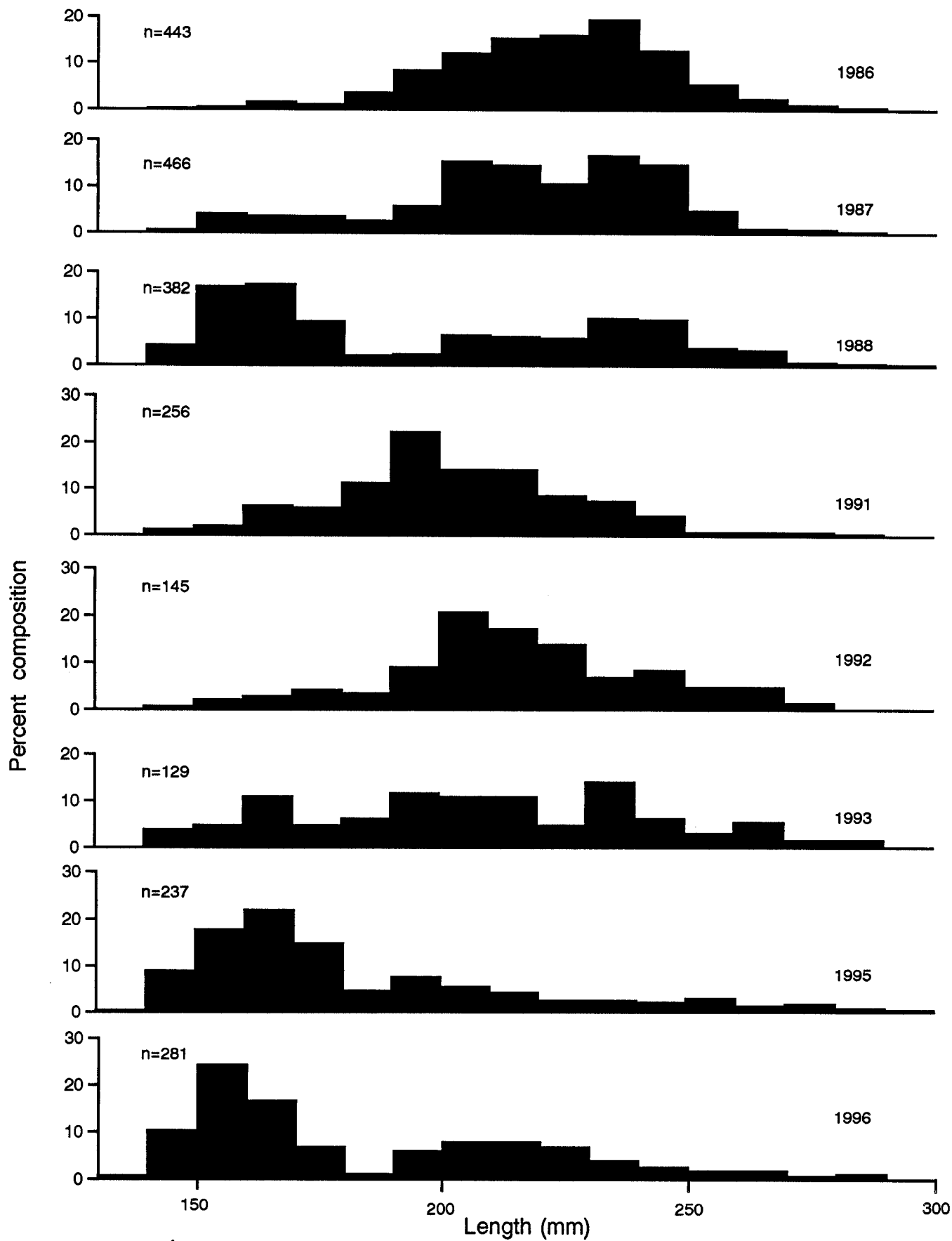


Figure 13. Length frequency distributions for yellow perch caught by gill netting in Lake Thirteen, 1986-1996.

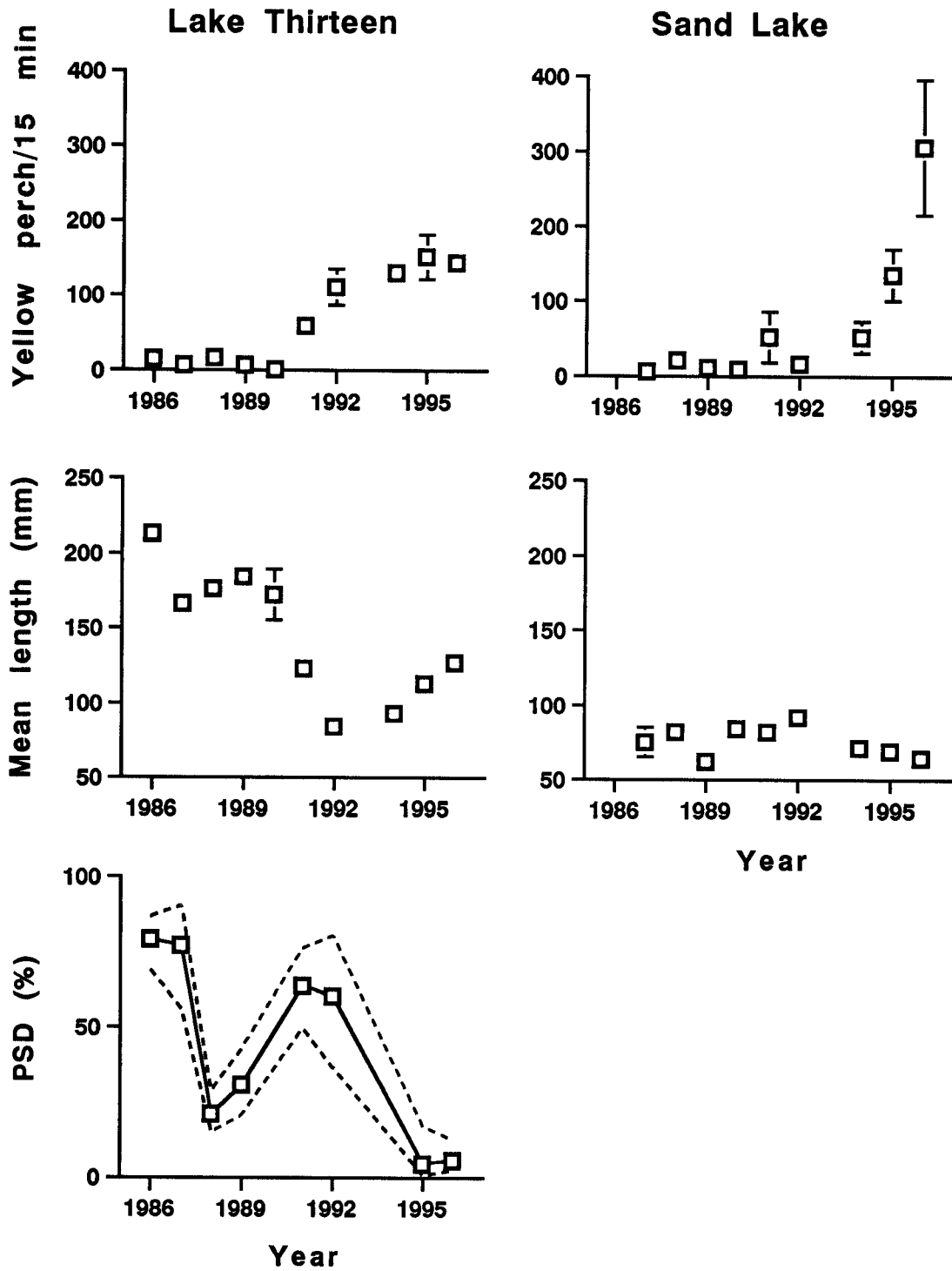


Figure 14. CPUE (\pm SE), mean length (\pm SE), and PSD (with 95% confidence limits) for yellow perch caught by electrofishing in Lake Thirteen and Sand Lake.

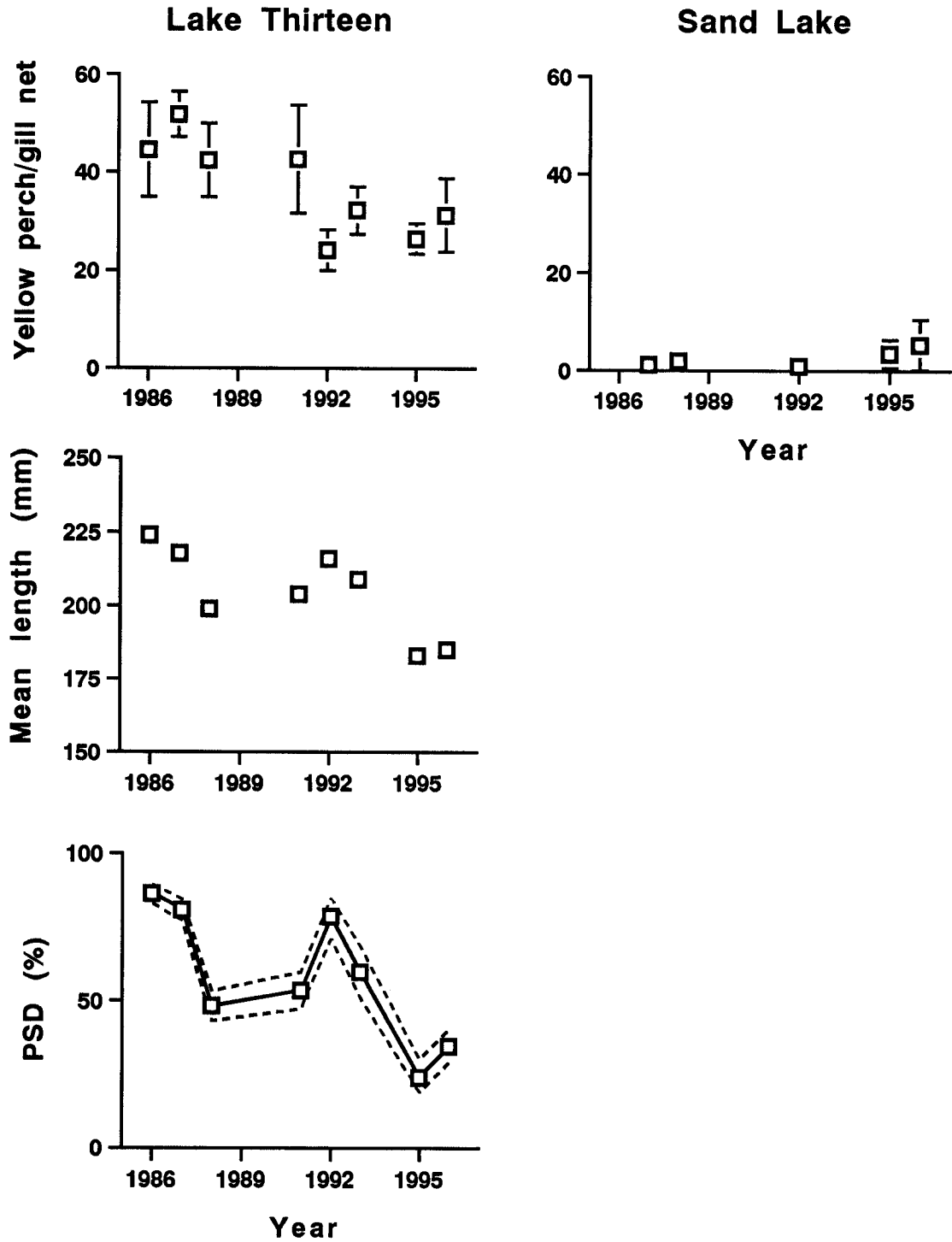


Figure 15. CPUE (\pm SE), mean length (\pm SE), and PSD (with 95% confidence limits) for yellow perch caught in gill nets in Lake Thirteen or Sand Lake.

crayfish, and decreased use of insects and amphipods. The most important insect orders found in yellow perch stomachs were Odonata, Ephemeroptera, and Diptera.

The yellow perch population in Sand Lake was quite different than in Lake Thirteen. Initially, the population in Sand Lake was typified by relatively low numbers of small yellow perch and a few rare larger individuals. Gill net catch rates in 1987-1988 were 1.2-2.0 perch/net and in 1995-1996 were only 3.5-5.3 perch/net (Figure 15). In all the years of gill netting, only 47 yellow perch larger than 150 mm were ever caught. Large increases in numbers of small (<70 mm) yellow perch were found in electrofishing catches during the last two years of the study (Figure 14).

Pumpkinseed

The pumpkinseed population in Lake Thirteen was 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 16-17). 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 mean lengths, age, and length frequency distributions of pumpkinseed caught by electrofishing and trap netting (Figures 18-20). The 1991 year class contributed substantially to the high catch rates found during 1995-1996.

Pumpkinseed in Lake Thirteen showed a trend of declining growth rates throughout the study. Growth of pumpkinseed was slow during early years of the study, with mean back-calculated lengths at age three being 88-89 mm (samples from 1987-1988). Growth got progressively worse, with mean back-calculated lengths at age three being 67-70 mm during 1995-1996. The trend of declining growth rates was also apparent in growth coefficients from the linear growth model (Figure 7). In addition to being poor years for pumpkinseed recruitment, linear growth modeling showed that the cold summers of 1992-

1993 were also poor years for pumpkinseed growth. Because of the trend of decreasing growth rates throughout the study, however, annual growth coefficients from the linear model were poorly related to mean daily temperatures during June-August ($R^2=0.19$; $P=0.11$).

Pumpkinseed ate a variety of food in Lake Thirteen, but aquatic insects and snails were the most abundant food items found in their stomachs. Stomach contents of pumpkinseed showed increased use of snails and decreased use of aquatic insects between 1987-1988 and 1995-1996 (Table 2). The most commonly eaten insects were from the orders Ephemeroptera and Diptera, but insects were also eaten from Tricoptera, Odonata, Megaloptera, and Lepidoptera.

Pumpkinseed were a much less important part of the fish community in Sand Lake than in Lake Thirteen. Catch rates in Sand Lake were low, with very few fish caught through 1991 (Figure 18). Highest catch rates (years 1992 and 1994) were only 5.0-5.5 fish per 15 min electrofishing transect. 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 three ranged from 89 to 142 mm each year. Linear growth modeling did not show the trend of decreasing growth rates found in Lake Thirteen (Figure 7). Rather, a regression model of annual growth coefficients showed that mean daily temperatures (June-August each year) could explain 65% of the variation in annual growth coefficients ($P<0.01$).

Small Cyprinids

Because of their small size and their similar roles as prey items for larger fish, electrofishing catches of all of the small cyprinids were pooled to look for changes in catch-per-unit-of-effort. Electrofishing catches of small cyprinids were quite variable during the study. In Lake Thirteen, catch rates during 1986-1990 were 0.6-4.0 fish per 15 min

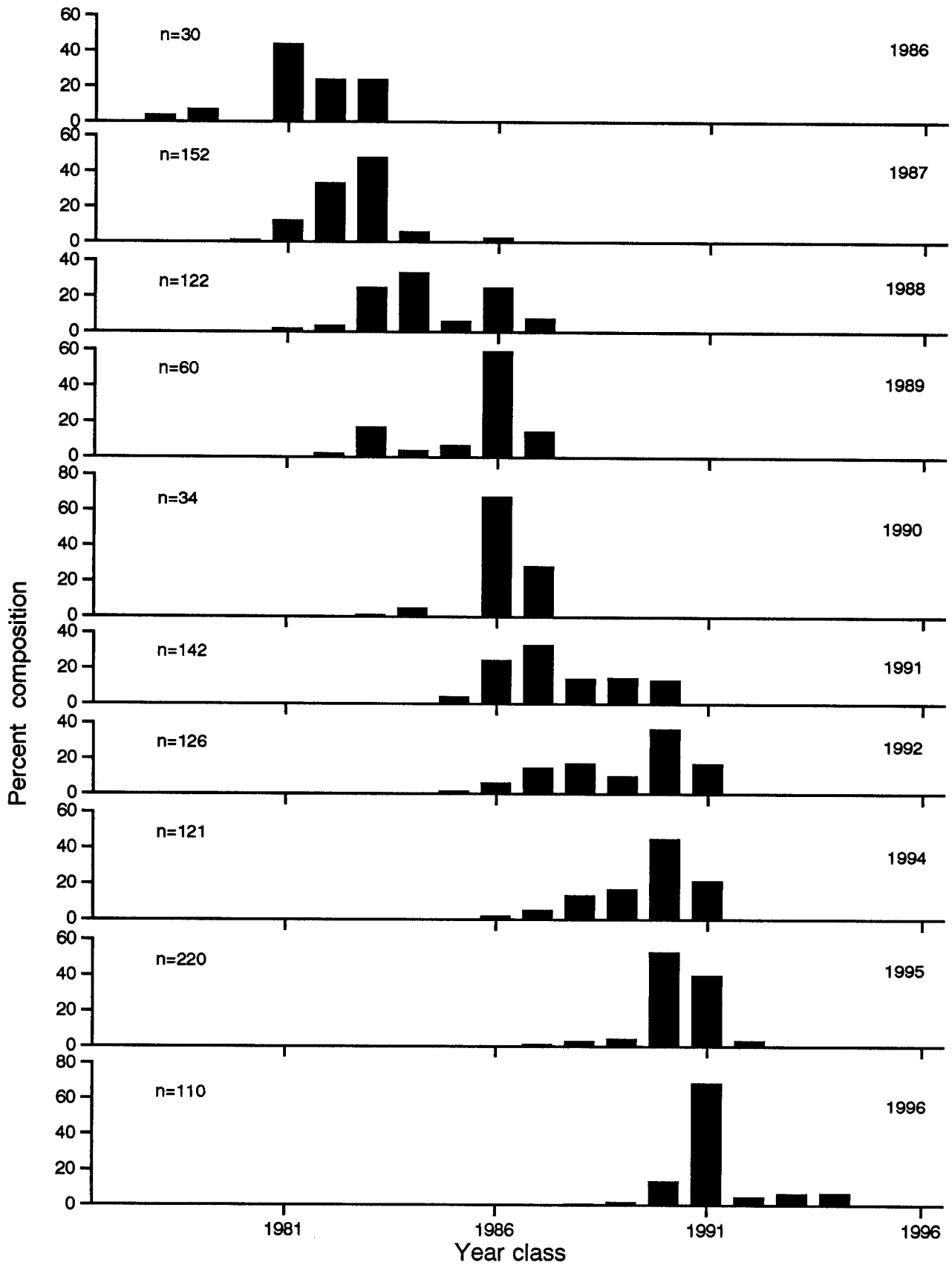


Figure 16. Percent composition of pumpkinseed year classes in electrofishing catches from Lake Thirteen, 1986-1996.

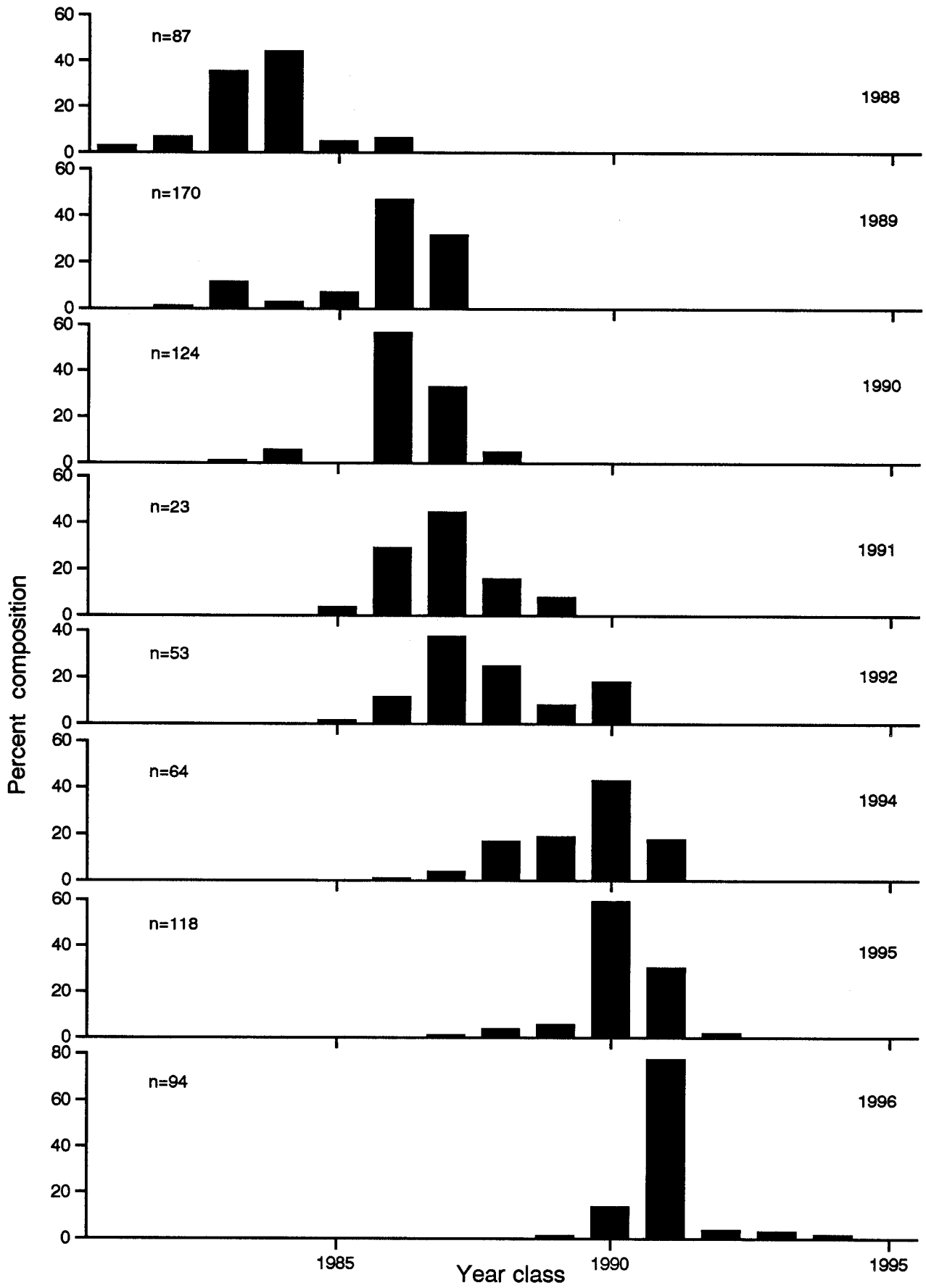
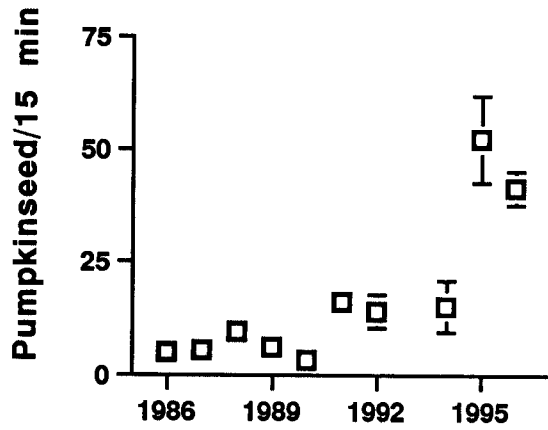


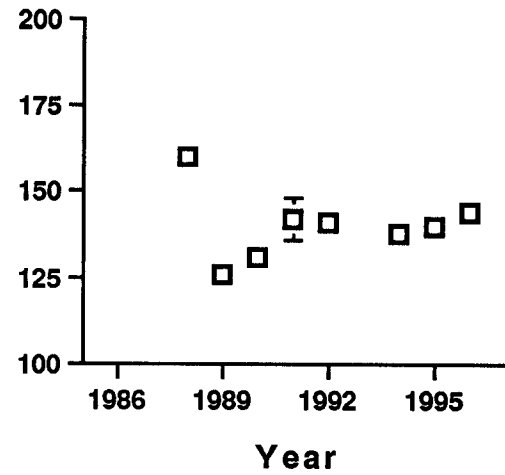
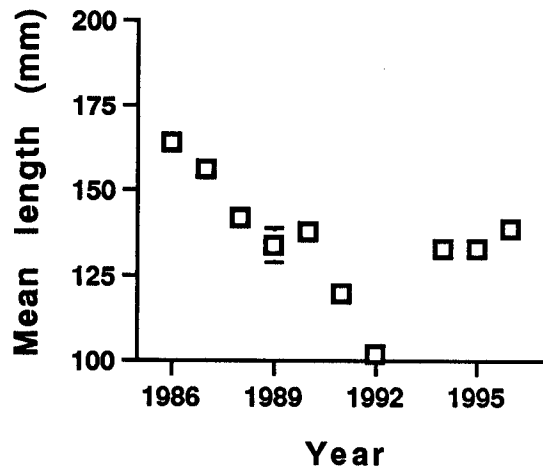
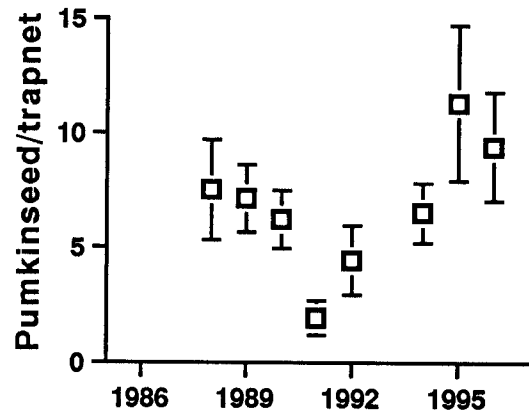
Figure 17. Percent composition of pumpkinseed year classes in trap net catches from Lake Thirteen, 1988-1996.

Lake Thirteen

Electrofishing



Trap netting



Sand Lake

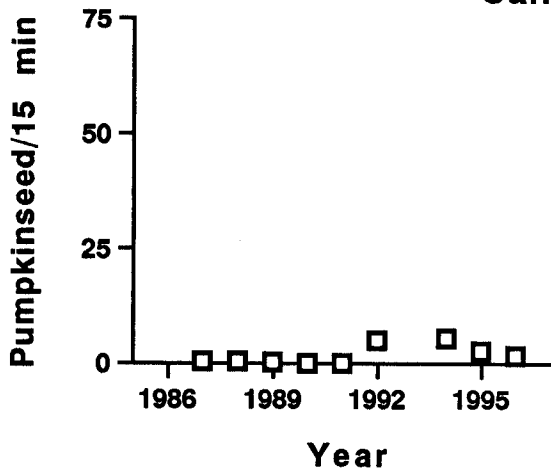


Figure 18. Electrofishing or trap net CPUE (\pm SE) and mean length (\pm SE) for pumpkinseed caught in Lake Thirteen, and electrofishing CPUE in Sand Lake.

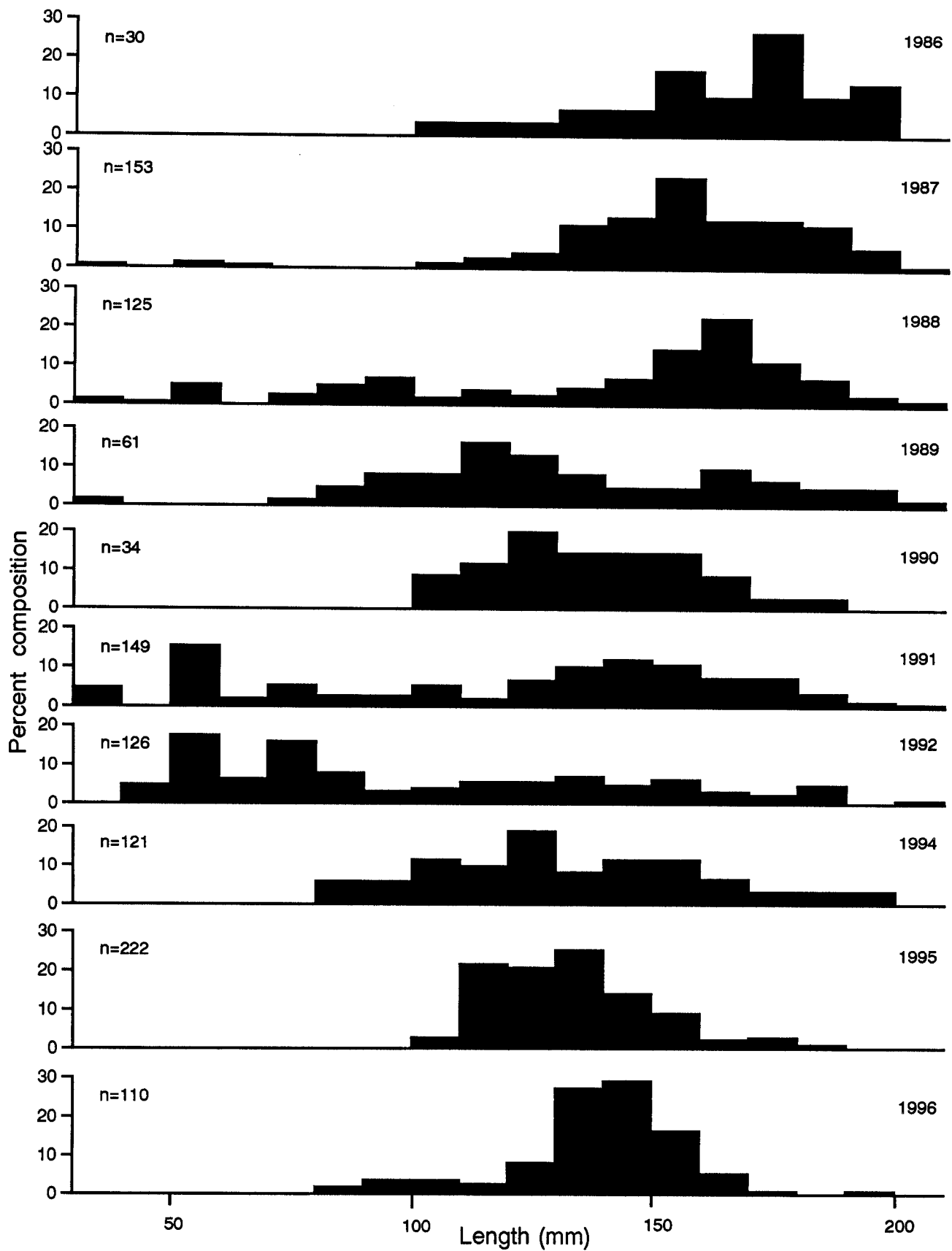


Figure 19. Length frequency distributions for pumpkinseed caught by electrofishing in Lake Thirteen, 1986-1996.

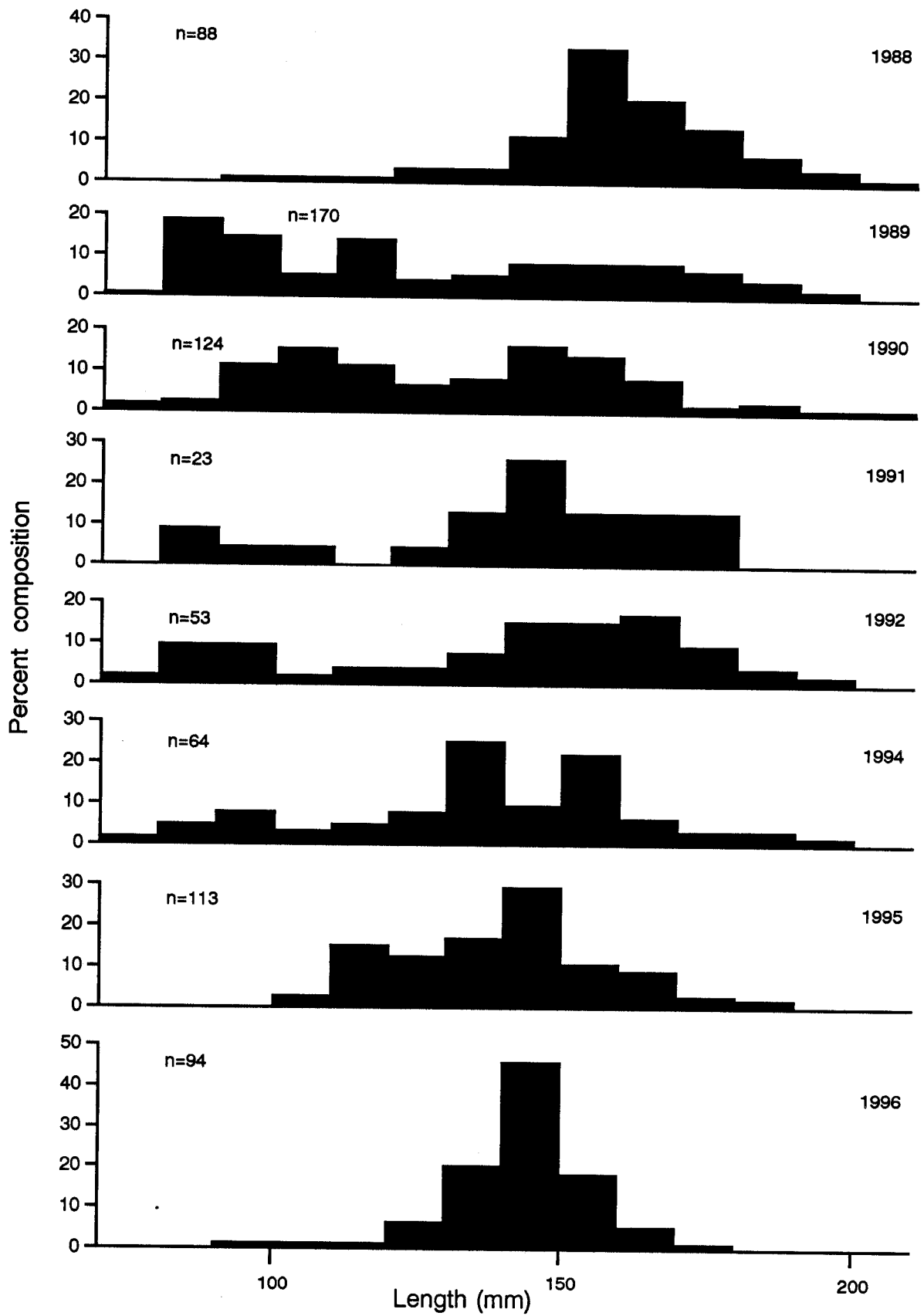


Figure 20. Length frequency distributions for pumpkinseed caught by trap netting in Lake Thirteen, 1988-1996.

(SE=0.3-1.9). After 1990, catch rates were 6.5-231.5 cyprinids per 15 min (SE=2.9-24.7). In Sand Lake, catch rates during 1987-1990 were 5.2-21.0 cyprinids per 15 min (SE=1.2-13.5) and after 1990 were 8.0-63.7 cyprinids per 15 min (SE=0-26.8).

Bluegill and rock bass

Bluegill and rock bass were two important fish species found in Sand Lake that were not found in Lake Thirteen. Catch rates for bluegill in Sand Lake were variable and were not consistent between capture gears. Bluegill catch rates in trap nets were 8.9-69.9 fish per net in each year and electrofishing catch rates were 64.2 to 151.0 fish per 15 min (Figure 21). Years with high electrofishing catch rates did not necessarily correspond to years of high trap net catch rates. For example, mean electrofishing catch rate in 1991 was relatively high whereas trap net catches were the lowest recorded. 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 21). Mean length of bluegill caught by trap netting was 150 mm or less each year, but the proportion of large (> 150 mm) bluegill varied substantially during the study.

Bluegill growth in Sand Lake was slow throughout the study. Mean back-calculated lengths at age three were 74-96 mm each year. The linear growth model showed that the slow growth rate did not vary much among years, except during the cold summers of 1992-1993, when growth was particularly slow (Figure 7). Over the duration of the study, however, the relationship between average summer temperatures and annual growth coefficients was not clear ($R^2=0.29$; $P=0.11$).

Catch rates for rock bass were quite variable during spring electrofishing in Sand Lake. Catch rates ranged from 1.6 to 23.3 rock bass per 15 min with no apparent trend (Figure 22). Similarly, there were no apparent trends in mean length or PSD of rock bass catches even though they were variable.

Growth of rock bass was strongly related to climatic conditions during the summer. Mean daily temperatures during June-August explained 75% of the variability in annual growth coefficients derived from the linear growth model ($P<0.01$; Figure 7). The variability in growth was also observed in back-calculated lengths of rock bass. Mean back-calculated lengths at age three were 104-128 mm for each year's samples.

Creel survey

In spite of discontinued walleye stocking, no change was observed in percentages of anglers that were specifically fishing for walleye. Anglers indicating they were specifically fishing for walleye were 25%, 17%, 19%, and 28% of the respondents to the voluntary creel survey in 1987, 1988, 1995, and 1996, respectively. Anglers fishing for northern pike were 2%, 7%, 7%, and 6% of the respondents each year, and those fishing for largemouth bass were 27%, 39%, 36%, and 33% of respondents.

There was a perceived decline in the quality of fishing in Lake Thirteen after walleye stocking was discontinued. The proportion of anglers indicating that fishing was worse than most lakes was 13% during 1987-1988 and increased to 30% during 1995-1996 (Chi-square=12.28; $df=1$; $P<0.01$). The perceived decline in fishing quality was evident even when anglers specifically fishing for walleye were excluded from the comparison (Chi-square=7.41; $df=1$; $P<0.01$).

Along with an apparent decline in fishing quality was a decrease in recreational fishing effort. Fishing effort, as indexed by angler counts, was lower in 1995-1996 than during 1987-1988. Average numbers of anglers per count for 1987, 1988, 1995, and 1996 were 6.1 (SE=1.0), 3.9 (SE=0.5), 2.8 (SE=0.8), and 1.5 (SE=0.4). The number of cards recovered from the voluntary creel survey served as a second indicator that fishing effort was lower in 1995-1996 than 1987-1988. The lowest numbers of cards were recovered during the last two years of the study. Num-

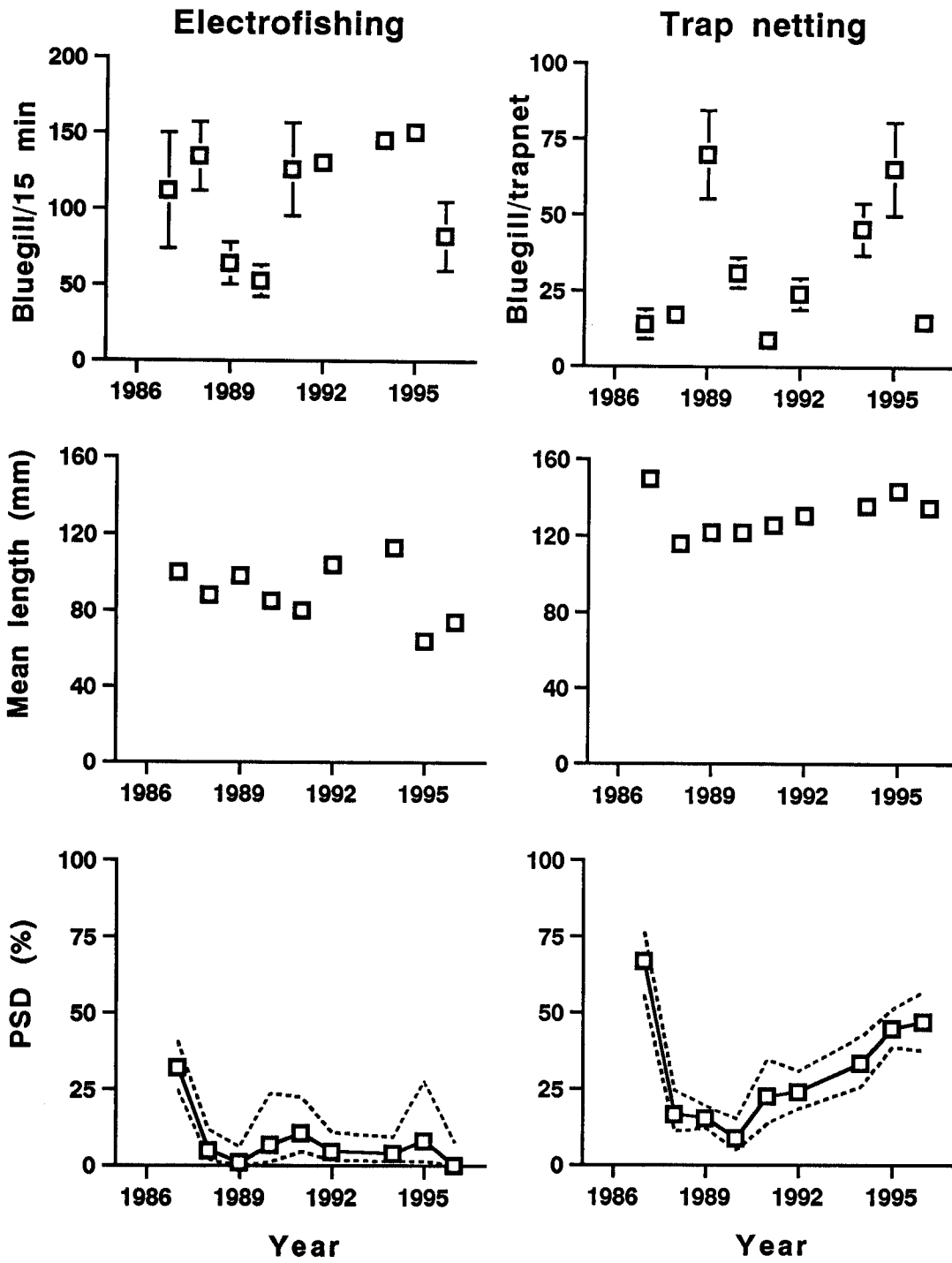


Figure 21. CPUE (\pm SE), mean length (\pm SE), and PSD (with 95% confidence limits) for bluegill caught by electrofishing and trap netting in Sand Lake.

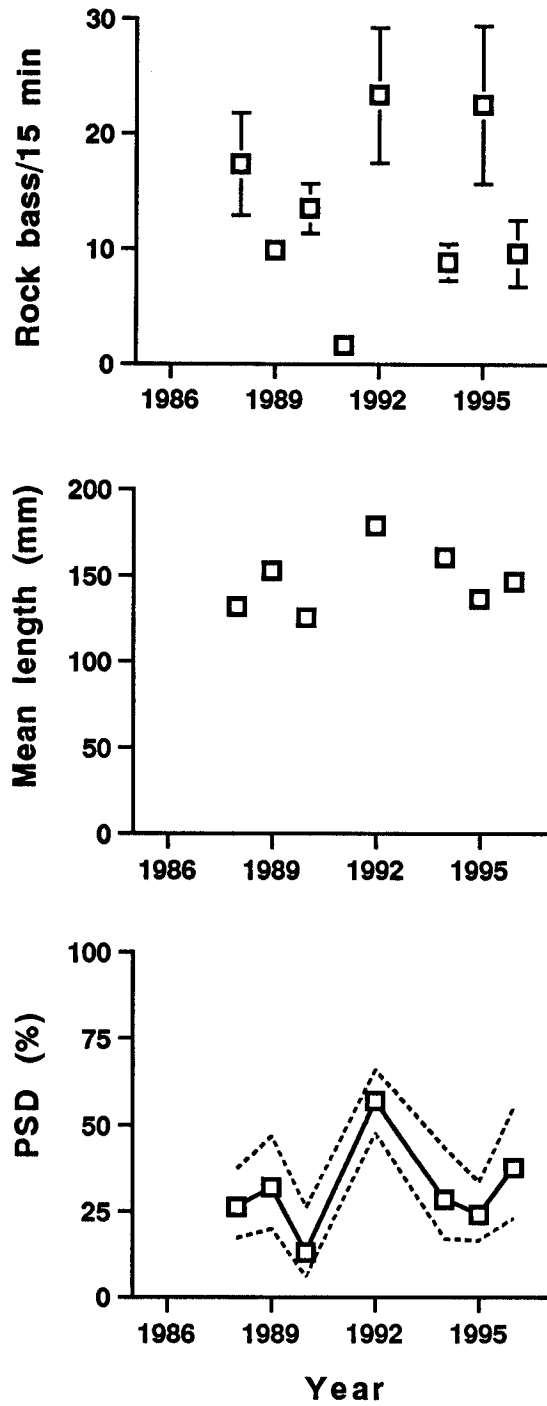


Figure 22. CPUE (\pm SE), mean length (\pm SE), and PSD (with 95% confidence limits) for rock bass caught by electrofishing in Sand Lake.

bers of cards recovered in 1987, 1988, 1995, and 1996 were 123, 116, 58, and 36.

Discussion

Studies of fish community interactions can be difficult to interpret because of confounding environmental influences. This study proved to be no exception. Climatic conditions, coupled with variable year class strength, had relatively large effects on the fish populations in Lake Thirteen and Sand Lake. Summer temperatures, especially the cool summers of 1985, 1992, and 1993, had pronounced effects on growth and recruitment of important fish species in both lakes. Location of both lakes near the northern edge of native distributions for centrarchids (as illustrated in Becker 1983) may explain the sensitivity to cool summer temperatures that we observed in centrarchid growth rates.

The sensitivity of growth rates to water temperature that we found was in contrast to results presented in other studies. Using size-specific growth rates, Osenburg et al. (1988) determined that year (annual climatic) effects did not explain the variation in growth rates of bluegill and pumpkinseed sunfish found among nine southwestern Michigan lakes during 1978-1985. Ross and Nelson (1992) concluded that annual temperature fluctuations in the Georges Bank region during 1963-1980 had only modest influences on growth of groundfishes. There was strong evidence for density dependence in growth rates in both studies, and stock size apparently exerted a larger effect on fish growth than water temperature. In Lake Thirteen, density dependent growth was apparent only in walleye. Yet, the pervasive effects of cold summers were evident in growth rates of several species from Lake Thirteen and Sand Lake.

The unusually strong 1988 year class of walleye from the last year of fry stocking also had important effects on this study. That large walleye year classes can have high predatory demand and reduced growth rates was documented in Lake Erie by Hartman and Margraf (1992). The 1988 year class in Lake Thirteen resulted in a large batch of slow

growing predators that were abundant throughout the period of discontinued stocking. Yet, with little natural reproduction, the walleye population at the end of the study consisted of no small (<467 mm) individuals. The lack of small walleye was a likely explanation for decreased use of shoal areas by walleye at the end of the study and for the shift in diet to increased use of fish and decreased use of invertebrates.

No climatic reasons could be found to explain the apparent lack of northern pike recruitment after 1990. Our results illustrated that recruitment was not related to spring water levels, nor were there any changes in fish habitat or shoreland development around the lake. It was also unlikely that other climatic effects hampered northern pike recruitment since recruitment was evident in Sand Lake and in other area lakes. Good year classes of northern pike were found during 1992-1993 in Crooked, Welsh, and Upper and Middle Sucker lakes, which were all located near Lake Thirteen (Minnesota Department of Natural Resources, files for 1995 lake surveys). One possible explanation for the loss of northern pike recruitment was predation by yellow perch. The lack of recruitment was coincident with the increase in numbers of small yellow perch, and yellow perch have been shown to be as important predators of larval northern pike (Hunt and Carbine 1951). Spawning habitat for northern pike seems to be limited to only a few small areas in the lake.

As a top level predator in Lake Thirteen, northern pike ate mostly fish, with yellow perch being a particularly important prey species. Therefore, northern pike were potential competitors with both walleye and largemouth bass. Because of their position in the food chain, northern pike may be somewhat buffered against year-to-year environmental changes. Their growth rates showed little interannual variation in either Lake Thirteen or Sand Lake. The effect of lack of northern pike recruitment, along with cessation of walleye stocking, was to decrease the relative abundance of younger age predators in Lake Thirteen.

Predation and its effects on other fish in aquatic systems has been described in a variety of studies. After introduction of northern pike to a small Wisconsin lake, He and Kitchell (1990) found decreases in prey biomass and mean size for species most vulnerable to predation. The decreases were a result of emigration as much as from direct predation. Johannes et al. (1989) concluded that golden shiner recruitment and population density were strongly influenced by predator density. More relevant to this study, yellow perch has been described as an important prey for walleye, northern pike, and largemouth bass (Seaburg and Moyle 1964; Forney 1980; Nielsen 1980; Reed and Parsons 1996). Stocking of northern pike, which can prey on a wide range of sizes of fish, has caused decreases in abundance of yellow perch (Anderson and Schupp 1986) whereas removal of northern pike has resulted in increased abundance of yellow perch and white sucker (Colby et al. 1987). Declines in both yellow perch and pumpkinseed populations in Escanaba Lake, Wisconsin, were attributed to increases in the numbers of walleye and northern pike (Kempinger et al. 1975). Predator-prey interactions are more complex, however, when the predators are size selective because of gape widths or other optimal foraging considerations. In an example, Rice et al. (1993) found size-dependent survival of young-of-the-year spot *Leiostomus xanthurus* in experimental enclosures. Survival rates depended on the sizes of a predator, southern flounder *Paralichthys lethostigma*, stocked in the enclosures. Such size-dependent survival was evident in the yellow perch population in Lake Thirteen.

Yellow perch was a key fish species in Lake Thirteen. It was the predominant prey fish for northern pike, walleye, and largemouth bass and it was also the species most sensitive to changes in the predator populations. Increases in relative abundance of small yellow perch (in electrofishing catches) coincided with reductions in numbers of small walleye and northern pike. It is likely that reduced predation caused an increase in numbers of small yellow perch (although reduced competition between small walleye and yellow perch for

invertebrate food resources may also have occurred). Conversely, the decreases in relative abundance of large perch (in gill net catches) corresponded with an increasing prominence of walleye from the 1988 year class as they grew to large sizes. There was also good recruitment of the 1994 year class of yellow perch in Sand Lake during 1995-1996. However, the increase in perch numbers occurred much later in Sand Lake than at Lake Thirteen.

Partitioning of food resources among the fish species in Lake Thirteen was evident early in the study, and shifts in diet were found after walleye stocking was discontinued. Largemouth bass and walleye diets overlapped primarily in their use of yellow perch, dipterans, and ephemeropterans early in the study. Later in the study, largemouth bass ate more yellow perch. The shift in diet reflected some combination of the absence of small walleye and northern pike, and the increased availability of small yellow perch. Slower growth rates and a shift toward increased use of snails in the diet of pumpkinseed suggest increasing levels of intraspecific competition or increasing interspecific competition with the expanding numbers of small yellow perch. Though stomach sampling was not year-round, the diets reported in this study are likely to be representative. In a more comprehensive study of diets and trophic position, Vander Zanden et al. (1997) found diets for walleye, northern pike, largemouth bass, pumpkinseed, and yellow perch to be very similar to our results.

Unusually high catches of largemouth bass and pumpkinseed during the last two years of sampling were a result of strong year classes of largemouth bass produced in 1994 and pumpkinseed produced in 1991. Environmental conditions were undoubtedly a factor influencing year class strength in those years. The importance of temperature to growth and year class strength of largemouth bass has been documented by other authors. Kramer and Smith (1960) found that largemouth bass growth during the first few months was directly related to water temperatures. Further, Newburg and Schupp (1986) suggested that strong year classes were a result of young bass

growing large enough during their first summer to survive the first winter. Miranda and Hubbard (1994a; 1994b) also discussed the value of larger size in relation to winter survival of age-0 largemouth bass. In our study, cool water temperatures affected both recruitment and growth of largemouth bass and pumpkinseed during the coldest summers.

Beyond the obvious environmental reasons for strong year classes, the changes that had occurred in the fish community may have set the stage for largemouth bass and pumpkinseed to be unusually successful in 1994 and 1991. In addition to overlapping use of food resources, walleye and largemouth bass habitat use overlapped everywhere there was sufficient dissolved oxygen to support fish. Both largemouth bass and pumpkinseed showed increases in catch rates of magnitudes that were not observed at Sand Lake at the end of the study. Taking a different perspective, results from Lake Thirteen also show that the increase in numbers of small yellow perch did not negatively affect numbers of pumpkinseed or largemouth bass. The long-term decline in pumpkinseed growth rates began before electrofishing catch rates for small yellow perch started to rise. It is possible, however, that poor growth rates for pumpkinseed were exacerbated by larger numbers of small yellow perch.

Management Implications

This study highlighted the significance of year-to-year climatic variation on fish growth and recruitment. In particular, summer temperatures should be monitored whenever we evaluate management actions designed to affect centrarchid growth. Weisberg's linear growth model was a useful tool for tracking the effects of temperature on growth.

Fry stocking was a viable technique for maintaining a walleye fishery in Lake Thirteen. Fry stocking provided walleye fishing opportunities and anglers perceived a decline in the "quality" of the fishery after fry stocking was discontinued. Furthermore, an important recreational fishery for largemouth bass was evident in spite of the earlier walleye stocking

regime. Anglers came from long distances (> 100 miles) and several states to fish for both largemouth bass and walleye in Lake Thirteen.

Walleye stocking had important influences on the size structure of the yellow perch population in Lake Thirteen. The presence of a large number, and just as importantly, a wide variety of sizes of top-level predators shaped the yellow perch population. Numbers of small yellow perch expanded rapidly in the absence of small walleye and northern pike. From an energetics viewpoint, resources in the fish community were stockpiled in small yellow perch rather than spread out to an additional trophic level.

Changes to the rest of the fish community were not readily evident. In the face of environmental variation and differing natural year class strengths, the fish community effects of walleye stocking seemed limited. We were unable to document any competitive effects of walleye stocking on the largemouth bass population in Lake Thirteen, even though food and habitat use overlapped considerably. Schlagenhaft and Murphy (1985) also found overlap in summer habitat use by the two species, but suggested that it was not extensive enough to limit production of either species in a Texas reservoir. With respect to northern pike, we will not be able to confirm if yellow perch predation is restricting northern pike recruitment until we can re-establish a walleye population capable of controlling the large numbers of small yellow perch. In summary, the documented fish community effects of discontinued walleye stocking were limited primarily to shifts in food habits of various fish species, and to a restructuring of the yellow perch population in Lake Thirteen.

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