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Post-Impoundment Response of a Boreal Northern Pike (*Esox lucius*) Population in Wupaw Bay, Southern Indian Lake, Manitoba, 1976-88

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POST-IMPOUNDMENT RESPONSE OF A BOREAL NORTHERN PIKE (*Esox lucius*) POPULATION IN WUPAW BAY, SOUTHERN INDIAN LAKE, MANITOBA, 1976-88

by

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ABSTRACT

Strange, N.E., R.J.P. Fudge, and R.A. Bodaly. 1991. Post-impoundment response of a boreal northern pike (Esox lucius) population in Wupaw Bay, Southern Indian Lake, Manitoba, 1976-88. Can. Tech. Rep. Fish. Aquat. Sci. 1823: v + 48 p.

A northern pike (Esox lucius) population in Wupaw Bay, Southern Indian Lake, was studied over the period 1976-1988 to determine effects of lake impoundment. Spawning success of pike was not enhanced by flooding, except in the first year after impoundment, and the abundance of adult pike declined over the study period. The proportion of pike stomachs with food increased immediately following lake impoundment and declined thereafter due apparently to a post-flooding trophic surge. The pattern seen in the percentage of stomachs with food was reflected in both condition factor and age adjusted size, which increased moderately just after impoundment, then declined significantly. Emerald shiner and cisco increased in abundance after flooding. The increase in water volume in the bay appeared to create an environment that favoured pelagic species such as emerald shiner and cisco over littoral species such as pike.

Key words: Northern pike; Esox lucius; lake impoundment; reproduction; feeding; emerald shiner; Notropis atherinoides; spottail shiner; Notropis hudsonius.

RÉSUMÉ

Strange, N.E., R.J.P. Fudge, and R.A. Bodaly. 1991. Post-impoundment response of a boreal northern pike (Esox lucius) population in Wupaw Bay, Southern Indian Lake, Manitoba, 1976-88. Can. Tech. Rep. Fish. Aquat. Sci. 1823: v + 48 p.

De 1976 à 1988, on a étudié une population de grands brochets (Esox lucius) de la baie Wupaw, lac Indian Sud, pour déterminer les effets de la création d'un réservoir. Le frai du brochet n'a pas été stimulé après l'inondation, sauf au cours de la première année suivant la création du réservoir, et l'abondance de brochets adultes a diminué pendant la période d'étude. La proportion de brochets dont l'estomac contenait des aliments a augmenté immédiatement après la création du réservoir et a diminué par la suite, apparemment en raison de la poussée trophique qui a suivi la création du réservoir. La même situation a été observée dans le cas du coefficient de condition et de la taille ajustée selon l'âge qui ont augmenté modérément juste après la création du réservoir pour diminuer ensuite de façon importante. L'abondance de ménés émeraudes et de ciscos s'est accrue après l'inondation. L'augmentation du volume d'eau dans la baie a semblé créer un environnement favorable aux espèces pélaqiques comme le méné émeraude et le cisco au détriment des espèces ripariennes comme le brochet.

Mots-clés: grand brochet; Esox lucius; création d'un réservoir; reproduction; alimentation; méné émeraude; Notropis atherinoides; queue à tache noire; Notropis hudsonius.

INTRODUCTION

The effects of impoundment on fish populations have been documented for reservoirs throughout the world (Runnstrom 1955; Gasaway 1970; Cooper 1971; Hamman 1980; Vostradovsky 1981; Kupchinskaya 1985). Most reservoirs experience increased fish production during and immediately following impoundment, followed later by a decline in production (Benson 1980). This has been shown to occur for northern pike (Esox lucius) in new reservoirs (Hassler 1969; Cooper 1971; Kupchinskaya 1985) and is attributed mainly to rising water levels which enhance spawning success. Spawning pike are attracted to areas of flooded vegetation and females lay eggs on or amongst submerged plants (Scott and Crossman 1973; Wright and Shoesmith 1988). Flooded vegetation is also thought to be important as a nursery area for fry (Hakkari and Bagge 1985) and strong year classes of pike have often been produced as a result (Beckman and Elrod 1971; Holland and Huston 1984).

Other conditions that have been found to contribute to strong pike year classes during and just after reservoir impoundment include stable water temperatures and levels, and calm weather at spawning time. Strong year classes of forage fish such as percids and cyprinids have also been produced under these conditions (Gasaway 1970; June 1976; Nelson 1977). Increased abundance of forage fish has often resulted in increased growth in adult pike (Domanevskii 1957; Hassler 1969; Vostradovsky 1981).

The subsequent decline in northern pike production to lower levels after full impoundment is thought to result from physical changes in the littoral zone, especially the degradation of the submerged vegetation which is important to reproductive success and fry survival (Benson 1980).

Northern pike is an economically important species for both the commercial and sport fisheries of northern Manitoba. Pike also acts as a host for Triaenophorus crassus, a cestode parasite which infects lake whitefish, Coregonus clupeaformis, and decreases their market value. The lake whitefish commercial fishery is important to residents of northern Manitoba (Bodaly et al. 1984).

The purpose of this paper is to describe the effects of impoundment of Southern Indian Lake (SIL) on the northern pike population of Wupaw Bay, an isolated bay in SIL. Bodaly and Lesack (1984) analyzed effects for the period 1976 through 1981. An additional six years of data have since been collected and will be presented here. Analyses and discussion will include data collected over the entire period of the study, 1976 to 1988.

MATERIALS AND METHODS

STUDY AREA

Southern Indian Lake (SIL) is located on the Churchill River in northern Manitoba (99°W 57°N). Historically, the natural flow of the Churchill passed through much of SIL, entering the southwestern part of the lake and exiting near the northern end at Missi Falls. In 1976, Manitoba Hydro completed control structures which diverted 75% of the Churchill River flow southward through the South Bay diversion channel, into the headwaters of the Rat-Burntwood Rivers system, eventually to join the Nelson River at Split Lake (Newbury and McCullough 1984). As a result, the water level of Southern Indian Lake rose 3 m between July and October of 1976, flooding shorelines and increasing the lake surface area by 21%.

Wupaw Bay, connected to the large southwestern part of SIL, is a long narrow bay approximately 10 km long and 0.75 km wide (Fig. 1). It is isolated somewhat from the rest of the lake, being connected only by a narrow (100-150 m) entrance. Because of the predominance of higher gradient shorelines, the surface area of Wupaw Bay increased by only 9% as a result of lake impoundment. Most of the flooding occurred in several distinct low-lying areas. Most of these heavily flooded sites were located in protected embayments and were sometimes associated with streams. Although the water

level of SIL was to have been be regulated within a 1 m (actually 3 ft) range according to the original operating license, this limit was frequently exceeded. However, compared with many other reservoirs, the water level fluctuations in SIL have been modest and there have been no large drawdowns. The water quality of Wupaw Bay has been largely unaffected by lake impoundment, with transparency actually increasing. Because of the relatively short wind fetches and lesser degree of terrestrial inundation, Wupaw Bay is not typical of SIL as a whole. There has been only limited commercial fishing in the bay over the period of study.

SAMPLING

Small fish - seining

The five seining sites described by Bodaly and Lesack (1984) continued to be sampled from 1982 to 1988, except in 1985 (Fig. 1). Sites were sampled usually once or twice a week during June, July and August. Whereas the number of seine hauls varied from site to site, the goal was always to catch as many of the fish at the site as was possible. In this paper, we define our unit of effort, the "seine haul" as the sum of all sweeps with the seine net at a site. One unit of effort at the Turkey Creek site consisted of three very short sweeps of the seine net in adjacent areas along the flooded creek bed, whereas at the Portage site a unit of effort was one long sweep. There were very few seinable areas in Wupaw Bay because of the tangle of submerged trees and shrubs and the relatively steep shorelines.

All of the fish caught in a seine haul were identified and counted. Representative subsamples of the catch were preserved in 10% formalin for length measurement and to confirm field identifications. Ages were determined by length frequency analysis. The abundance of each year-class was determined by multiplying the proportion of fish of each age (from the preserved subsample) by the total catch. Catch per unit of effort was calculated as the number of fish per seine haul. In addition, mean catches and 95% confidence intervals were derived as antilogs of statistics calculated from log $(X+1)$ transformed data.

Large fish - gill netting

The gill net sampling program described by Bodaly and Lesack (1984) was continued for the period 1982 to 1988, although no fish were collected in 1985. Gill nets were set perpendicular to shore, usually for 4-6 hours during the day. A few overnight sets were used to increase total effort (i.e. hours set), especially in the later years of the study when sampling trips to Wupaw Bay from the SIL field camp were less frequent. Gill nets of white multifilament nylon mesh, 46 m (50 yd) long by 2.1 m (7 ft) deep were attached to standing flooded trees. On each sampling day, two sites were chosen randomly from a total of 36 distributed around the bay (Fig. 1). At one site, a 70 mm (2 3/4") mesh net and an 89 mm (3 1/2") mesh net were set tied together; at the second site 51 mm (2") and 108 mm (4 1/4") mesh nets were set together. Mesh sizes are stretched measure. Orientation of the nets was reversed every set, so that meshes set onshore one day would be set offshore the next.

Catches of all fish species were noted for each mesh size. Fork length, round weight and sex were recorded for pike only. Catch per unit of effort (CUE) was calculated in two ways. For the five most abundant species, CUE was determined by standardizing the catch to an 8 hour fishing period. For northern pike only, statistics were also calculated for an 8 hour period as antilogs of statistics derived from log $(X+1)$ transformed data. Statistical tests for normal distributions, such as analysis of variance, could then be applied to CUE data. The condition factor (K), a measure of fitness, was calculated for individual pike as follows:

$$K = \frac{100\ (\text{Round weight})}{\text{Fork length}^b}$$

where b is the slope of the linear regression of log round weight on log fork length for all pike captured over the period 1976-1981 ($b = 2.93$, $n = 3654$).

Northern pike ages were determined using scales and cleithra. Scales, collected from 1976 to 1987, were cleaned with household bleach and rinsed with water. Ages were determined by the same person for all scales used in the study. Cleithra, collected in 1986, 1987 and 1988, were also all aged by one person using the methodology described by Casselman (1983). Subsamples, stratified by length distribution according to Ketchen's method, were used to calculate age distributions (Ricker 1975) and annual survival rates (Robson and Chapman 1961). Survival rates were recalculated after deleting the most numerous year class if a significant Chi-square test statistic resulted. Length frequency curves for pike were smoothed by plotting running averages for three length groups.

Stomach contents of pike were counted and identified to species whenever possible and empty stomachs were noted.

RESULTS

SMALL FISH - ABUNDANCE IN SEINE NETS

Fish species caught in seine nets are listed in Table 1. In this report, we will discuss the most abundant species (emerald shiners - Notropis atherinoides, spottail shiners - Notropis hudsonius and yellow perch - Perca flavescens), as well as young-of-the-year northern pike.

Total catches in each year of the study are shown in Table 2. Effort varied widely over the study, from 35 hauls in 1988 to 109 hauls in 1980. Therefore, total catches may be compared only within a given year. Shiners (spottails plus emeralds) dominated the seine catches every year, comprising from 75% of the total catch in 1980 to 99% in 1988. For 7 of the 11 years of seining data, shiners comprised more than 90% of the catch. In 1977, emerald shiners were scarce in seine nets, but the total catch of emeralds over the entire study (1977-88) was nearly 1.5 times that of spottails.

The relative abundance of the two shiner species changed noticeably over time (Fig. 2). Emeralds first became more numerous in seine nets in 1981, after which they dominated total annual catches. The decline in spottails relative to emeralds is not due to a decrease in the number of spottails in the catch, but rather to an increase in emeralds (Fig. 3). In fact, it appears that spottails have increased in number over the years, from an average of 61 per haul in 1977 to 130 per haul in 1988. Variability in the average catch per seine haul of shiners was high, especially for emeralds. Years of high shiner abundance (1981, 1984 and 1988) seem to be correlated with warm weather years, especially warm Augusts (Fig. 4), and with years in which the maximum water level in the reservoir was lower than average (Fig. 5).

Yellow perch comprised between 1% (1988) and 23% (1980) of the seine catch over the years (Table 2, Fig. 2). Fluctuations in the percentage of perch were due mainly to fluctuations in shiner catches (Fig. 3). Average catches of perch increased from 3.4 per haul in 1977 to 18.6 per haul in 1980. Catches remained at approximately this level (except for 1983) until 1986, then appear to have declined to near 1977 levels again.

Young-of-the-year (YOY) northern pike were scarce in seine nets. The average number per haul ranged from 0.03 in 1980 to 1.17 in 1977 (Table 2, Fig. 6). The 1977 year class was twice as abundant in seine catches as the next largest year class (198-1). From 1978 to 1984, there was a loose relationship between YOY pike catches and average air temperatures (Fig. 4). The most successful YOY pike year classes (1977, 1981, 1984) occurred in years of low water level fluctuation (Fig. 5). Pike fry were caught at all seining sites but catch per unit of effort was highest at the Portage, Portage Bay Road and Turkey Creek sites (Fig. 7). The Sandbank Slice site produced consistently low YOY pike catches whereas catches at Sloughtooth Creek were high in 1977 and 1978 but declined thereafter.

The mean catch per seine haul of major species and 95% confidence intervals derived from log $(X+1)$ transformed data are shown in Fig. 8-11.

Because seine catches fit a binomial distribution, these means best represent probabilities, or in other words, expected catches. Means for spottail shiners are much higher than those for emeralds. This implies that the expected catch of spottails in a seine haul was higher than the expected catch for emeralds, which were caught much less frequently in seine nets (Fig. 12). The average catches of emeralds were elevated by a few very large catches each year.

Log transformed means for emerald shiners indicate that they have increased in number over the period of study (Fig. 8). Catches in 1977 were significantly lower than in all other years. Log transformed means for spottail shiners indicate that only in 1982 and 1988 were catches significantly larger than those in the first few years of the study, and that overall abundance has been stable over the period of study (Fig. 9). Log transformed means for yellow perch catches increased significantly in the early years of the study, peaked in 1982, then declined (Fig. 10). The plot of log transformed means for YOY pike shows that the catch in 1977 was significantly higher than in all other years (Fig. 11). After 1977, the percentage of seine hauls with no YOY pike increased, against the trend for shiners and perch (Fig. 12).

Most of the shiners and perch caught in seine nets during the study were young-of-the-year or one-year-old fish. The most successful year-class overall for the three species occurred in 1981. Emerald shiners produced strong year-classes in 1979, 1980, 1981, 1983 and 1987 (Fig. 13). The 1985 year-class also appeared to be large, based on the abundance of one-year-olds in 1986. Most of the emerald shiners caught in the other high abundance years (1984, 1988) were one year old. It would appear that the CUE for emerald shiners increased beginning in 1981 because of good over winter survival of perhaps every year class. The lack of data for 1985 makes determination of survival of the 1984 and 1985 year-classes difficult. The most successful spottail shiner year- classes occurred in 1979, 1981, 1987 and 1988 (Fig. 14). One-year-olds dominated the large catches of spottails in 1982 and 1988, whereas YOY's dominated the large 1987 catch (Fig. 14). The decline in yellow perch CUE in 1983 and 1987 appears to be attributable to poor survival of the previous year-class. Yellow perch YOY were most abundant in 1981, 1982, 1983 and 1986 (Fig. 15). The CUE in 1988 was low because of a poor 1988 year-class.

Other species of small fish comprised a small percentage of seine catches (Fig. 2). The most abundant of these were lake chub (Couesius plumbeus) and johnny darter (Etheostoma nigrum) (Table 2). Lake chub appeared to undergo large fluctuations in abundance, almost disappearing from catches from 1982 to 1984, then re-appearing in large numbers. Johnny darter showed a similar decline and rebound in abundance. In general, most of these minor species were in greatest abundance in seine catches for the first 3-5 years of the study.

LARGE FISH

All species - abundance in gill nets

Large fish species caught in gill nets in this study are listed in Table 1. Northern pike and white sucker (Catostomus commersoni) dominated the gill net catch (Table 3). Pike comprised 42% of the total catch over the entire study, ranging from 20% in 1984 to 68% in 1980 (Fig. 16). In most years, pike comprised 30%-45% of the catch. White sucker ranged from 16% (1981) to 41% (1978) of the annual catch, averaging 35% for the 13-year totals. Walleye (Stizostedion vitreum), cisco (Coregonus artedii and C. zenithicus) and lake whitefish (Coregonus clupeaformis) together comprised 23% of the total gill net catch.

All five fish species showed the same trends in catch per unit of effort over the years (Table 4, Fig. 17). Catches were high in 1976, 1978, 1982 and 1986; catches were low in 1977, 1980, 1984 and 1987. It appears that the degree to which pike dominated gill net catches was due mainly to the extreme fluctuations in sucker CUE, which reaches

higher maximums and lower minimums than pike CUE.

Overall, northern pike average catch per unit of effort appears to have declined (Fig. 17). Examination of log transformed data confirms this downward trend (Fig. 18). Compared with 1976 (the year of impoundment), mean CUE values were significantly lower in 9 of the next 11 years for which we have data. Year-to-year differences in CUE were found to be highly significant by analysis of variance ($F_{11,201}$ = 11.16, $p<0.01$). A least significant difference test confirmed the significant downward trend in catches (Fig. 19). The two smaller meshes (51 mm and 70 mm) caught more pike than the two larger meshes (89 mm and 108 mm) (Fig. 18).

White sucker CUE was extremely variable, but at the end of the study CUE values were similar to those at the beginning (Fig. 17). The percentage of cisco in gill nets increased over the years (Fig. 16) because cisco catch per unit of effort increased (Fig. 17). Walleye consistently comprised approximately 8-12% of the annual catch, except for 1984 when it increased to 32% of the catch. This was not due to a dramatic increase in walleye CUE, but rather to a modest increase combined with a decline in CUE for all other species (Fig. 17). Lake whitefish declined in relative importance due to a real decline in CUE values. Although no data are presented here, it should be noted that sauger (Stizostedion canadense) were beginning to appear in gill net catches in modest but increasing numbers in the final few years of the study.

There appears to be some correlation between gill net catch and water levels. In years of high CUE (1976, 1978, 1982, 1986 and 1988), fluctuations in water level were usually high (Figs. 5, 17). The maximum water level in most of these years was higher than the previous year's maximum, and the level was usually rising during the open-water season. In 1978, CUE values were high but water levels were more stable.

In low catch years (1977, 1980, 1983, 1983 and 1987), there was generally little fluctuation in water levels. The exception is 1983, where the maximum lake level was only slightly above the 1982 level, and it occurred in September. In addition, a relationship between gill net catch and air temperature appears to exist, such that years of high CUE (1976, 1978, 1982, 1986, 1988) correlate with lower than normal seasonal temperatures. In years of low CUE (1977, 1980, 1983-84, 1987), 1983 and 1984 were warm, 1987 warmer than most years while 1977 and 1980 were average. In the very warm year 1981, catches were higher than in 1980 but still quite low, especially for pike and white sucker.

Northern pike growth, condition and length frequency

Regressions of fork length on scale age suggest that pike were smaller at age over the period 1982-88 (Fig. 20) than pike caught from 1976 to 1981 (see Fig. 4, Bodaly and Lesack 1984). Age adjusted mean fork lengths of each year's pike were found to be significantly different by analysis of covariance ($F_{10,1296}$ = 3.85, $p<0.01$). A least significant difference test of these age adjusted fork lengths indicates that they increased slightly until 1978, then declined significantly for 1980 and 1981 (Fig. 21). Adjusted lengths increased in 1982 and stabilized thereafter. From 1980 to 1988, adjusted lengths were significantly lower than the 1978 maximum in five of the seven years for which we have data.

Northern pike condition factor (K) generally declined over the period of study (Table 5). Analysis of variance for condition was highly significant ($F_{11,1685}$ = 10.82, $p<0.01$). Northern pike condition was significantly lower in five of the next eight years sampled after 1979 than for the period 1976-79 (Fig. 22).

Modal length of northern pike increased from 1976 to 1979, remained constant until 1982, then decreased from 1983 to 1986 (Fig. 23). Modal length appears to have increased again in 1987-1988. Length-frequency plots for 1976 and 1984 are strikingly similar. Both are bimodal at 420 mm and 470 mm and there is no evidence in either plot of

three-year-old pike in the sample. These fish usually range from 275 to 350 mm in length and are present in every other year. Both plots also show a distinct mode at 675 mm which translates into eight-year-old fish, according to Fig. 20.

The large 1977 year-class first appears in length-frequency plots in 1980, with a mode at 340 mm. It seems to have reached the sample mode by 1984. Although this year-class was abundant in its first year (Fig. 6), it does not appear to have been unusually abundant beyond four years of age.

Northern pike stomach contents

Northern pike stomach contents varied considerably over the study. The average number of fish and invertebrates per stomach increased from 1976 to 1978, then decreased (Table 6, Fig. 24). The percentage of stomachs that were empty decreased from 76% in 1976 to 50% in 1978, then increased slowly to near 1976 levels by 1988.

More detailed descriptions of the most common pike stomach contents are presented in Fig. 25 and 26. Cannibalism of young-of-the-year pike appeared to be correlated with their abundance (Fig. 6, 11). The importance of shiners in the pike diet declined after 1977 and the large number of shiners found in stomachs in 1986 appears to be an anomaly to the overall trend. The number of shiners in stomachs was lowest in 1981 when shiners were most abundant in seine catches (Fig. 3). In 1977, yellow perch were found in only 4% of stomachs containing food. By 1981, perch had increased in occurrence to 12% of stomachs, after which their occurrence in stomachs declined. Ephemeroptera were very common in stomachs by 1978 (22%), declined in occurrence for a few years, then disappeared from stomach contents by 1983. Crayfish increased in pike diets until 1980, after which they declined in importance. The occurrence and number of coregonids (cisco and whitefish) increased in the diet of pike from 1977 to 1981 then declined. Occurrence was highest in 1984, but this is based on a small sample size.

Northern pike sex ratio and annual survival rate

The ratio of females to males increased over the period of study (Table 4). Differences among years were highly significant (2 x 11 contingency table: $X^2_{10\ df} = 25.45$, $p<0.01$).

The annual survival rate of northern pike increased from 1976 (0.43) to 1977 (0.52) then decreased to a low of 0.39 in 1978 (Table 4). From that point, survival generally increased through to 1988. Survival rates based on scale ages were likely underestimated (see next section).

Northern pike age distribution

The age distribution derived from scales of the Wupaw Bay pike population is presented in Fig. A1.1 (also see Fig. 7 in Bodaly and Lesack 1984). Age-frequency plots derived from cleithra for the period 1986-88 are illustrated in Fig. A1.2. Clearly, the age distribution derived from cleithra was quite different than that derived from scales (Figs. A1.3, A1.4). Examination of the relationship between scale age and cleithra age for Wupaw Bay pike caught in 1986 and 1987 (n = 152) shows that cleithra consistently aged pike older than scales (Fig. A1.5), and that the difference in estimated age increased with increasing pike fork length. Because of the inaccuracies apparent in scale aging, one must be cautious about drawing any conclusions from these data.

Commercial fishing

Due to decreasing catches of pike and consistently low numbers of whitefish (Table 3), it would have been unprofitable to fish in Wupaw Bay. There were very few sightings of commercial fishermen or their nets by field personnel, especially in the second half of the study period. It is therefore assumed that commercial fishing had no significant impact on the fish populations in Wupaw Bay.

DISCUSSION

Emerald shiners in Wupaw Bay appear to have benefitted from lake impoundment. The shift in the balance between emerald and spottail shiners was due to a large increase in the number of emeralds. A similar increase in emerald shiner abundance occurred in Lake Francis Case, South Dakota, a reservoir on the Missouri River (Gasaway 1970). Stomach content analyses of 1977 samples indicated that spottail and emerald shiners were eating the same food items, cladocerans and chironomids. Therefore, food supply probably did not favour one shiner over the other. The rise in lake level resulted in cooler water temperatures (Patalas and Salki 1984). Wupaw Bay, in contrast to the larger basins of SIL, became clearer as a result of flooding (Hecky et al 1979). Thus, the creation of a deeper, clearer body of water (more favourable habitat) probably favoured the pelagic emerald shiner relative to the more littoral species such as the spottail shiner. It is likely that this stimulatory effect on emerald shiner abundance was limited to Wupaw Bay and similar shallow isolated bays where the post-impoundment increase in mean depth was significant.

Spottail shiner and yellow perch populations in Wupaw Bay seemed to be relatively unaffected by impoundment. The abundance of these littoral species fluctuated over the study period but showed no overall trend. Figure 10 suggests an increase in perch abundance from 1977 to 1982, followed by a decline to 1988. The CUE data (Fig. 3), however, suggest generally stable abundance year-to-year. This implies that Fig. 10 should be interpreted instead as relatively stable perch abundance interrupted by unusually high abundance in 1982 and 1984. In both years, survival over winter of the previous year class (1982 and 1983) was much better than average (Fig. 15). Survival of young-of-the-year was also high from 1979 to 1980 and from 1987 to 1988, but in both cases poor spawning success lowered overall abundance.

Spottail shiners were much more abundant in 1982 and 1988 (Fig. 9), due to the high over winter survival rate of 1981 and 1987 year-classes respectively (Fig. 14). The years with highest overwinter survival for both spottail shiners and perch (1981, 1983 and 1987) were warmer than average (Fig. 4). Warmer water temperatures generally result in faster growth of fish, which enhances their ability to avoid predators. Also, the larger a fish grows, especially at this critical stage, the fewer potential predators it must avoid. Thus, it appears that weather over the open-water season had a greater impact on the abundance of spottail shiners and yellow perch in Wupaw Bay than did the flooding of the lake.

Vogel and June (1987) found that yellow perch abundance in Lake Sharpe, South Dakota, decreased markedly during and after flooding. They blamed reduction of the brood stock and degradation of spawning and nursery grounds in embayments. We have no estimates of brood stock in Wupaw Bay. Perch spawning and nursery areas were not degraded as seriously in Wupaw Bay as they were in Lake Sharpe because the relatively short wind fetches in the bay slowed erosion. Whether erosion of these areas will eventually impact perch abundance is unclear. In Lake Frances Case, South Dakota, yellow perch increased in abundance during and after flooding, with clear water and submerged vegetation given as the reasons (Gasaway 1970). The largest year-class occurred when the water level was high and a large amount of vegetation was flooded. Because we have no pre-impoundment seine catch data, we cannot be certain that there was no stimulatory effect on abundance of perch. If the 1977 perch year-class was significantly larger than pre-flood year-classes, why were subsequent year-classes (1981, 1982 and 1986) even more successful? One would expect a response similar to that shown by young-of-the-year pike. Perhaps perch and spottail shiners were affected positively by clearer water and submerged vegetation, and negatively by slow degradation of spawning and nursery areas, and the two have balanced to result in no net change in abundance since impoundment. Other species caught in seine nets were generally too scarce to permit determination of trends in abundance (Table 2).

The impoundment of Southern Indian Lake significantly impacted the spawning success of the pike population in Wupaw Bay. The lake level rose during the open-water season of 1976, dropped slightly over the winter, and then rose again until June of 1977 (Fig. 5). In the spring of 1977, the first year with flooded terrestrial vegetation, YOY pike were much more abundant than in any other year of the study. The association of strong pike year-classes with newly flooded reservoirs has been well documented (Beckman 1987; Domanevski 1957; Gasaway 1970; Holcik 1968). Pike spawning success in 1977 was unusually strong, likely because flooded terrestrial vegetation provided pike with an abundance of substrate on which to lay their eggs. Flooded vegetation probably also provided a favourable nursery area for the pike fry.

Pike prefer to lay their eggs in shallow water amongst submerged vegetation (Scott and Crossman 1973). Holcik (1968) found that pike in Klicava Reservoir spawned on "gently sloped shoreline with vegetation remains". Wright and Shoesmith (1988) reported that maximum pike egg density occurred on flooded grass, while Hakkari and Bagge (1985) found that high young-of-the-year pike densities were correlated with a variety of organic substrates, including sedges, grasses, mosses and detritus. The most extensively flooded habitats in Wupaw Bay were gently sloped embayments, dominated by black spruce, Labrador tea, sphagnum and feather mosses, and grasses and sedges. These areas were probably preferred spawning habitat. Holland and Huston (1984) reported catches of YOY pike in areas with submerged vegetation as 10X catches in areas with no vegetation. More YOY pike were caught in Wupaw Bay at the sites with extensive vegetation, i.e. Turkey Creek and the Portage (Fig. 7). Young-of-the-year pike abundance was lowest at the Sandbank Slice site, where there was relatively little submerged vegetation (no moss or grass) and an unstable sandy-clay bottom.

Fry have two main requirements - food and protection from predation. After hatching, food supply is believed to be more important than physical factors (Hassler 1970). In the Mississippi River, young-of-the-year pike up to 60 mm in length ate primarily invertebrates, including ephemeropterans, isopods and amphipods (Holland and Huston 1984). At 70 mm, fish comprised 50% (by volume) of their diet and at 100 mm pike were eating only fish. Analysis of stomach contents of 60 YOY pike caught in 1977 revealed that the larger the pike fry, the more they fed on fish. Large fry also fed regularly on ephemeropterans and chironomids. The diet of smaller fry was dominated by chironomids, ephemeropterans, amphipods and cladocerans. Benthic organisms increased significantly in number in SIL after flooding from 3200 individuals per m^2 in 1972, to 5700 individuals per m^2 in 1977 (Giberson et al. 1991). More specifically, Pontoporeia sp. (Amphipoda) increased in number from 1972 to 1983. Hexagenia sp. (Ephemeroptera) declined significantly from 1977 to 1981 but maximum densities occurred in 1977. Both perch and adult pike are known to feed on pike fry (Grimm 1981). Remaining amongst flooded vegetation probably reduces the frequency of encounters with these predators. Thus, a highly successful spawn, combined with an abundance of preferred food and protection from predators were the factors responsible for a highly successful pike year-class in Wupaw Bay in 1977.

In 1978, YOY pike were only 1/6 as abundant as in 1977. Explanations for such a decline in abundance, observed in many reservoirs, have included: (1) siltation affecting egg survival and food supply, (2) either stable or frequently fluctuating water levels affecting the quality of the spawning/nursery habitat and food supply and (3) the degradation of flooded vegetation (Gasaway 1970; Hassler 1970; Cooper 1971; June 1976). Because of the relatively short wind fetches and the predominance of rocky shorelines, siltation was not likely significant in Wupaw Bay. Deposition was minimal in an important YOY pike nursery area near the Portage seining site (C. O'Neill, Winnipeg, personal communication). The water level in Wupaw Bay in 1978 peaked on May 30 (Fig. 5), slightly above the 1977 maximum. From that point on, throughout the open-water season, the lake level generally dropped or remained stable. The drop in water level coincided with the spawning period and the critical early life

stages of pike fry. The pike year-class success could have been reduced either directly, through the death of eggs laid in receding shallow water, or indirectly, through the absence of newly flooded terrestrial vegetation. The terrestrial vegetation flooded in the previous year had probably degraded significantly by 1978. Since food (invertebrates) would not have been in short supply in 1978 (Giberson et al. 1991), these physical changes in the near shore habitat were likely the principal cause of a much weaker pike year-class. In addition, newly hatched 1978 fry may have fallen prey to members of the large 1977 year-class. The success of northern pike year-classes after 1978 was quite variable. It is unknown whether such year-to-year variability existed before flooding.

The adult northern pike population in Wupaw Bay appears to have suffered since lake impoundment. A downward trend in both catch per unit of effort and condition factor was observed for the period 1976 to 1988. From 1976 to 1978, fish of the same age were larger each year; after 1978, size at age decreased (Fig. 21). A significant drop in both condition and age-adjusted fork length occurred in 1980, when the 1977 year-class first appeared in gill net catches in reasonable numbers. To determine whether the lower condition factors and fish sizes were caused only by the dominance of this year-class, we examined the percentage frequency of each pike year-class (from the 1972 to the 1984 year-class) as that year class aged from 3 to 7 years of age. This enabled us to determine what percentage of the population (gill net catch) each of the year-classes comprised when it was 3, 4, 5, 6 and 7 years old. Perhaps surprisingly, the analysis showed that the large 1977 year-class was median of all the year-classes at all ages. Even at age 3 (in 1980), this large year-class comprised only 9% of the total catch, about average for the year-classes studied. We conclude, therefore, that the significant decreases seen in CUE and condition reflected the status of the entire population. Unlike Wupaw Bay, post-impoundment year-classes of pike in the Kuybyshev Reservoir were dominant 3-4 years later (Kuznetsov 1981).

The decline in pike abundance appears to be related to physical changes in Wupaw Bay. Before flooding, most of the bay ranged from 0 to 3 m in depth and there were a few large areas of macrophyte growth (R.E. Hecky, personal communication). Since flooding, the depth ranges from 0 to 6 m and there are no macrophytes. Much of the bay was suitable pike habitat before flooding, but since flooding, favoured pike habitat has been restricted to a few peripheral areas where gently sloped shorelines were flooded extensively. Northern pike spend some time in deeper water but they tend to prefer warm weedy bays of lakes (Scott and Crossman 1973). The loss of the macrophytes and fluctuating water levels have probably contributed significantly to decreased spawning success. Flooded terrestrial vegetation was a successful alternative for one year, but degraded quickly. Thus, a habitat well suited for pike was transformed into one that, at least in relative terms, favoured pelagic species. This conclusion is confirmed by the increase in abundance of cisco and emerald shiners. Also favoured by the changes in Wupaw Bay were fish that spawn over rocks or sand (walleye, sauger and emerald shiner), as predicted by Benson (1980). Whitefish have not done well since flooding and may be declining in abundance (Fig. 17), perhaps due to the decline in invertebrate abundance from 1983 to 1987 (Giberson et al 1991).

The deterioration in condition of Wupaw Bay pike is puzzling, considering that food (shiners, perch, cisco) was apparently more abundant after impoundment of SIL. The percentage of pike stomachs that were empty declined immediately after flooding but increased from 1979 to 1988. Craig and Babaluk (1989) found that the summer condition of pike in 37 lakes in central Canada was positively correlated with water clarity. Secchi disk readings in Wupaw Bay more than doubled from 1975 (pre-flood) to 1977 (post-flood), indicating much clearer water and therefore pike feeding would not have been restricted by water clarity. It is possible that pike condition factors before impoundment may have been significantly lower than in the impoundment year (1976) and all subsequent post-impoundment years (1977-88).

In conclusion, the flooding of Wupaw Bay has negatively impacted the pike population. Reproductive success improved initially because of the post-flooding trophic surge brought on by submergence of terrestrial vegetation and the subsequent nutrient input; however the flooded vegetation degraded quickly and reproductive success dropped significantly. Flooding transformed the bay from a very favourable pike habitat into one that, in relative terms, favoured pelagic species such as cisco and emerald shiner. This resulted in fewer pike which were in poorer condition.

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Table 1. Fish species caught in gill nets and seine nets in Wupaw Bay, 1976–88.

	Scientific name	Common name
Gill net:		
(1)	*Esox lucius*	Northern pike
(2)	*Catostomus commersoni*	White sucker
(3)	*Coregonus clupeaformis*	Lake whitefish
(4)	*Coregonus artedii and Coregonus zenithicus*	Cisco
(5)	*Stizostedion vitreum*	Walleye
(6)	*Stizostedion canadense*	Sauger
(7)	*Lota lota*	Burbot
(8)	*Perca flavescens*	Yellow perch
(9)	*Catostomus catostomus*	Longnose sucker
Seine net:		
(1)	*Notropis atherinoides*	Emerald shiner
(2)	*Notropis hudsonius*	Spottail shiner
(3)	*Perca flavescens*	Yellow perch
(4)	*Esox lucius*	Northern pike
(5)	*Couesius plumbeus*	Lake chub
(6)	*Etheostoma nigrum*	Johnny darter
(7)	*Percopsis omiscomaycus*	Trout–perch
(8)	*Pungitius pungitius*	Ninespine stickleback
(9)	*Culaea inconstans*	Brook stickleback
(10)	*Cottus cognatus*	Slimy sculpin
(11)	*Catostomus commersoni*	Common white sucker
(12)	*Catostomus catostomus*	Longnose sucker
(13)	*Lota lota*	Burbot
(14)	*Coregonus clupeaformis*	Lake whitefish
(15)	*Stizostedion vitreum*	Walleye
(16)	*Cottus ricei*	Spoonhead sculpin
(17)	*Stizostedion canadense*	Sauger
(18)	*Semotilus margarita*	Pearl dace

Table 2. Total small fish catch in seine nets from all sites in Wupaw Bay, 1977–88.

Species	1977	1978	1979	1980	1981	1982	1983	1984	1986	1987	1988	Totals
Main species:												
(1) Emerald shiner	12	1831	1746	2688	28085	5392	4198	9810	3708	4918	10532	72920
(2) Spottail shiner	4980	5857	3403	3945	8577	7211	3142	2286	1381	5095	4565	50442
(3) Yellow perch	275	1115	1107	2028	1448	1136	176	721	910	176	139	9231
(4) YOY pike	96	19	27	7	47	2	5	22	15	8	6	254
Main species totals	5363	8822	6283	8668	38157	13741	7521	12839	6014	10197	15242	132847
"Other" species:												
(5) Lake chub	15	39	364	123	224	3	18	5	124	233	42	1190
(6) Johnny darter	55	50	46	16	62	3	3	3	6	15	9	268
(7) Trout-perch	8	12	1	2	1	4	2	0	7	6	0	43
(8) Ninespine stickleback	0	0	4	18	9	16	0	0	9	3	0	59
(9) Brook stickleback	23	24	18	11	9	0	0	1	5	5	3	99
(10) Slimy sculpin	0	0	1	0	3	2	0	0	0	0	0	6
(11) White sucker	6	2	4	31	1	16	1	10	2	5	0	78
(12) Longnose sucker	1	0	0	2	0	4	0	0	0	0	0	7
(13) Burbot	20	12	6	0	1	0	0	1	0	0	0	40
(14) Lake whitefish	0	4	28	0	1	0	0	0	0	0	0	33
(15) Walleye	0	15	0	0	0	0	0	0	0	0	0	15
(16) Spoonhead sculpin	0	2	2	2	2	0	0	0	0	0	0	8
(17) Sauger	0	0	0	1	0	0	0	0	0	0	0	1
(18) Pearl dace	2	0	0	0	0	0	0	0	0	0	0	2
"Other" species totals	130	160	474	206	313	48	24	20	153	267	54	1849
Effort (no. of hauls)	82	100	82	109	83	70	50	55	51	49	35	766
Totals for all species	5493	8982	6757	8874	38470	13789	7545	12859	6167	10464	15296	134696

Table 3. Total gill net catch of the most abundant fish species in Wupaw Bay, 1976–88.

Year	Effort (hr)	Northern pike	Walleye	Lake whitefish	Cisco	White sucker	Totals
1976	238.33	403	112	71	70	285	941
1977	1129.33	1030	184	115	37	801	2167
1978	422.11	531	202	83	100	648	1564
1979	234.24	231	65	24	62	253	635
1980	172.83	125	9	4	17	30	185
1981	184.05	174	45	19	33	52	323
1982	127.15	198	41	33	58	198	528
1983	76.87	54	7	3	13	21	98
1984	151.40	23	38	2	12	42	117
1985	0.00	–	–	–	–	–	–
1986	92.46	88	17	8	40	61	214
1987	277.00	117	17	14	68	120	336
1988	67.12	47	12	1	15	44	119
Totals:	3172.89	3021	749	377	525	2555	7227

Table 4. Average condition factors (K), annual survival rates (based on scale ages) and sex ratios for northern pike captured in gill nets in Wupaw Bay, 1976–1988. (n= number of fish examined; s.d.= standard deviation).

Year	Condition factor (K)			Annual survival		Sex Ratio
	n	mean K	s.d.	Rate	95% CI	(females/males)
1976	71	0.89	0.09	0.43	0.07	-
1977	551	0.90	0.15	0.52	0.02	1.03
1978	533	0.87	0.09	0.39	0.04	1.39
1979	242	0.88	0.10	0.44	0.04	1.00
1980	120	0.82	0.13	0.43	0.08	1.05
1981	170	0.82	0.13	0.47	0.07	1.14
1982	198	0.84	0.18	0.45	0.07	1.83
1983	54	0.83	0.08	0.50	0.13	2.45
1984	31	0.85	0.09	0.42	0.20	3.88
1985	-	-	-	-	-	-
1986	90	0.79	0.09	0.58	0.08	1.43
1987	74	0.84	0.10	0.68	0.06	3.29
1988	47	0.84	0.07	0.62	0.08	2.21

Table 5. Stomach contents of northern pike captured in gill nets in Wupaw Bay, 1976–88. Data for 1976–81 are from Bodaly and Lesack (1984).

Year	n	Empty stomachs		Mean number per stomach (includes empty stomachs)		
		%	95% CI	fish	invertebrates	YOY pike
1976	21	76	56–97	0.14	0.10	0.00
1977	228	58	52–65	0.50	0.14	0.06
1978	538	50	46–55	0.50	0.51	<0.01
1979	242	52	46–59	0.38	0.39	0.01
1980	121	69	63–80	0.20	0.20	0.00
1981	174	62	54–70	0.45	0.17	0.00
1982	198	62	55–69	0.36	0.24	0.00
1983	54	74	62–87	0.42	0.00	0.00
1984	31	68	50–86	0.35	0.00	0.00
1985	–	–	–	–	–	–
1986	90	61	51–72	0.37	0.12	0.01
1987	–	–	–	–	–	–
1988	47	70	56–84	0.17	0.11	0.00

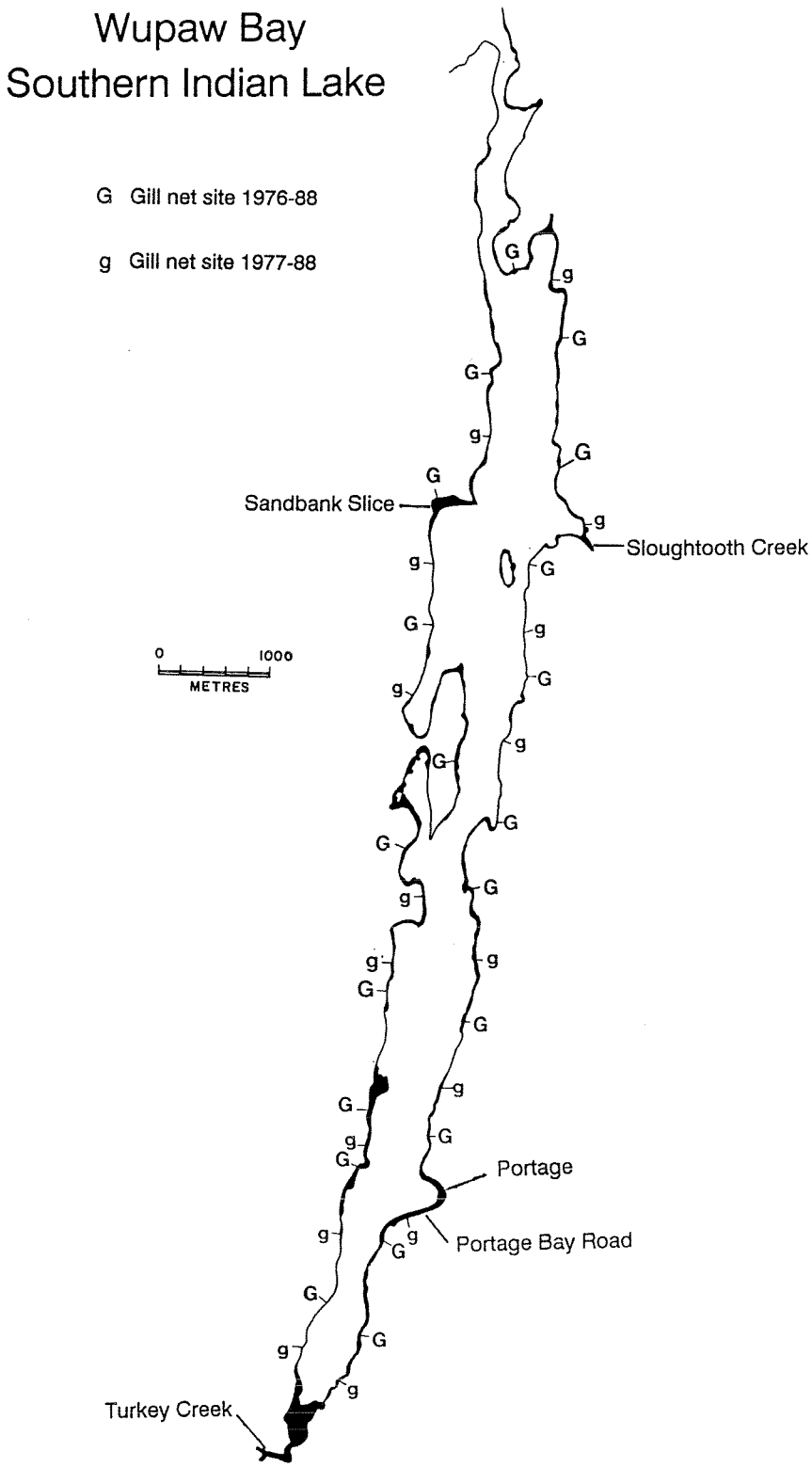


Fig. 1. Map of Wupaw Bay with seining and gill net sites. Flooded areas are indicated by dark shading. (Adapted from Bodaly and Lesack 1984). Seining sites are Sandbank Slice, Sloughtooth Creek, Portage, Portage Bay Road and Turkey Creek.

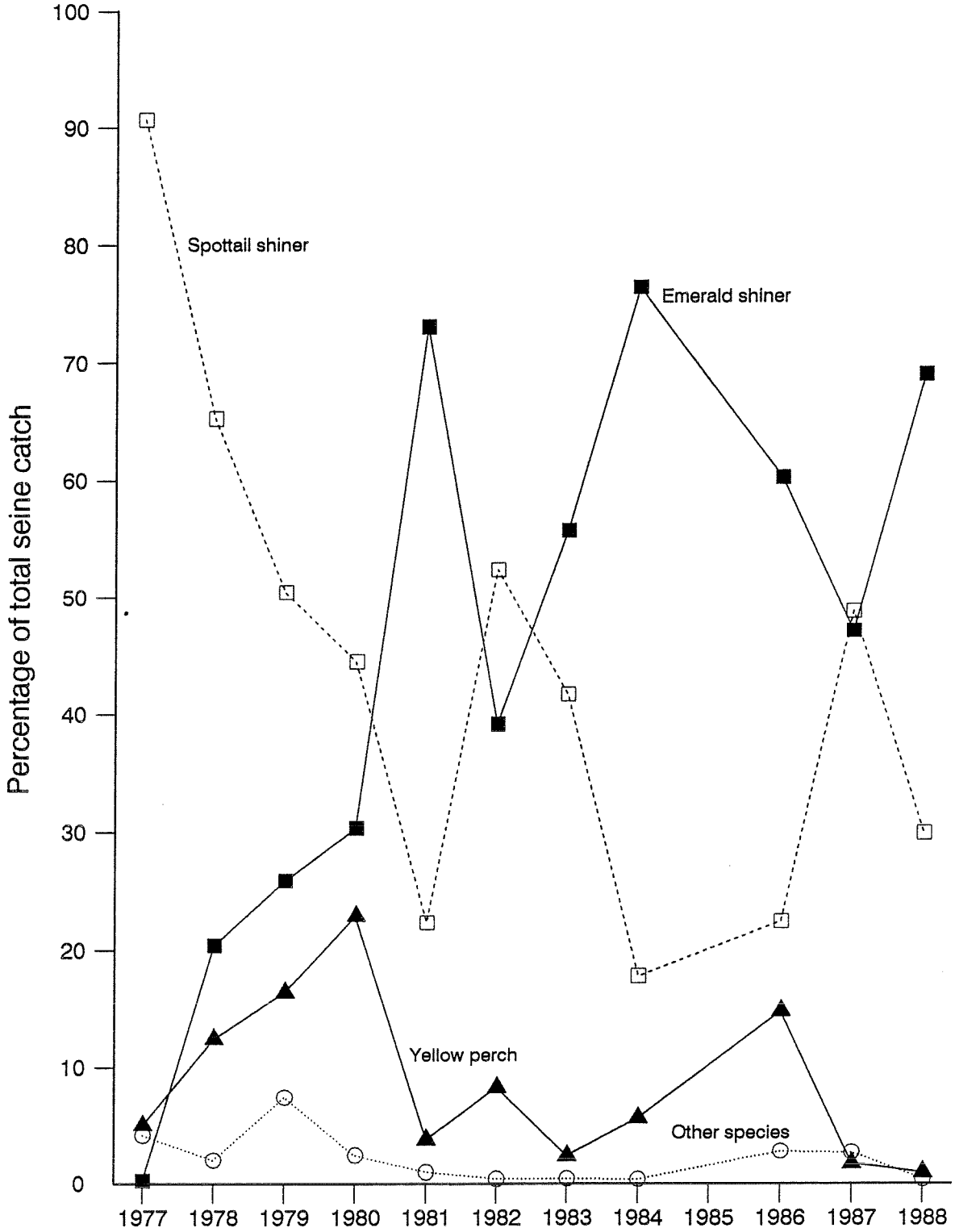


Fig. 2. Composition of seine catch in Wupaw Bay, 1977-88. No fish were collected in 1985.

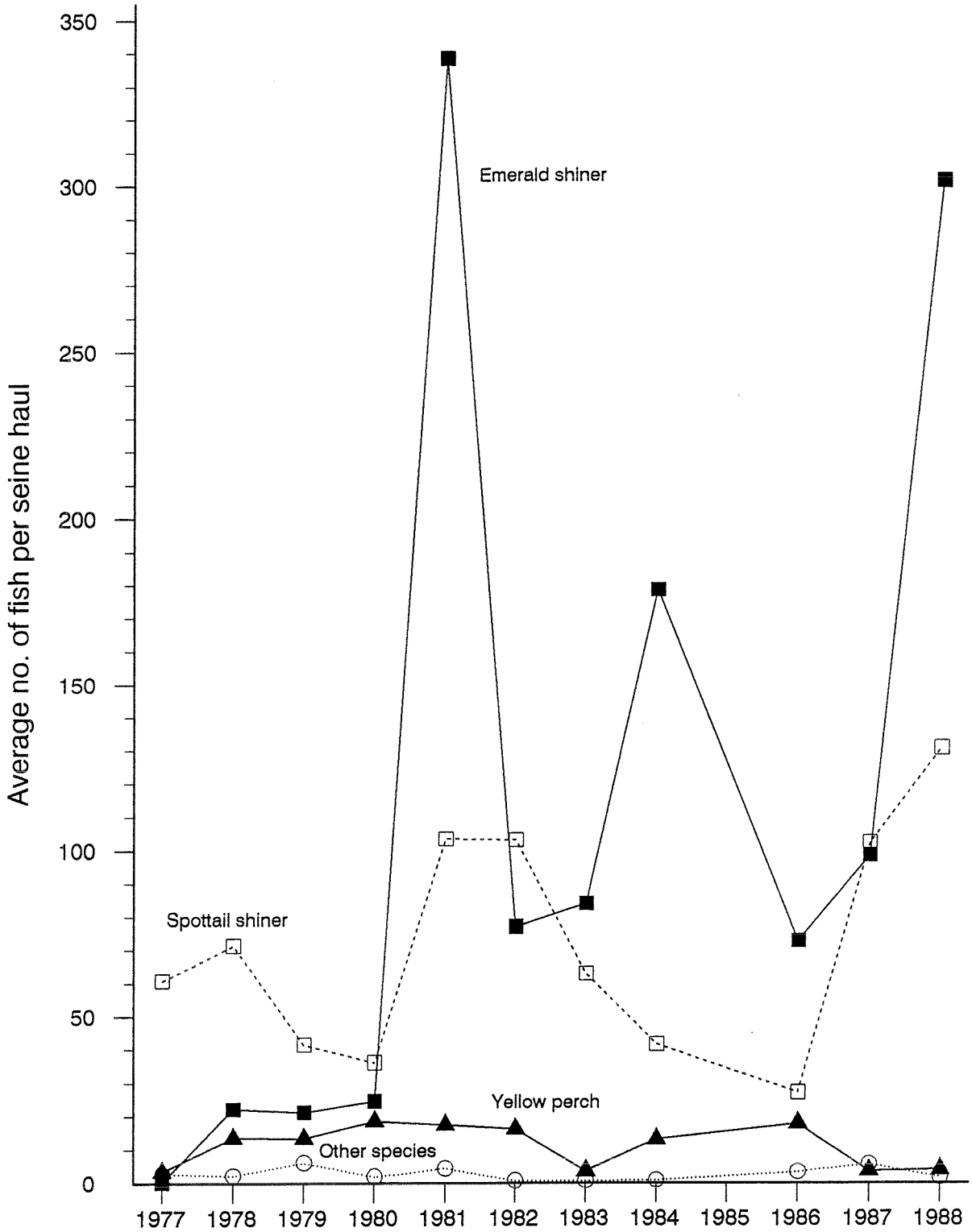


Fig. 3. Average catch per seine haul in Wupaw Bay, 1977-88. No fish were collected in 1985.

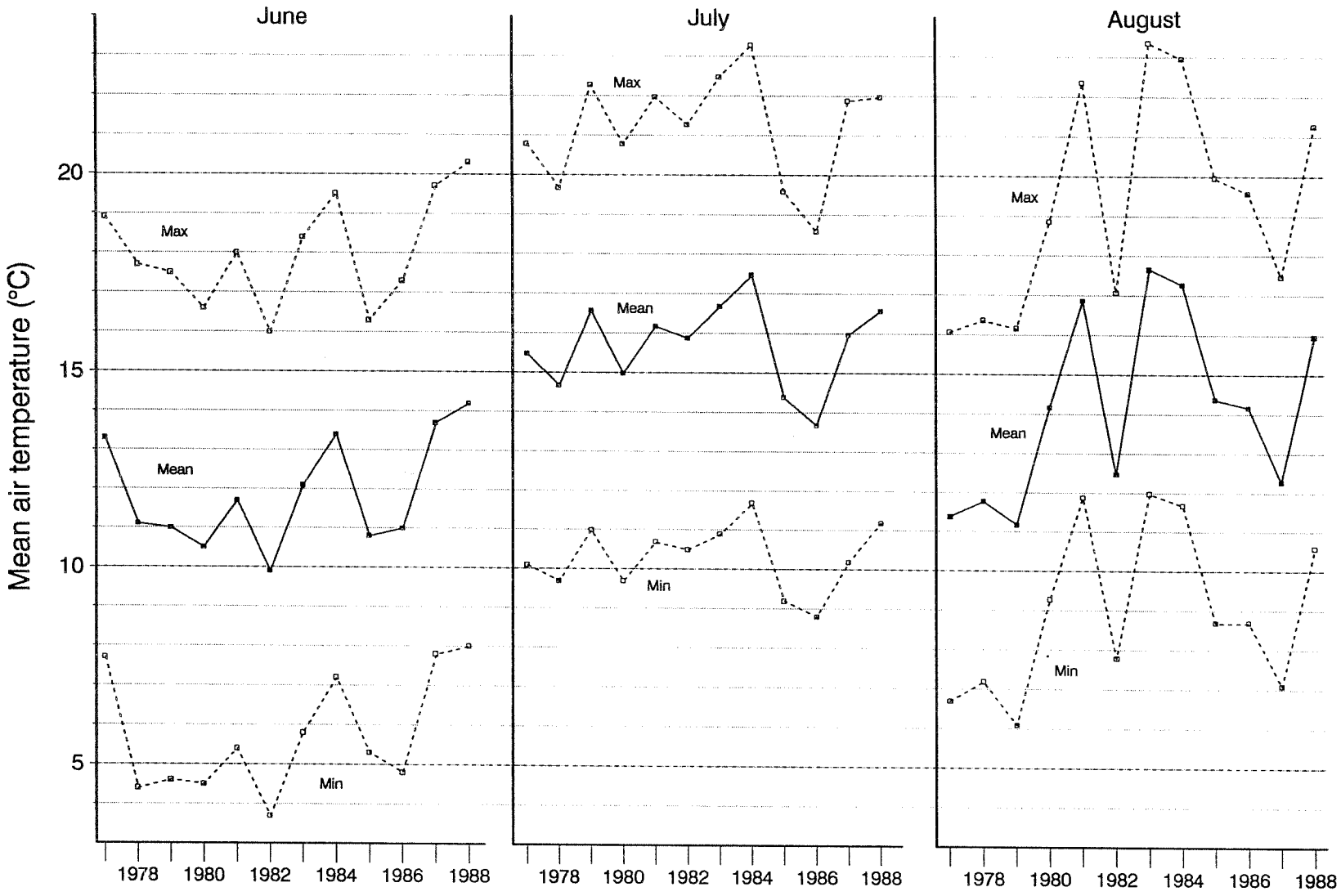


Fig. 4. Mean minimum, mean maximum and overall mean daily air temperatures for June, July and August at Southern Indian Lake, 1977-88.

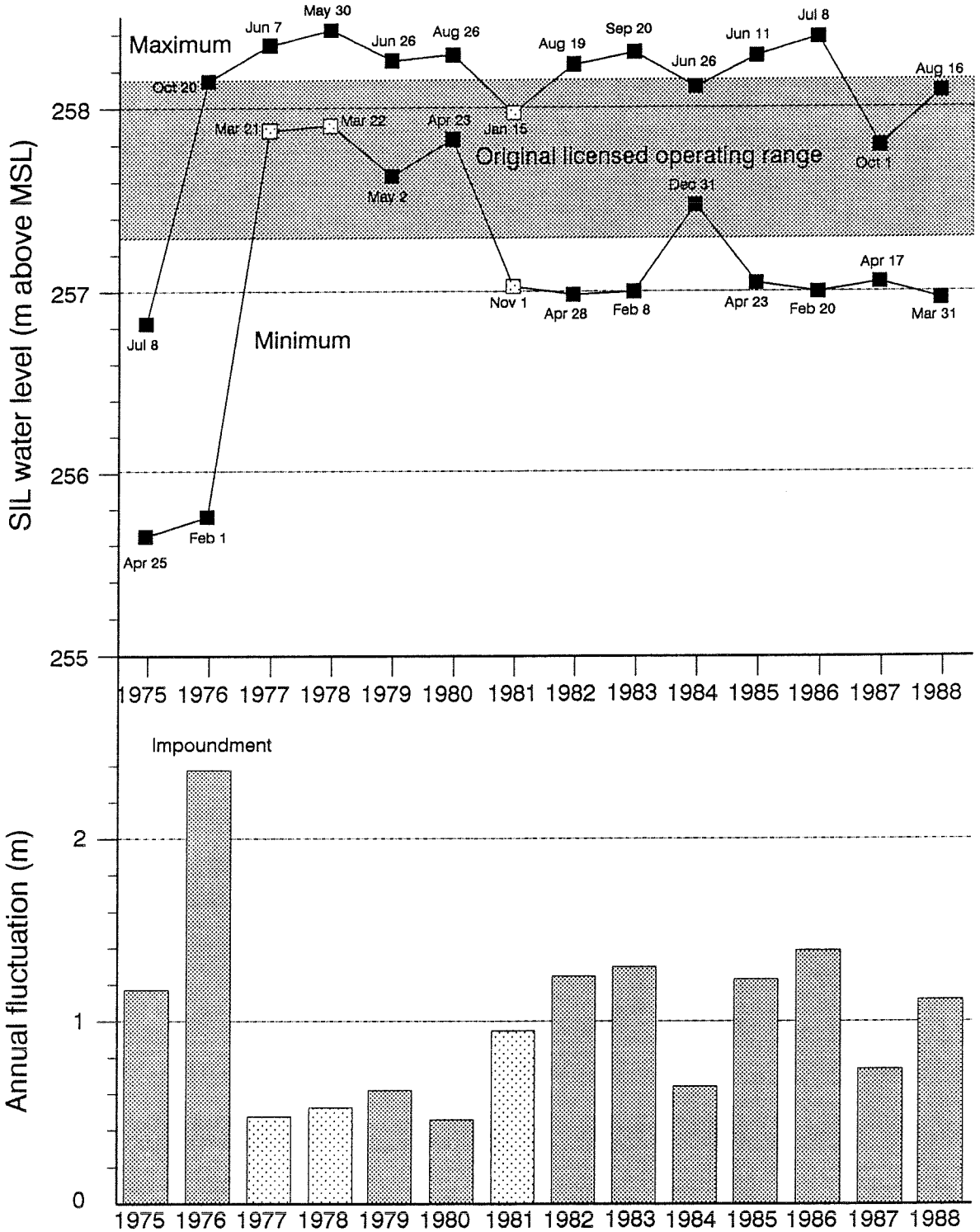


Fig. 5. Southern Indian Lake water levels for the period 1975-88. Dates of annual minimum and maximum water levels are shown. Lighter toned bars and points indicate data derived from incomplete records. Data from Water Survey of Canada (1975-88).

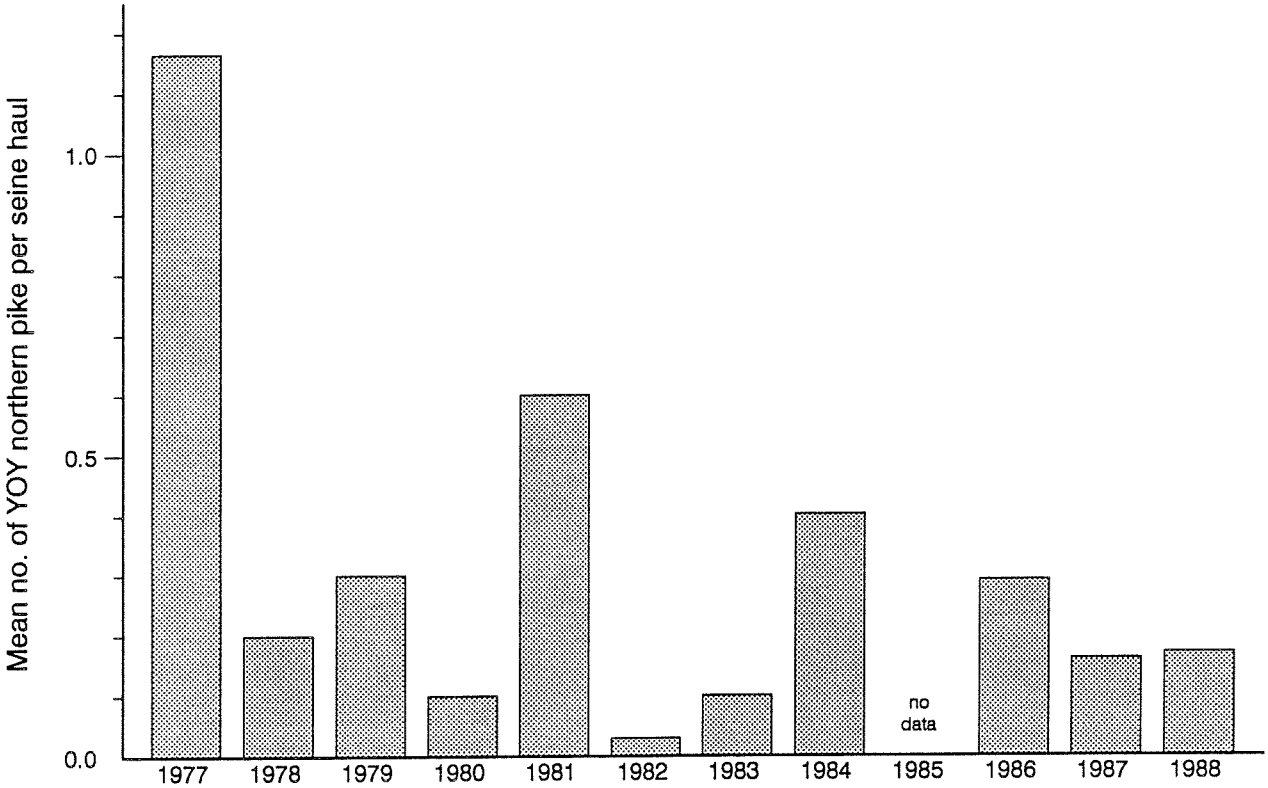


Fig. 6. Mean catch per seine haul of young-of-the-year northern pike from all Wupaw Bay seining sites combined, 1977-88.

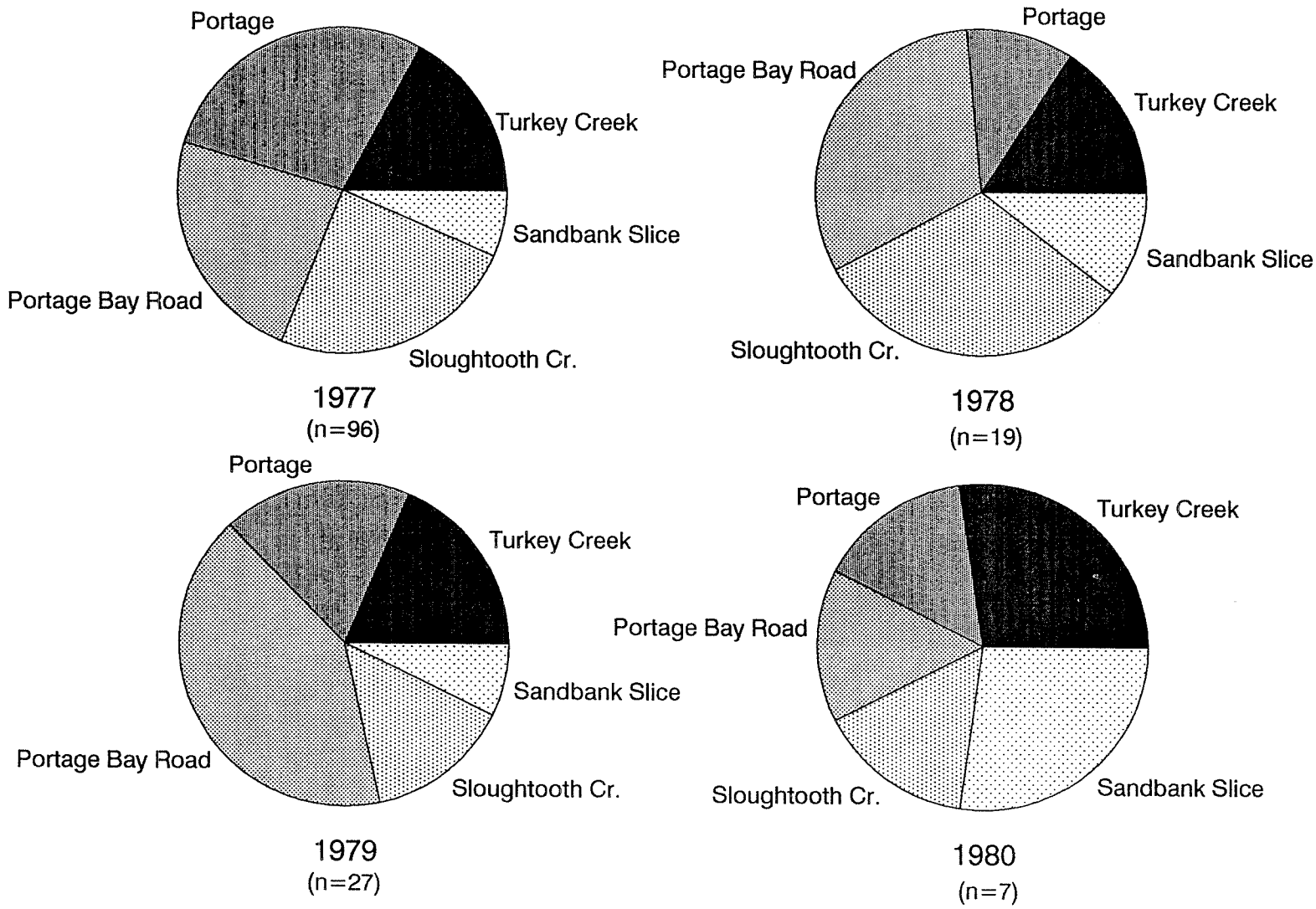
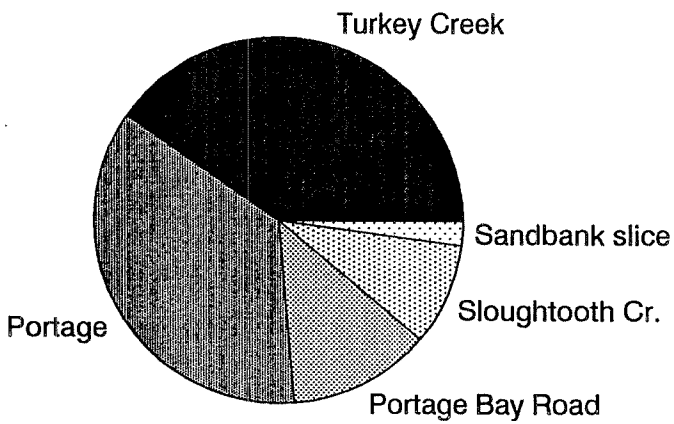
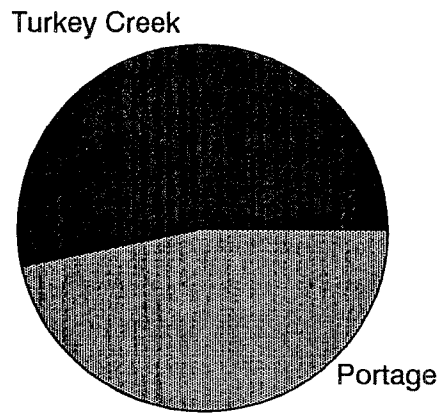


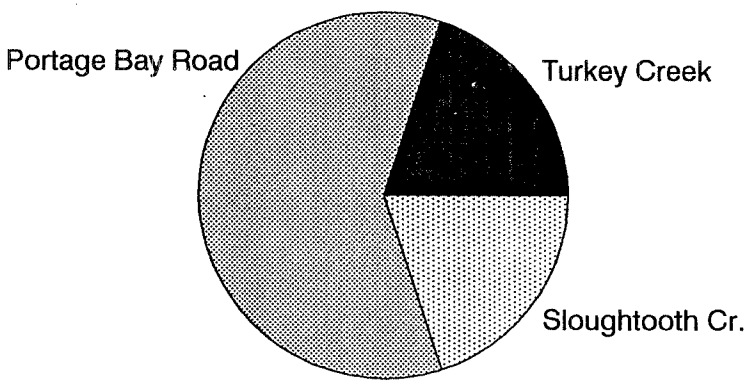
Fig. 7. Relative catch per unit of effort for young-of-the-year northern pike seined at each site in Wupaw Bay, 1977-88. No fish were collected in 1985 (n= total catch).



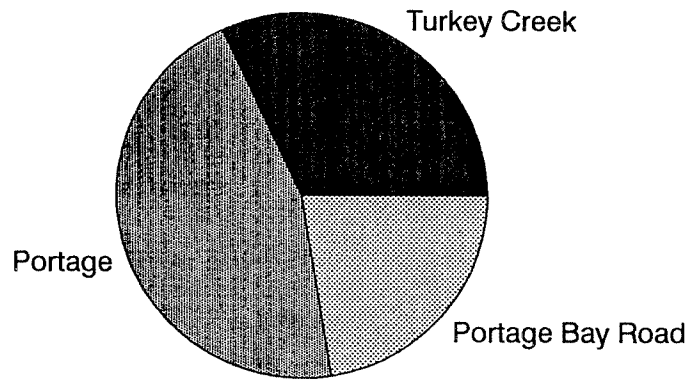
1981
(n=48)



1982
(n=2)



1983
(n=5)



1984
(n=22)

Fig. 7 (cont'd).

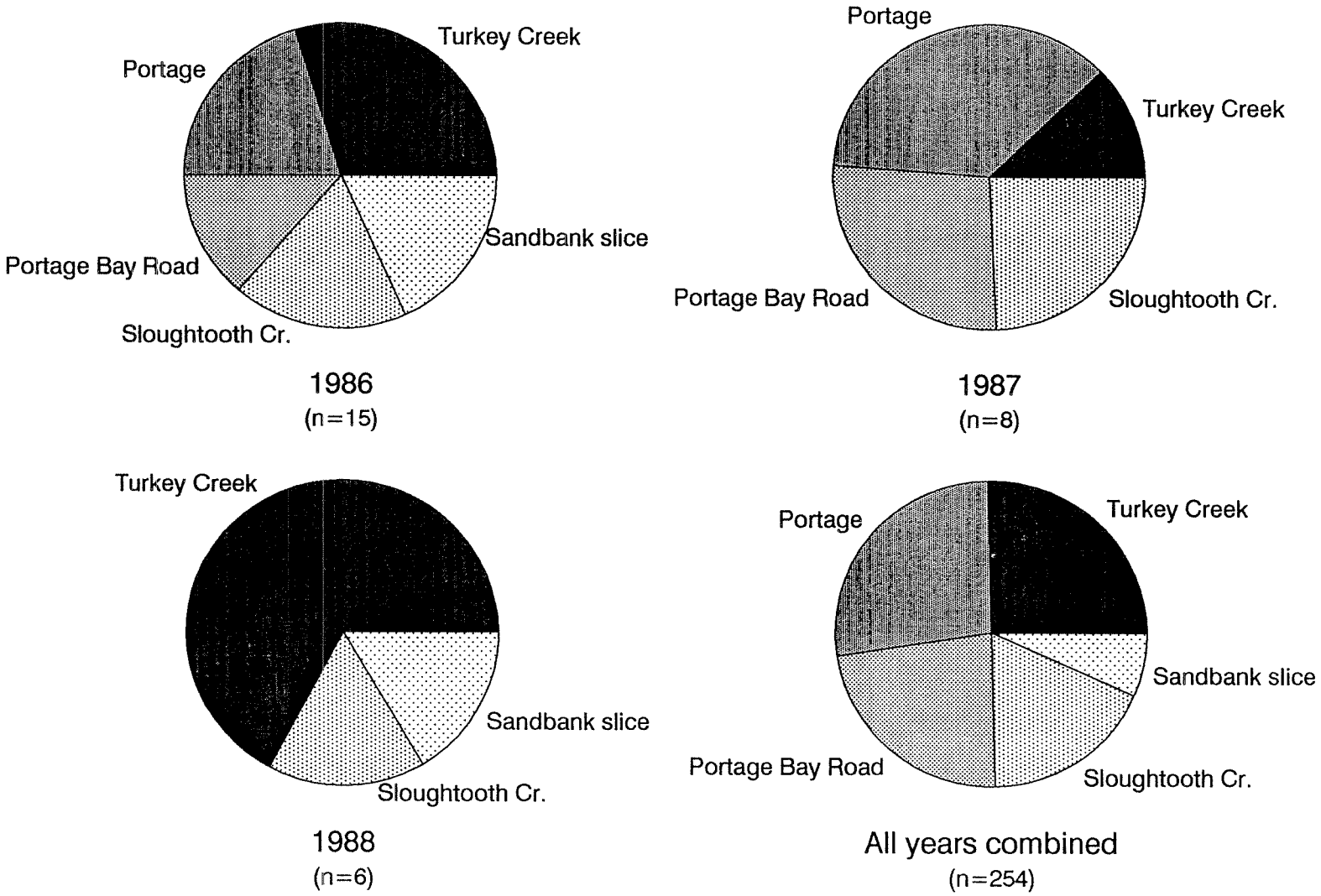


Fig. 7 (concluded).

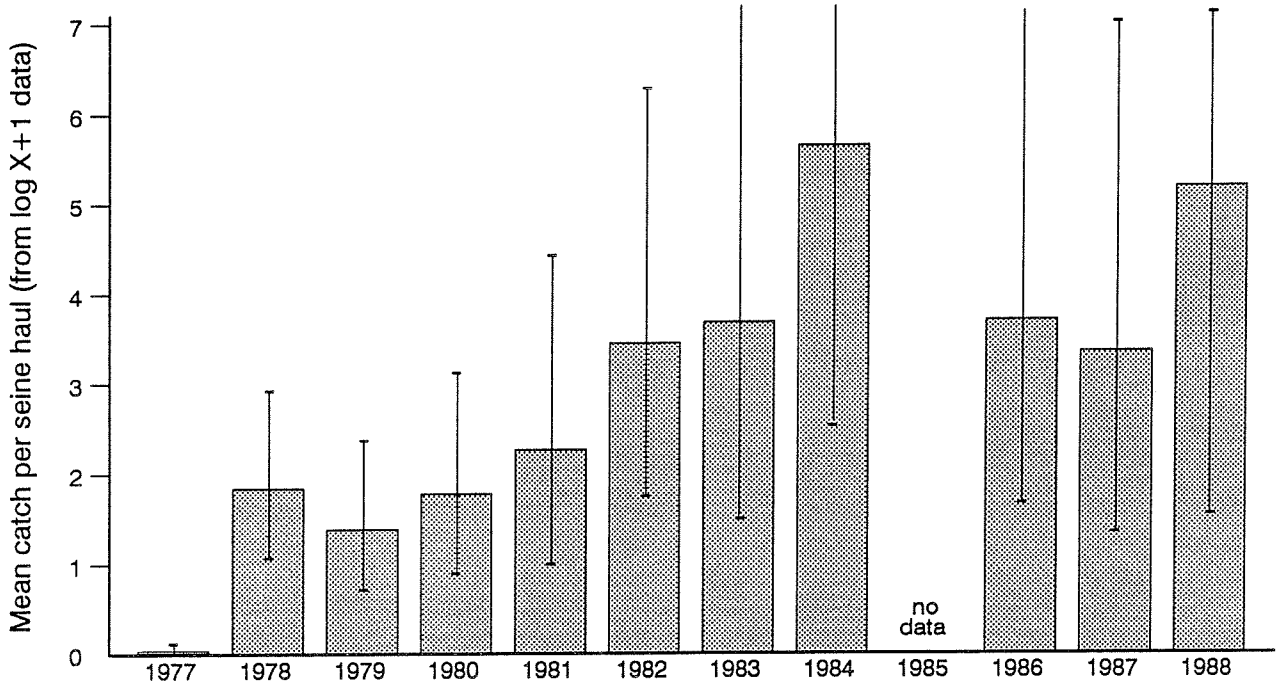


Fig. 8. Mean catch per seine haul and 95% confidence intervals for emerald shiners from Wupaw Bay seining sites, 1977-88. Values are antilogs of log(X+1) transformed data.

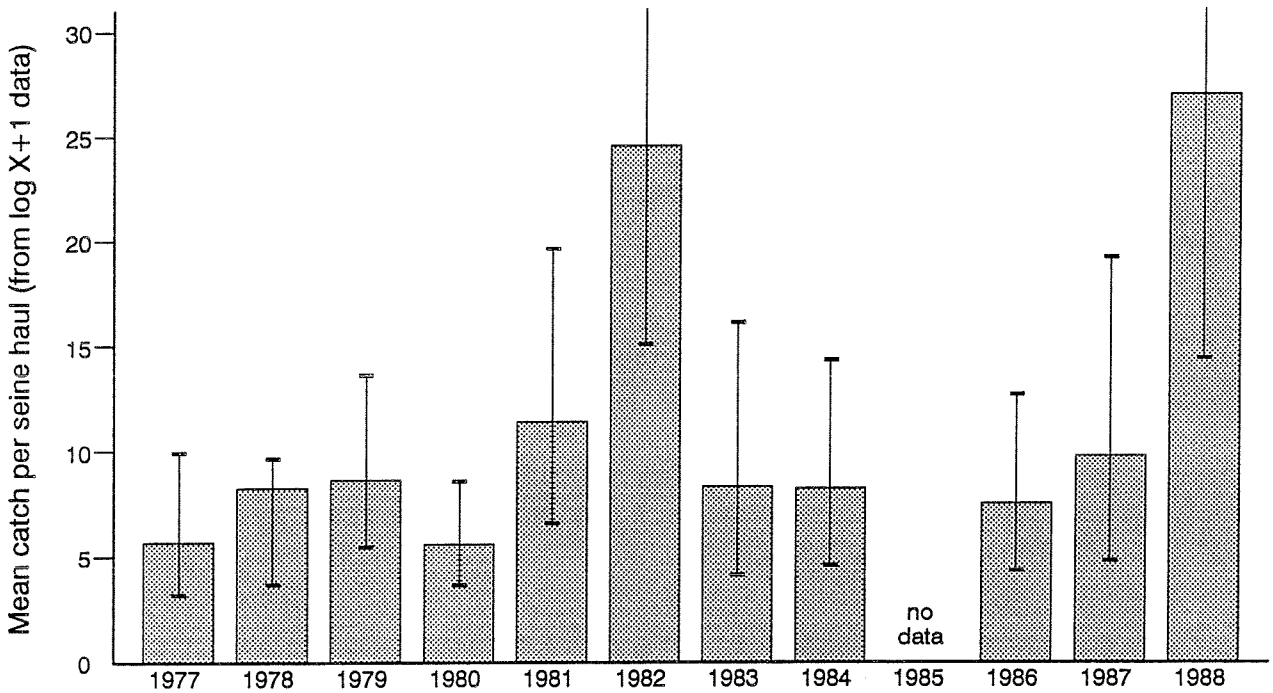


Fig. 9. Mean catch per seine haul and 95% confidence intervals for spottail shiners from Wupaw Bay seining sites, 1977-88. Values are antilogs of log(X+1) transformed data.

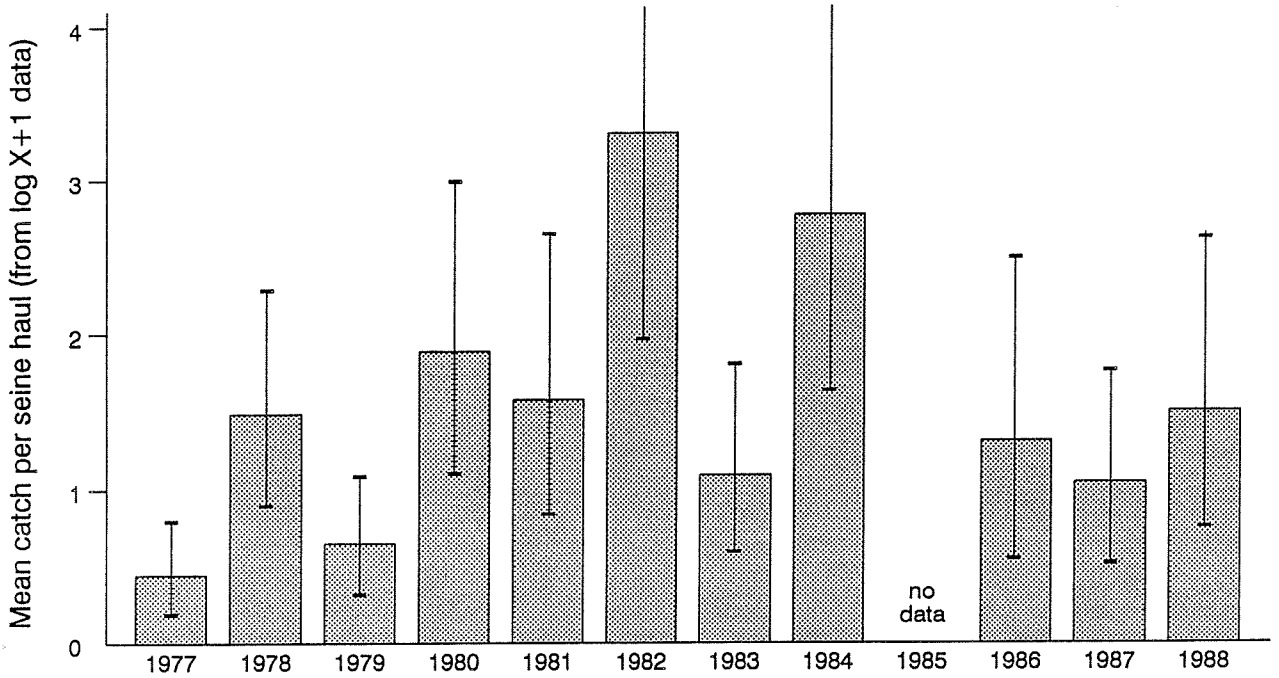


Fig. 10. Mean catch per seine haul and 95% confidence intervals for yellow perch from Wupaw Bay seining sites, 1977-88. Values are antilogs of log (X+1) transformed data.

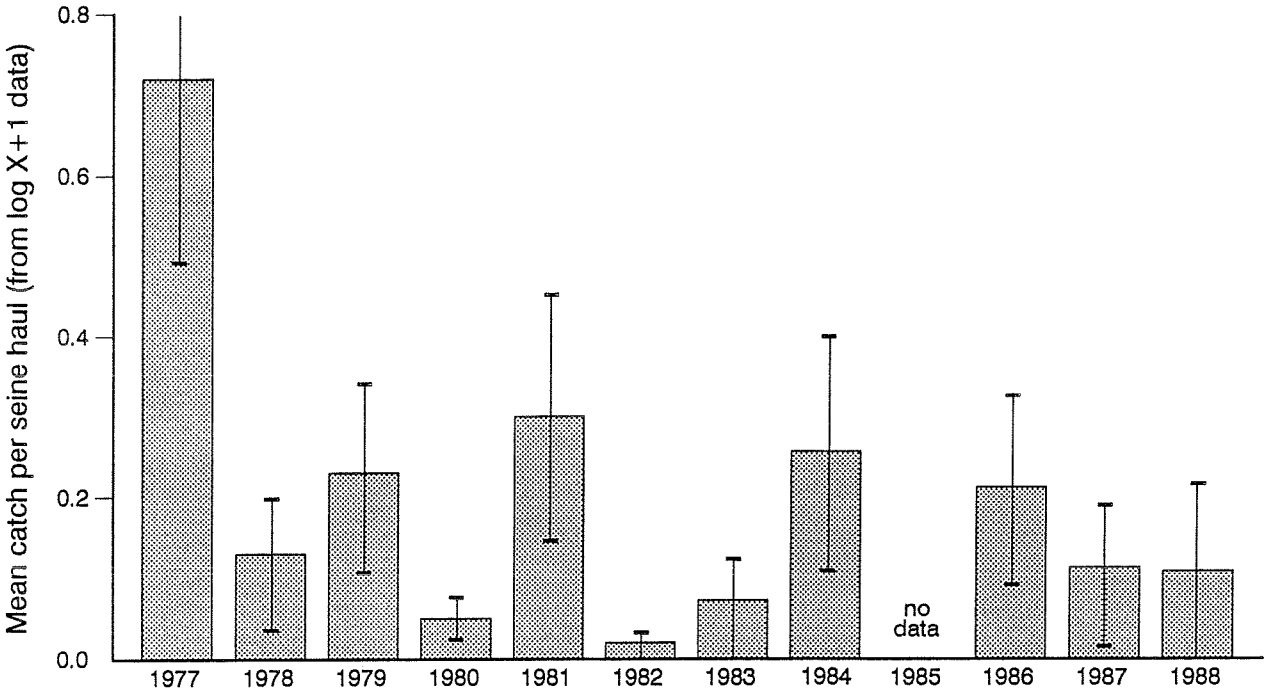


Fig. 11. Mean catch per seine haul and 95% confidence intervals for young-of-the-year northern pike from Wupaw Bay seining sites, 1977-88. Values are antilogs of log (X+1) transformed data.

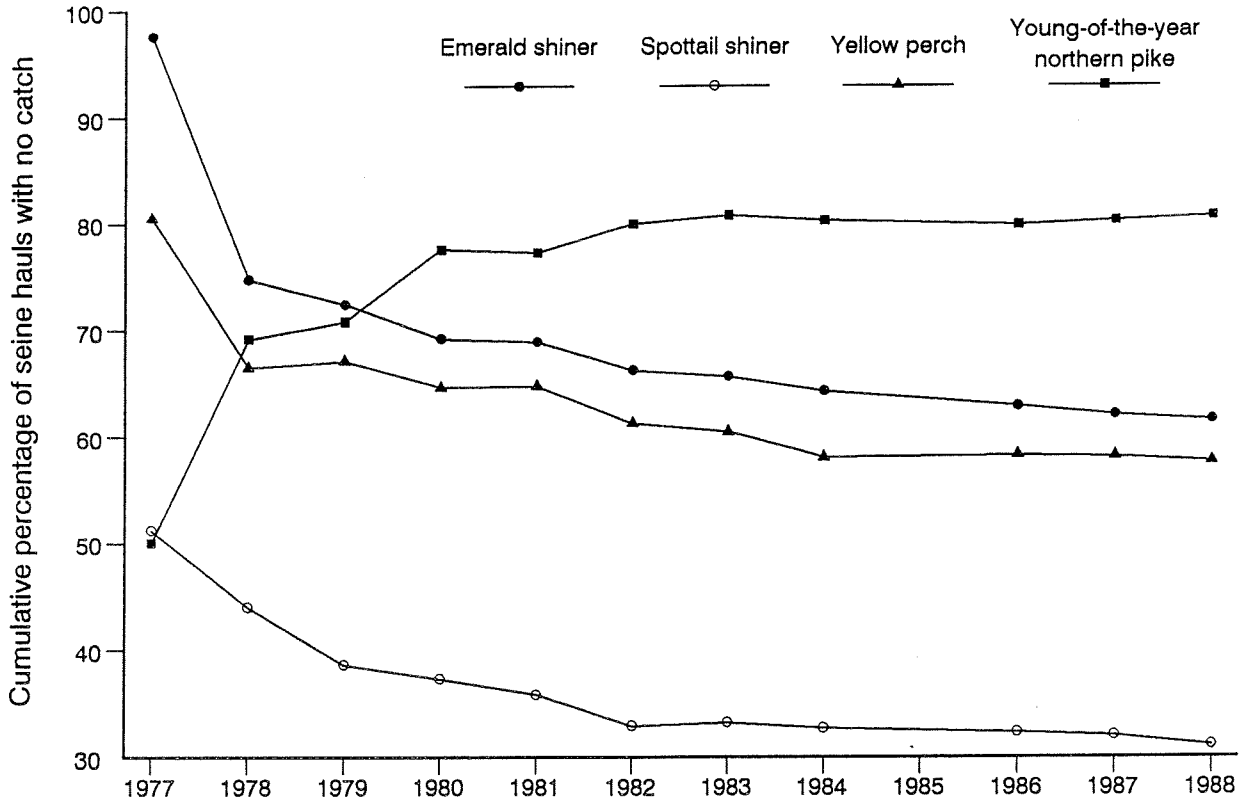


Fig. 12. Cumulative percentage of seine hauls with no catch of each of four species of small fish in Wupaw Bay, 1977-88. No fish were collected in 1985.

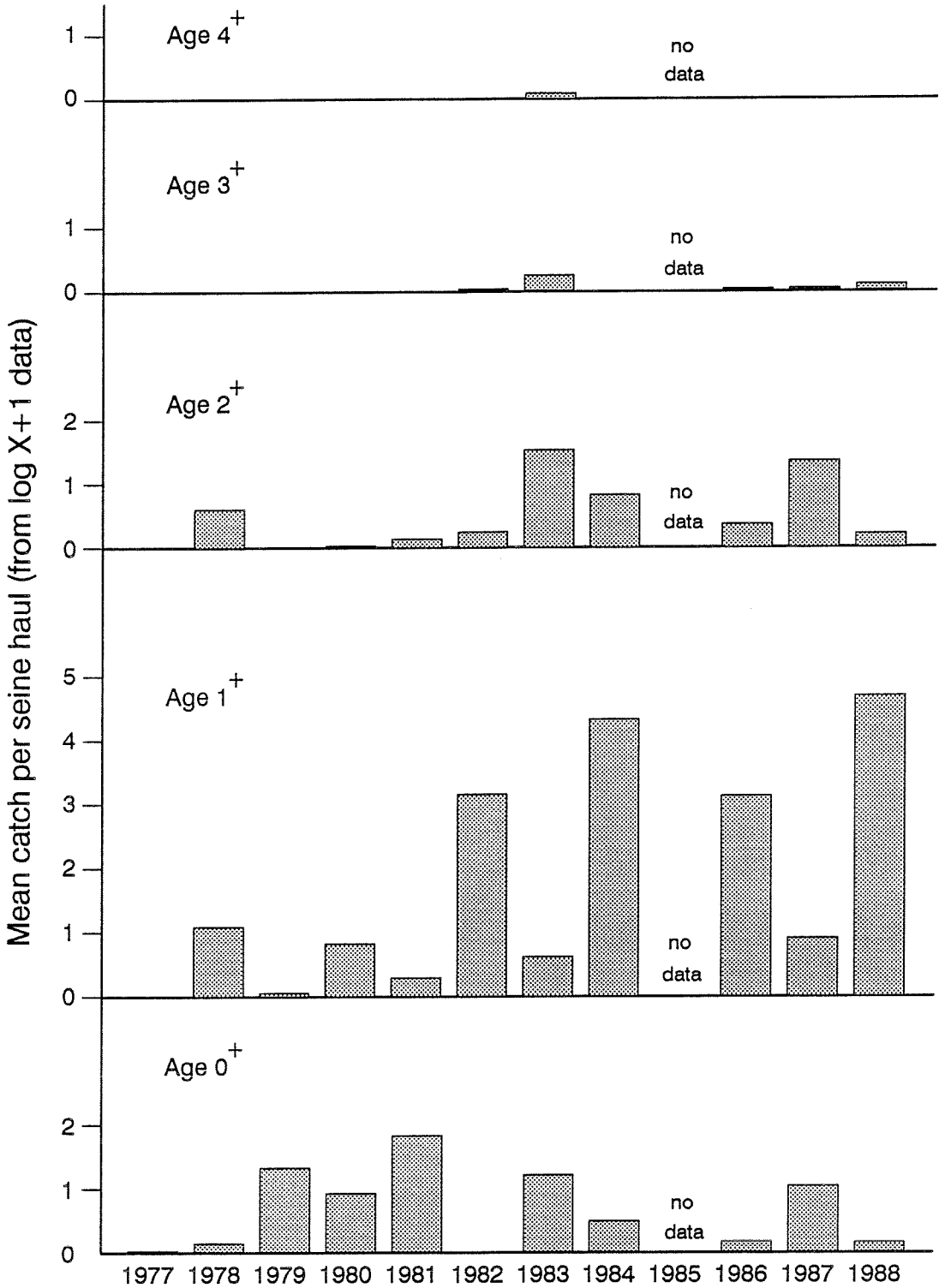


Fig. 13. Mean catch per haul for each age class of emerald shiners in seine nets, Wupaw Bay, 1977-88. Means are antilogs of means calculated from log (X+1) transformed data.

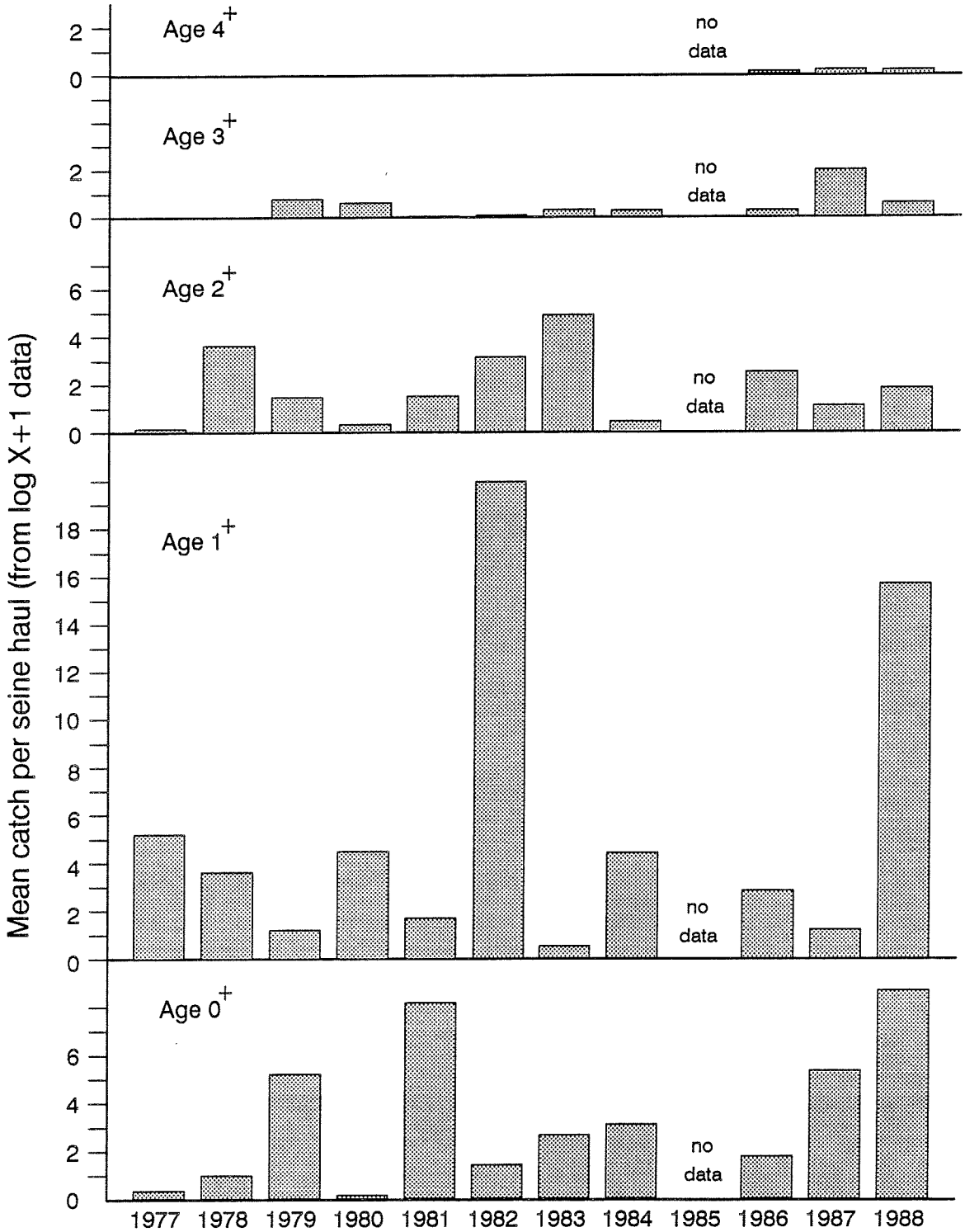


Fig. 14. Mean catch per haul for each age class of spottail shiners in seine nets, Wupaw Bay, 1977-88. Means are antilogs of means calculated from log (X+1) transformed data.

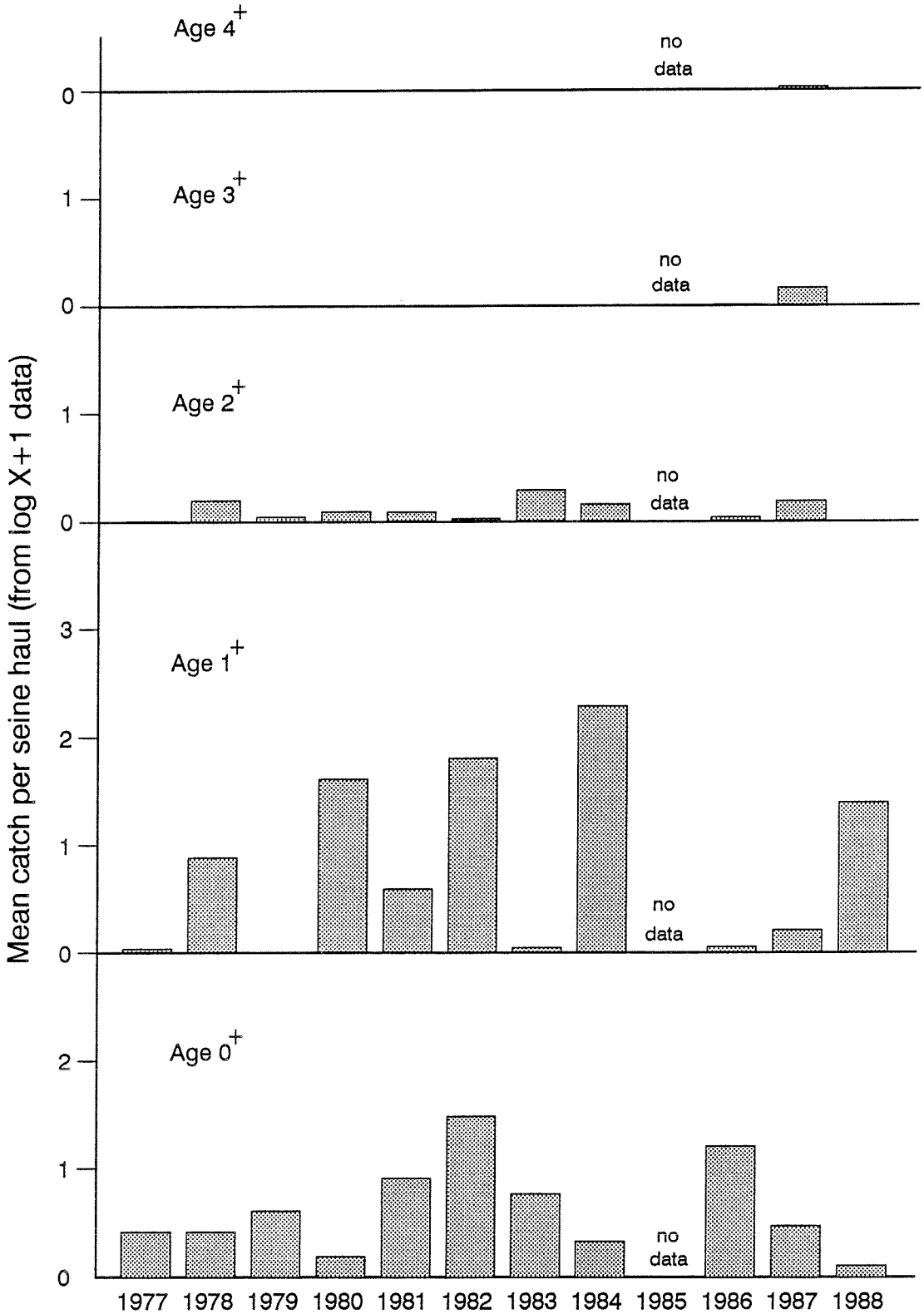


Fig. 15. Mean catch per haul for each age class of yellow perch in seine nets, Wupaw Bay, 1977-88. Means are antilogs of means calculated from log (X+1) transformed data.

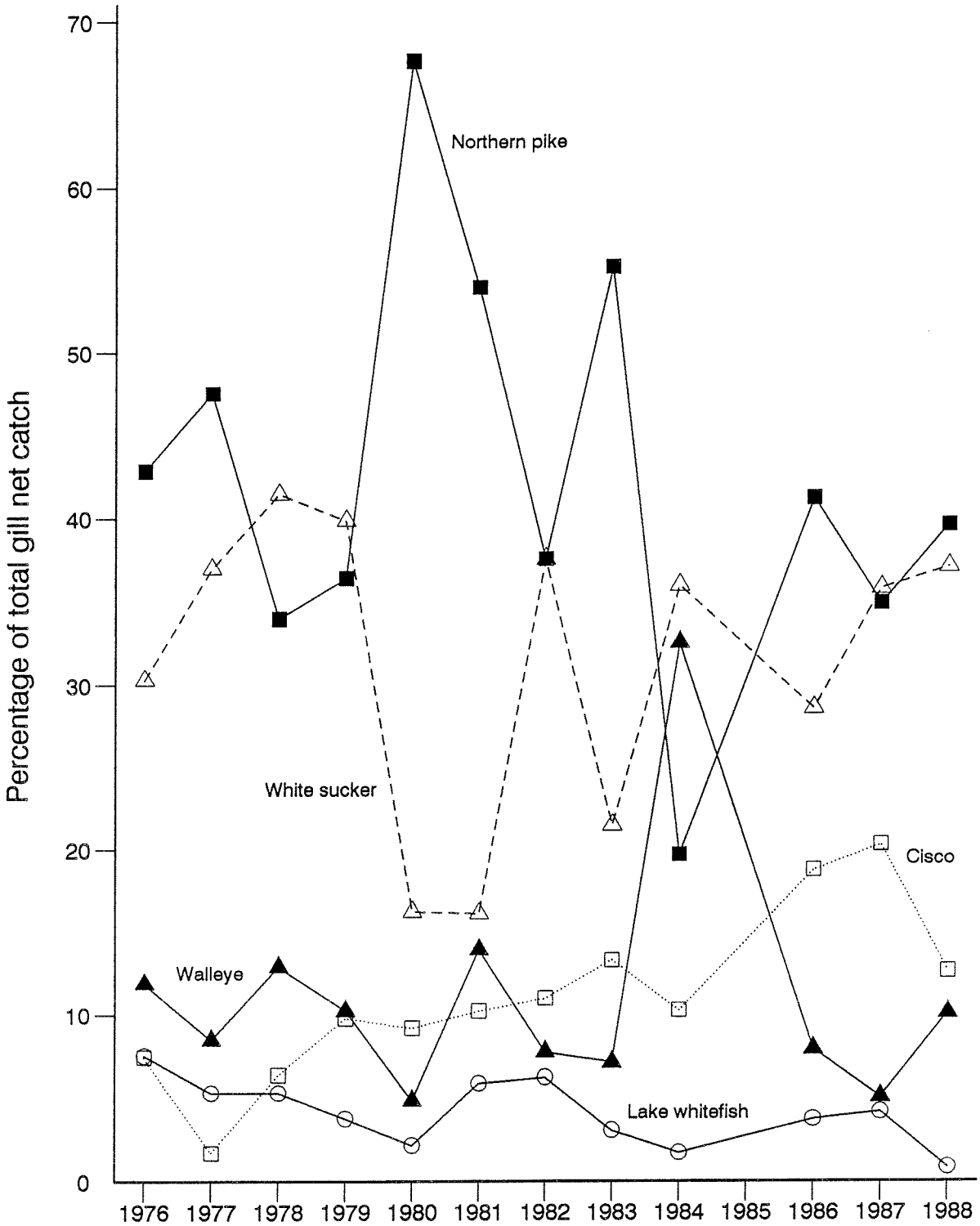


Fig. 16. Composition of the gill net catch in Wupaw Bay, 1976-88. No fish were collected in 1985.

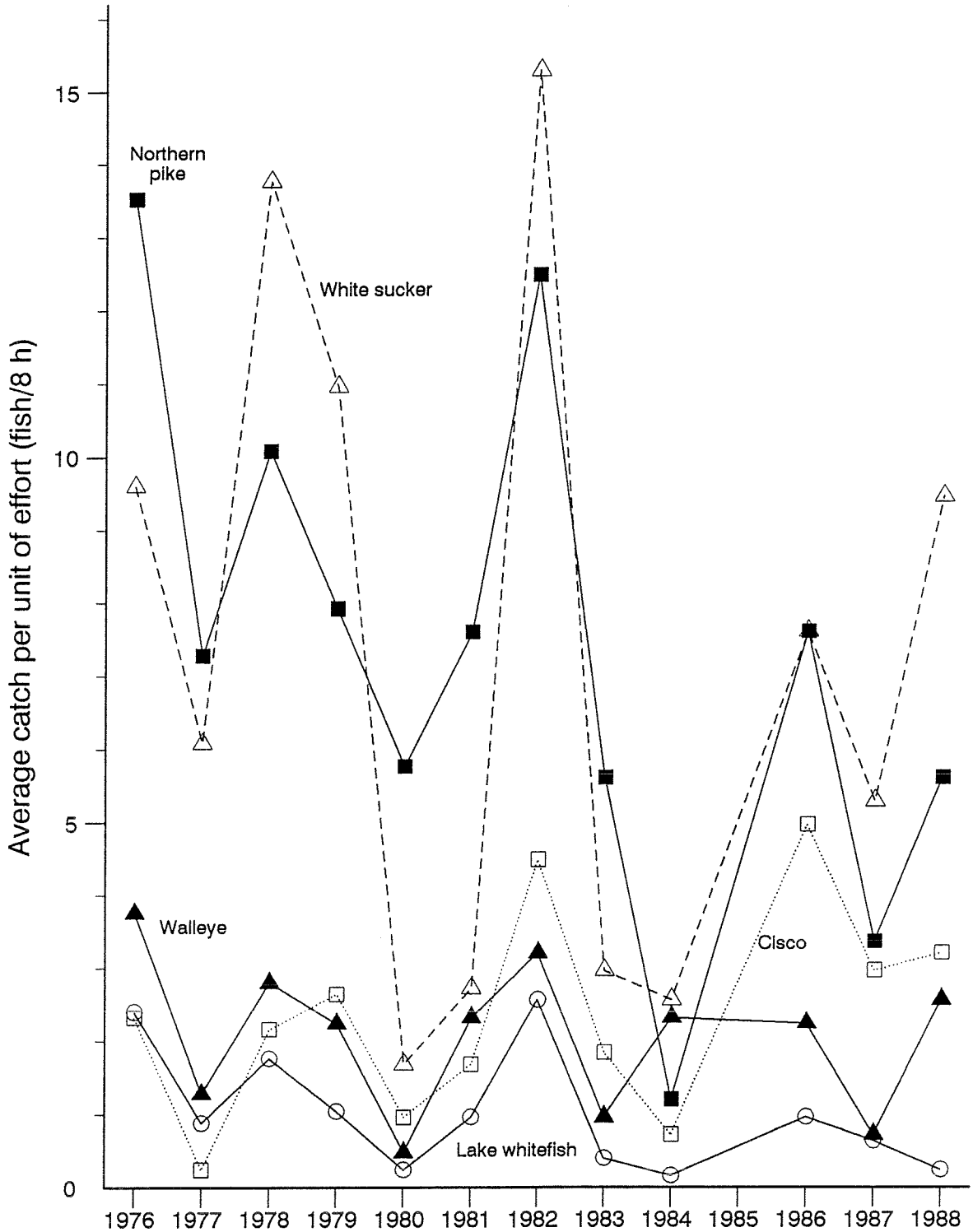


Fig. 17. Average catch per unit of effort for fish caught in gill nets in Wupaw Bay, 1976-88. No fish were collected in 1985.

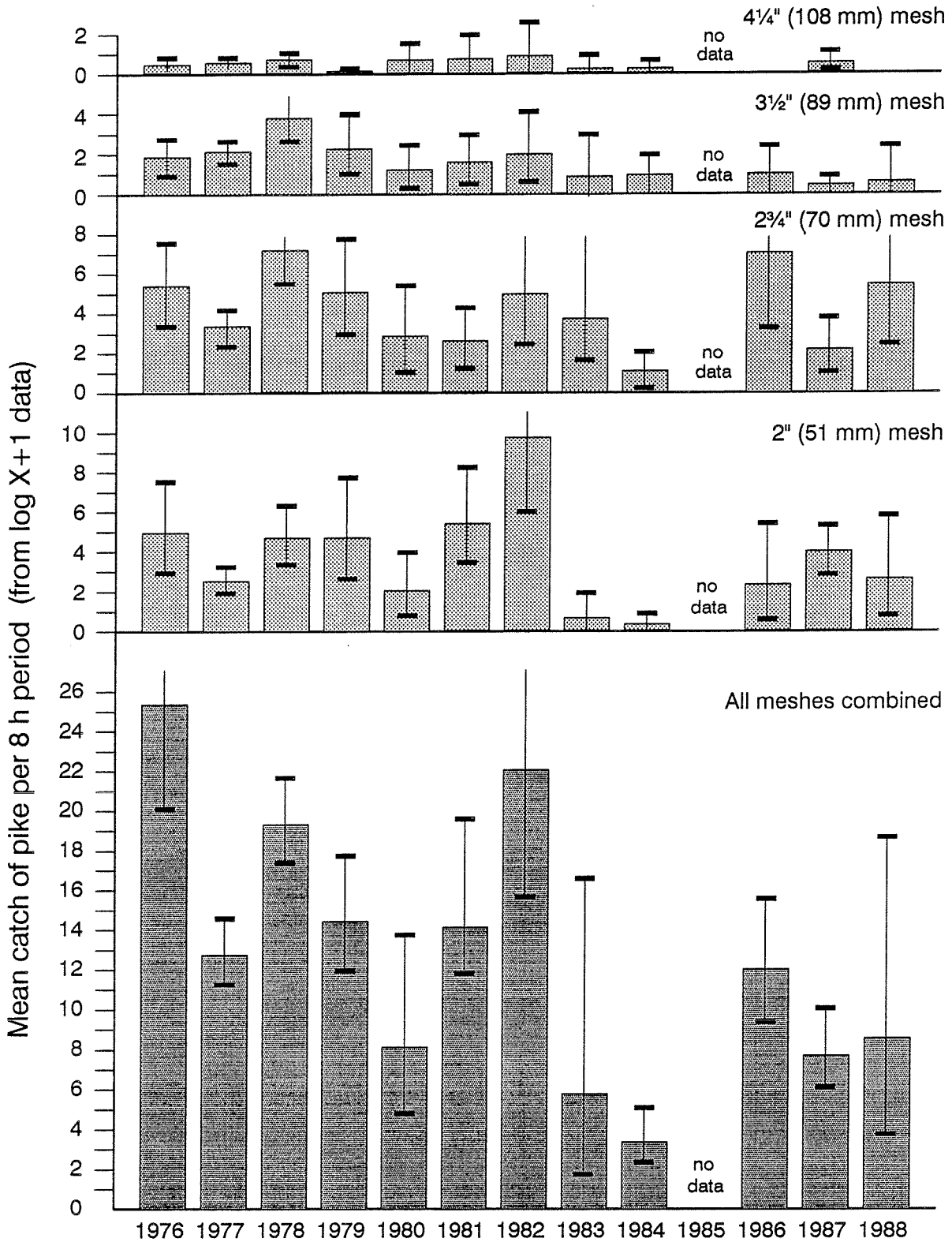


Fig. 18. Mean catch per 8 h set and 95% confidence intervals for northern pike caught in gill nets in Wupaw Bay, 1976-88. Values are antilogs of log (X+1) statistics. No fish were collected in 1985.

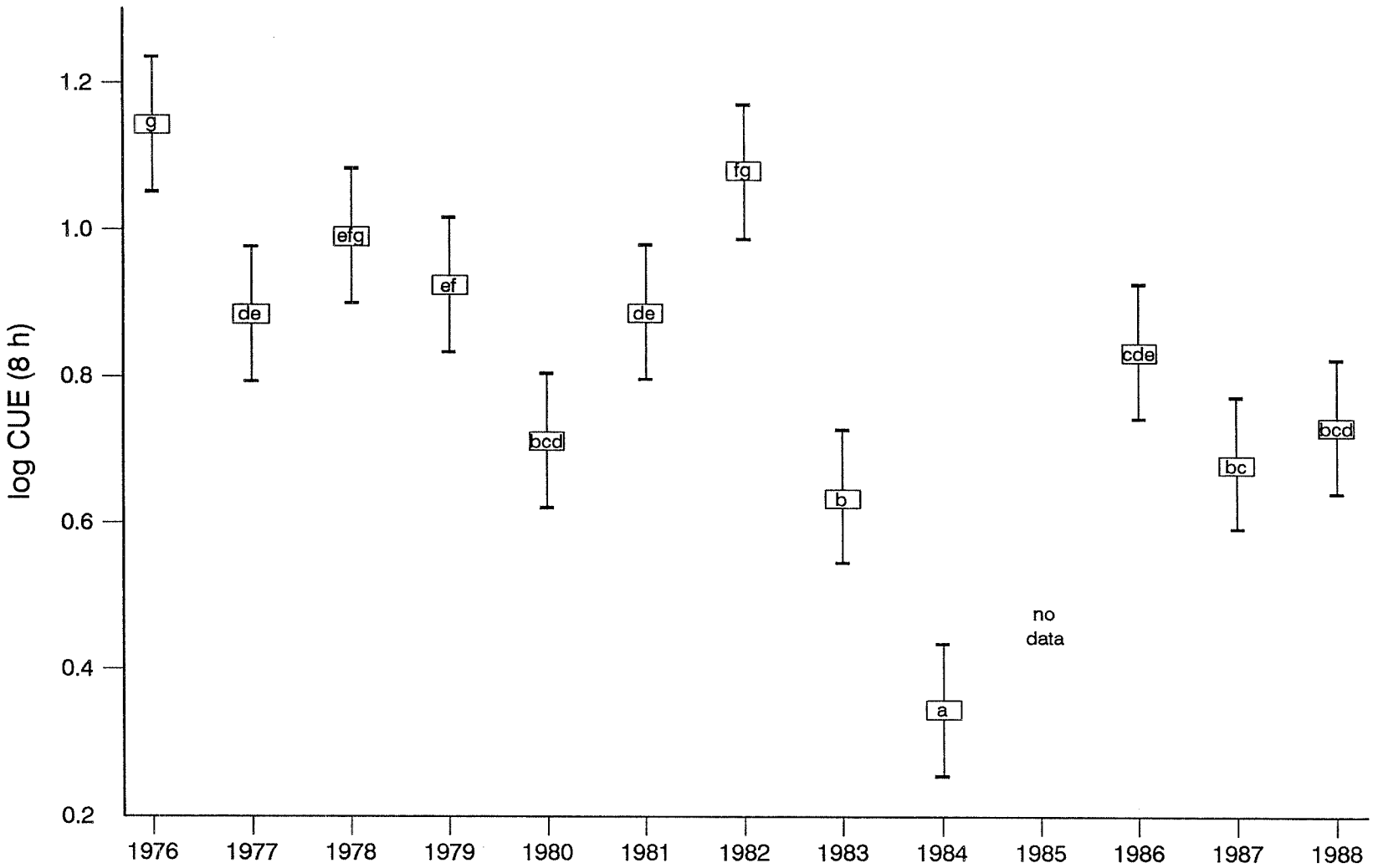


Fig. 19. Least significant difference plot for catch per unit of effort (CUE) of northern pike caught in gill nets in Wupaw Bay, 1976-88. Means with any letter in common are not significantly different (α=0.05). Bars are 95% confidence intervals for the LSD test.

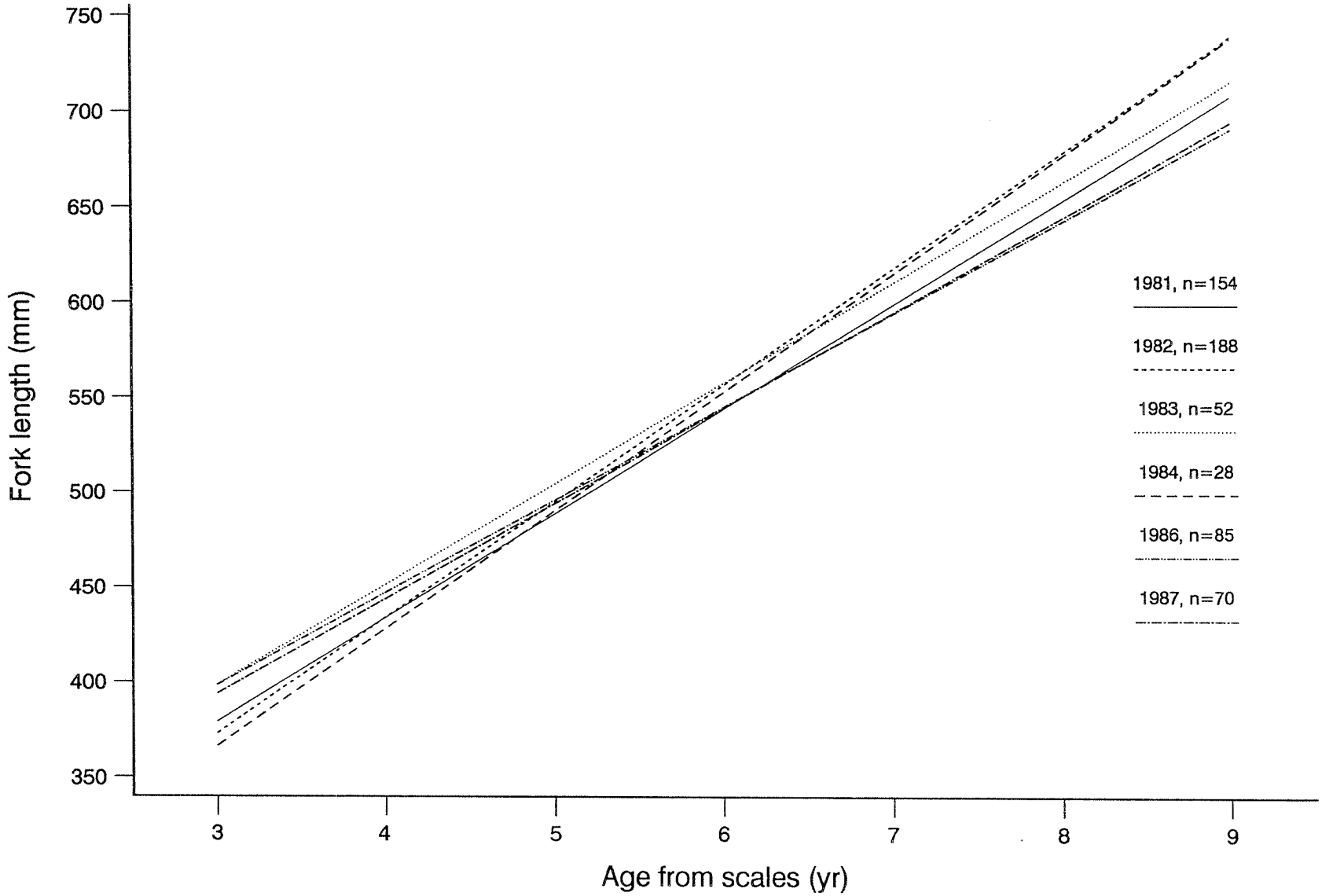


Fig. 20. Linear regressions of fork length on scale age for northern pike, Wupaw Bay, 1981-88.

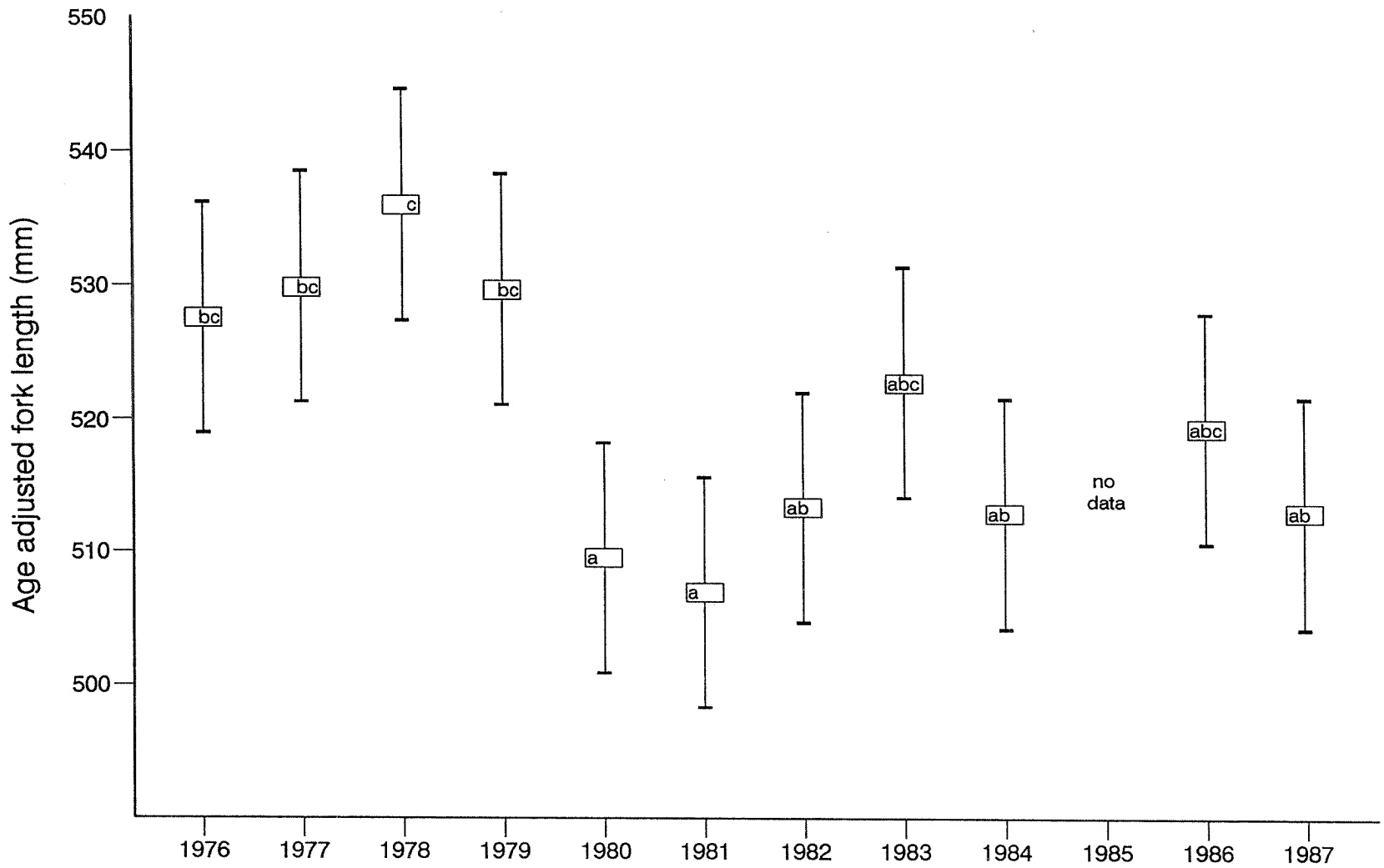


Fig. 21. Least significant difference plot for age adjusted fork lengths, 1976-87. Means were adjusted by analysis of covariance. Means with any letter in common are not significantly different($\alpha = 0.05$). Bars are 95% confidence intervals for the LSD test.

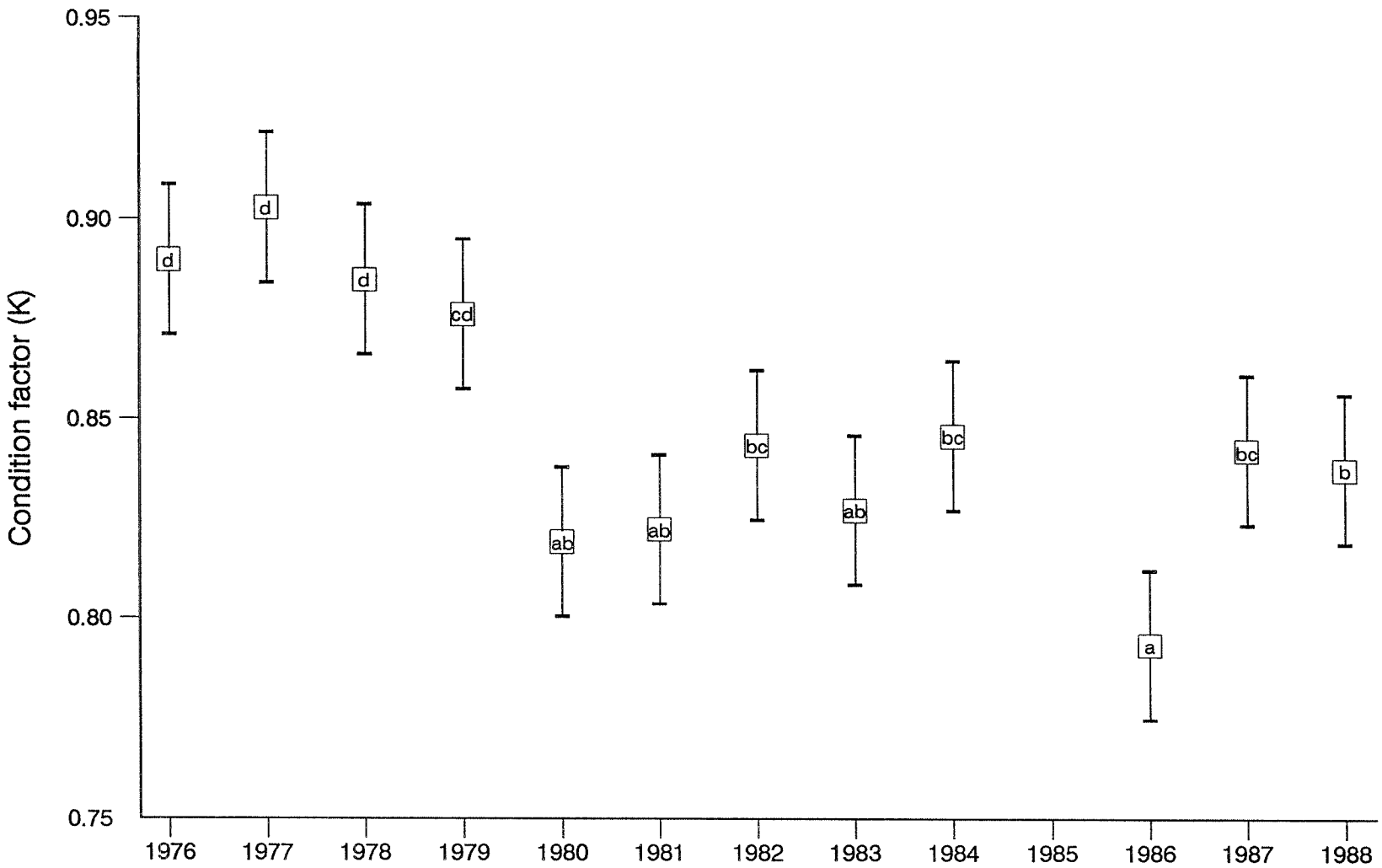


Fig. 22. Least significant difference plot of condition factor (K) of northern pike caught in gill nets in Wupaw Bay, 1976-88. Means with any letter in common are not significantly different (α=0.05). Bars are 95% confidence intervals for the LSD test.

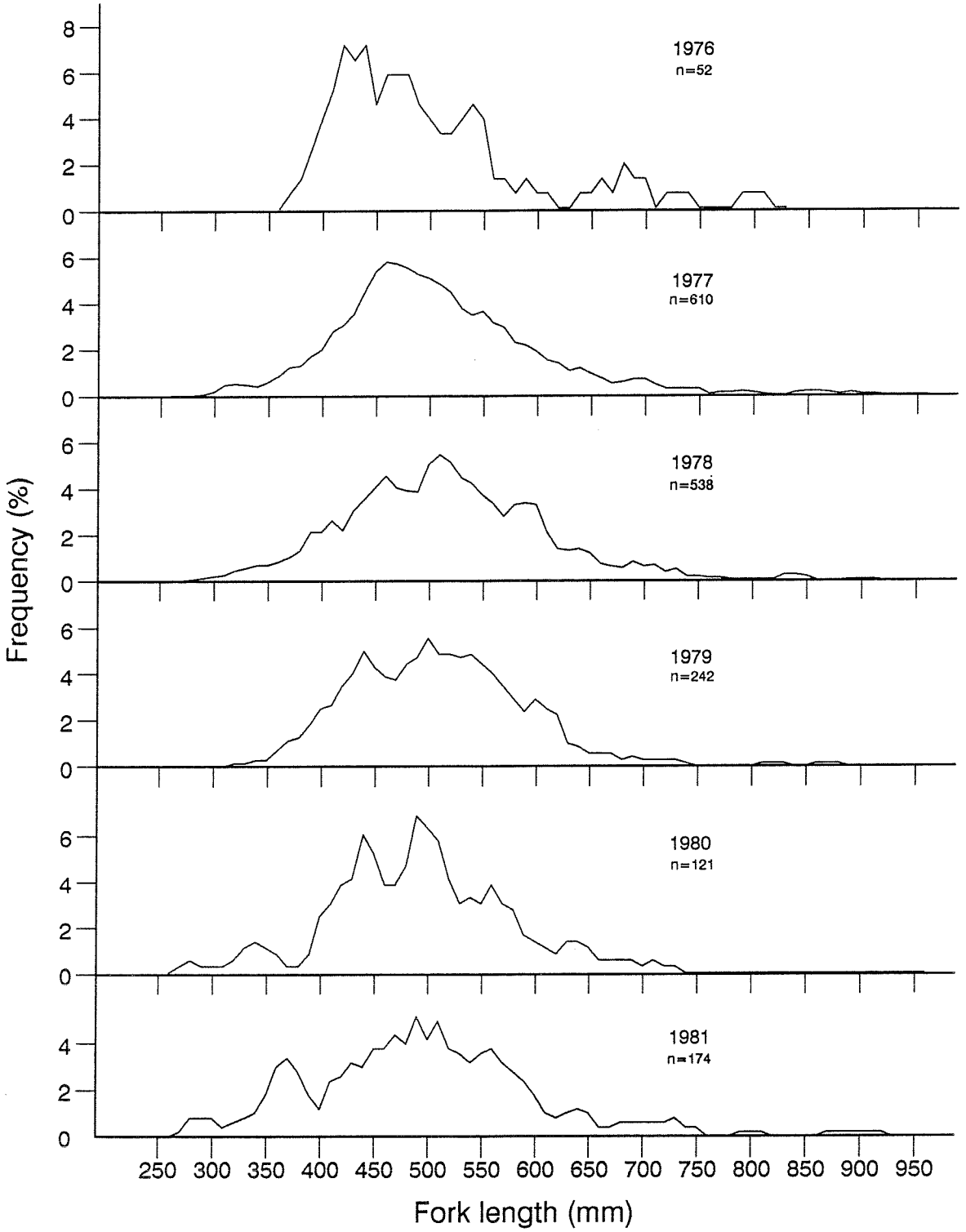


Fig. 23. Length-frequency plots for northern pike caught in gill nets in Wupaw Bay, 1976-88 (Adapted from Bodaly and Lesack 1984).

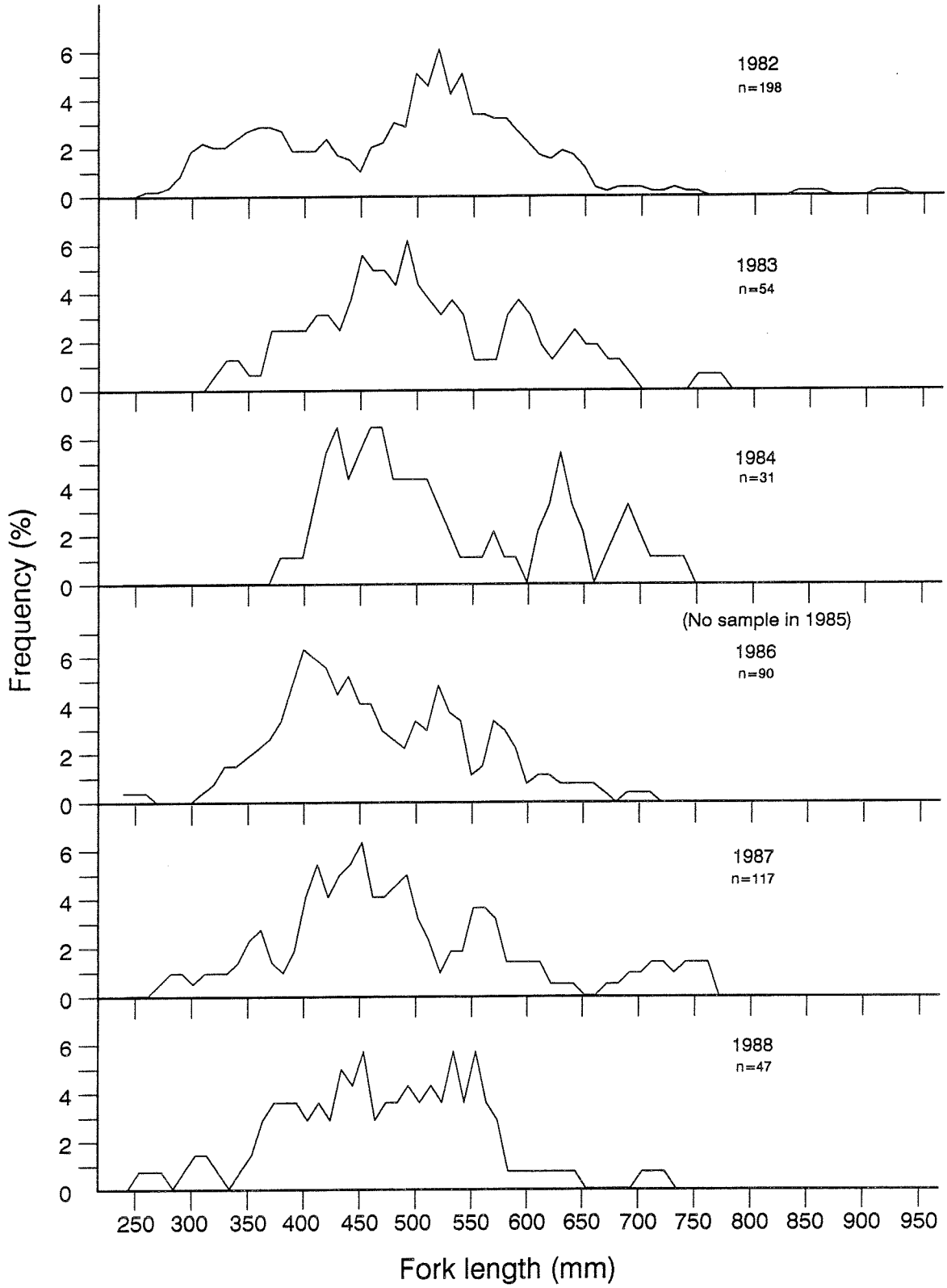


Fig. 23 (concluded).

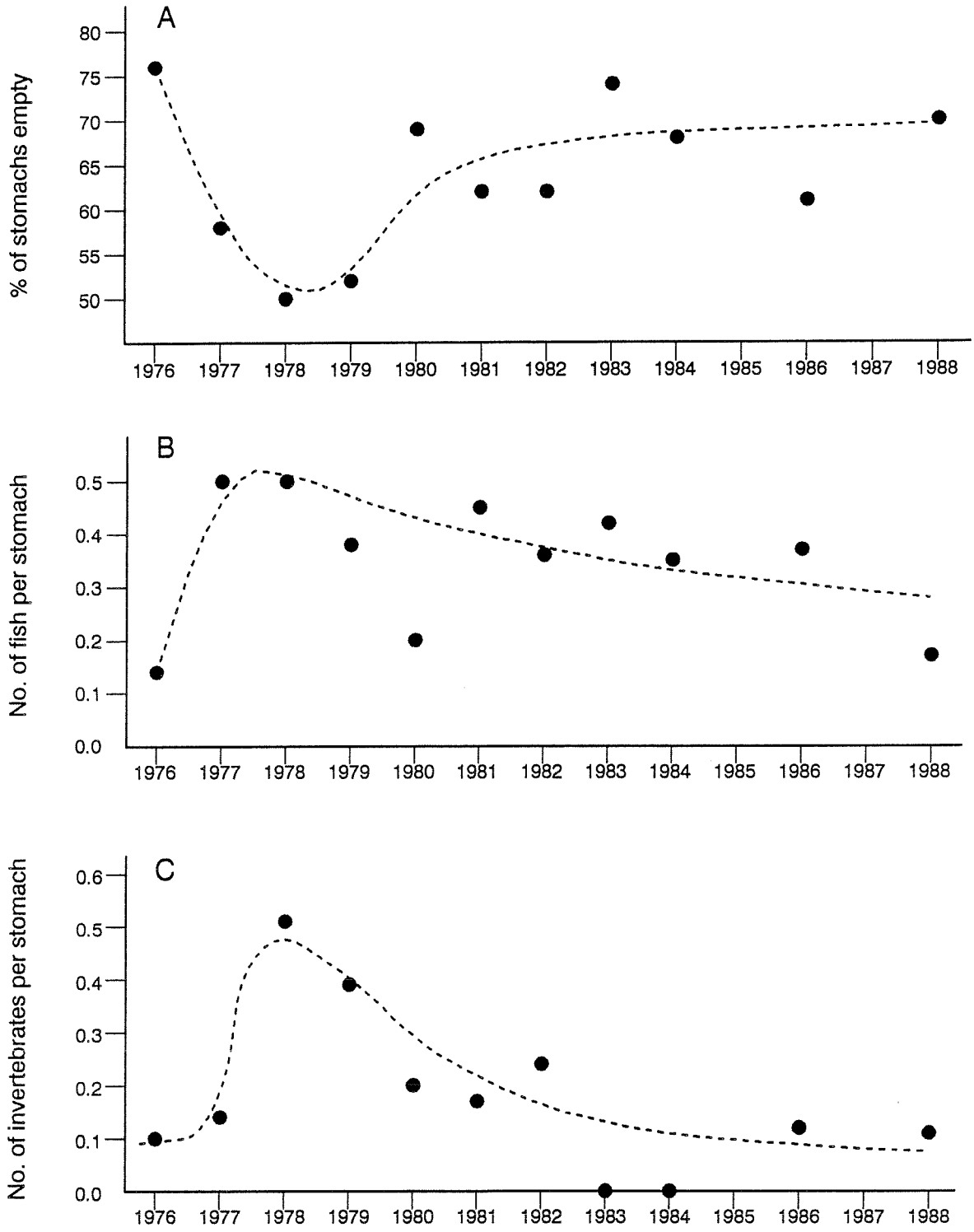


Fig. 24. Trends in northern pike feeding in Wupaw Bay, 1976-88. Means in B and C represent all stomachs, including empty stomachs. Dashed lines represent the authors' interpretation of trends.

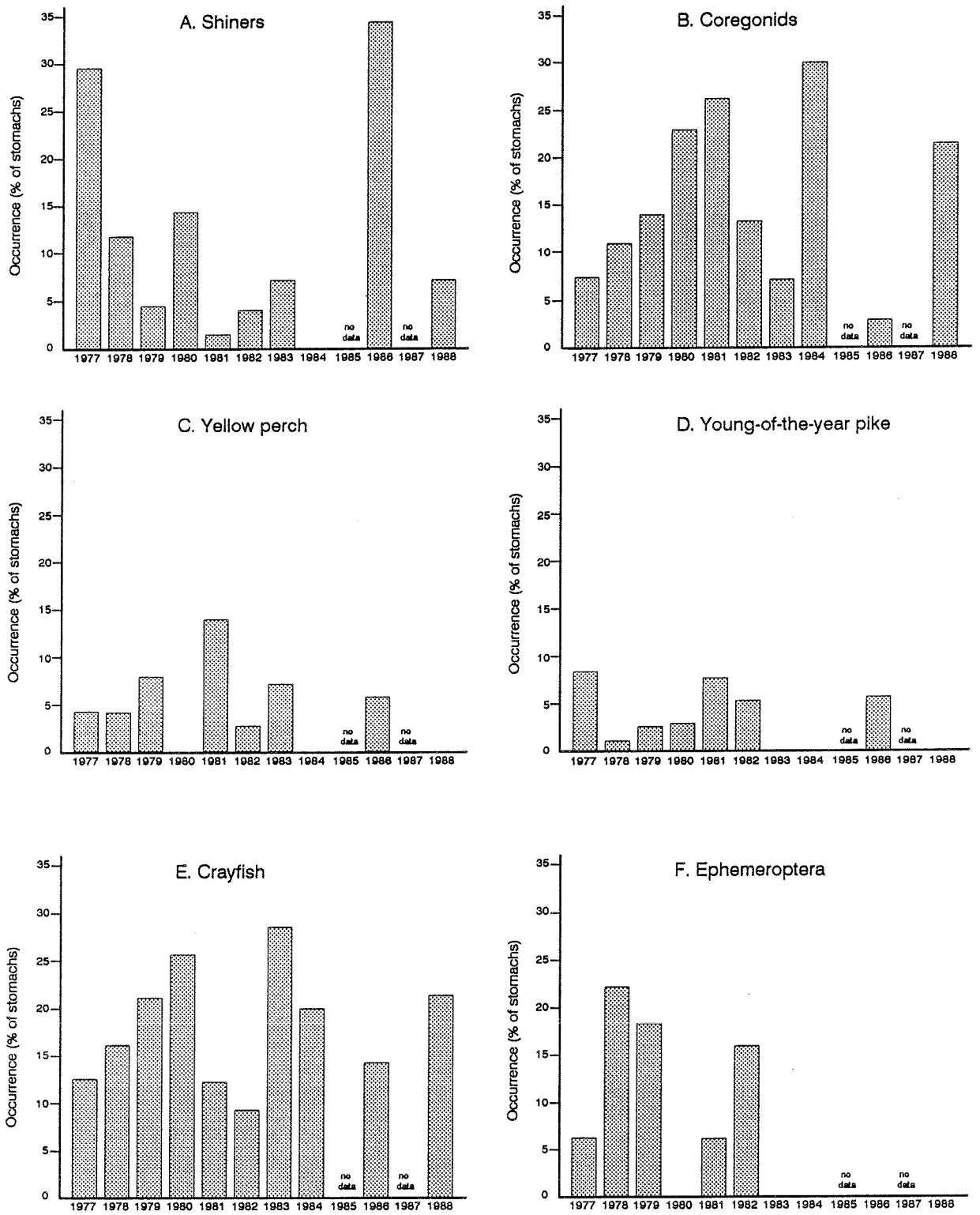


Fig. 25. Percentage occurrence of food items in northern pike stomachs that contained food. Empty stomachs were not included in calculation of means.

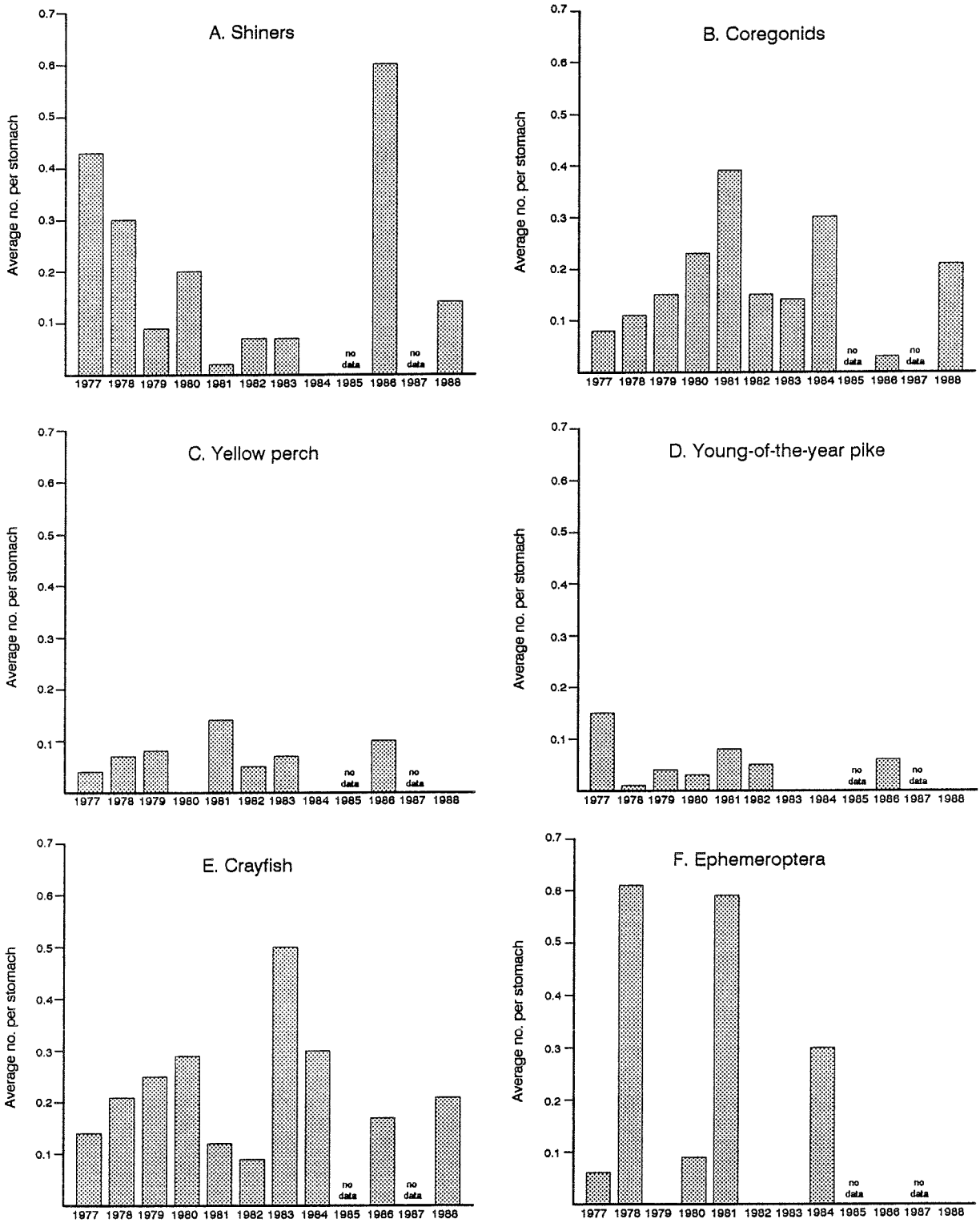


Fig. 26. Average number of food items found in northern pike stomachs that contained food. Empty stomachs were not included in calculation of means.

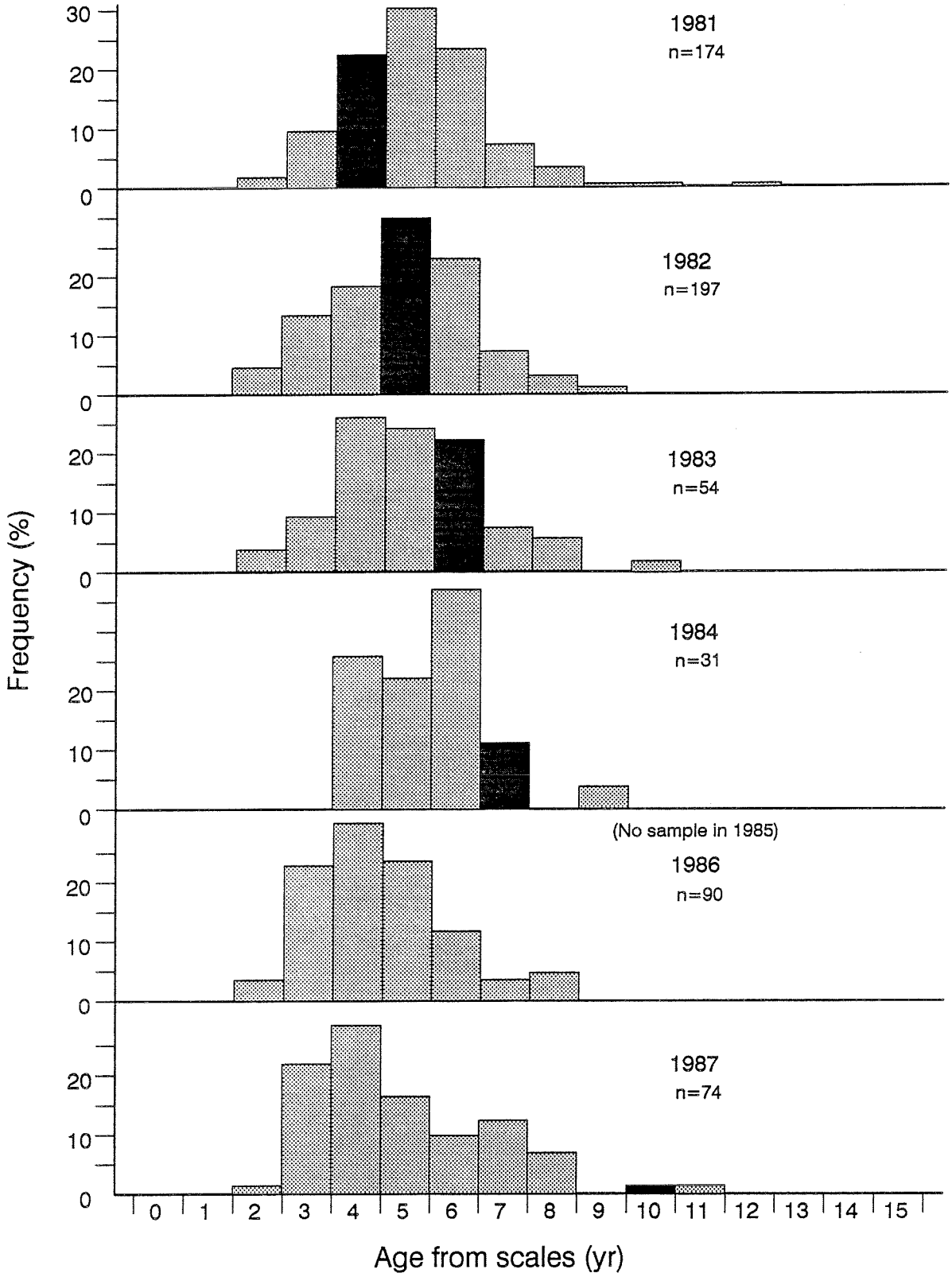


Fig. A1.1. Age frequency plots of Wupaw Bay northern pike, 1981-87. Ages were determined from scales. The 1977 year class is darker toned.

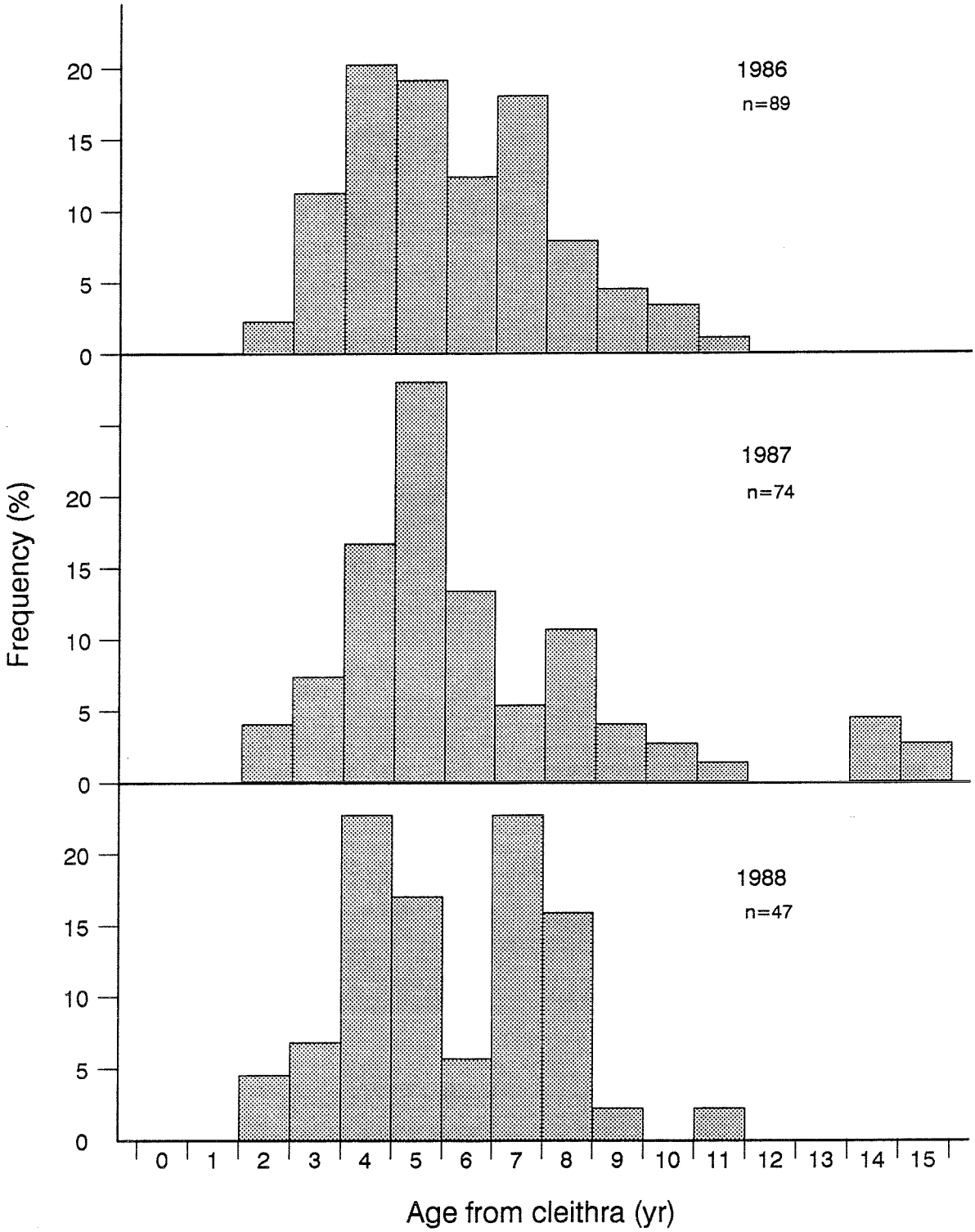


Fig. A1.2. Age frequency plots of Wupaw Bay northern pike, 1986-88. Ages were determined from cleithra.

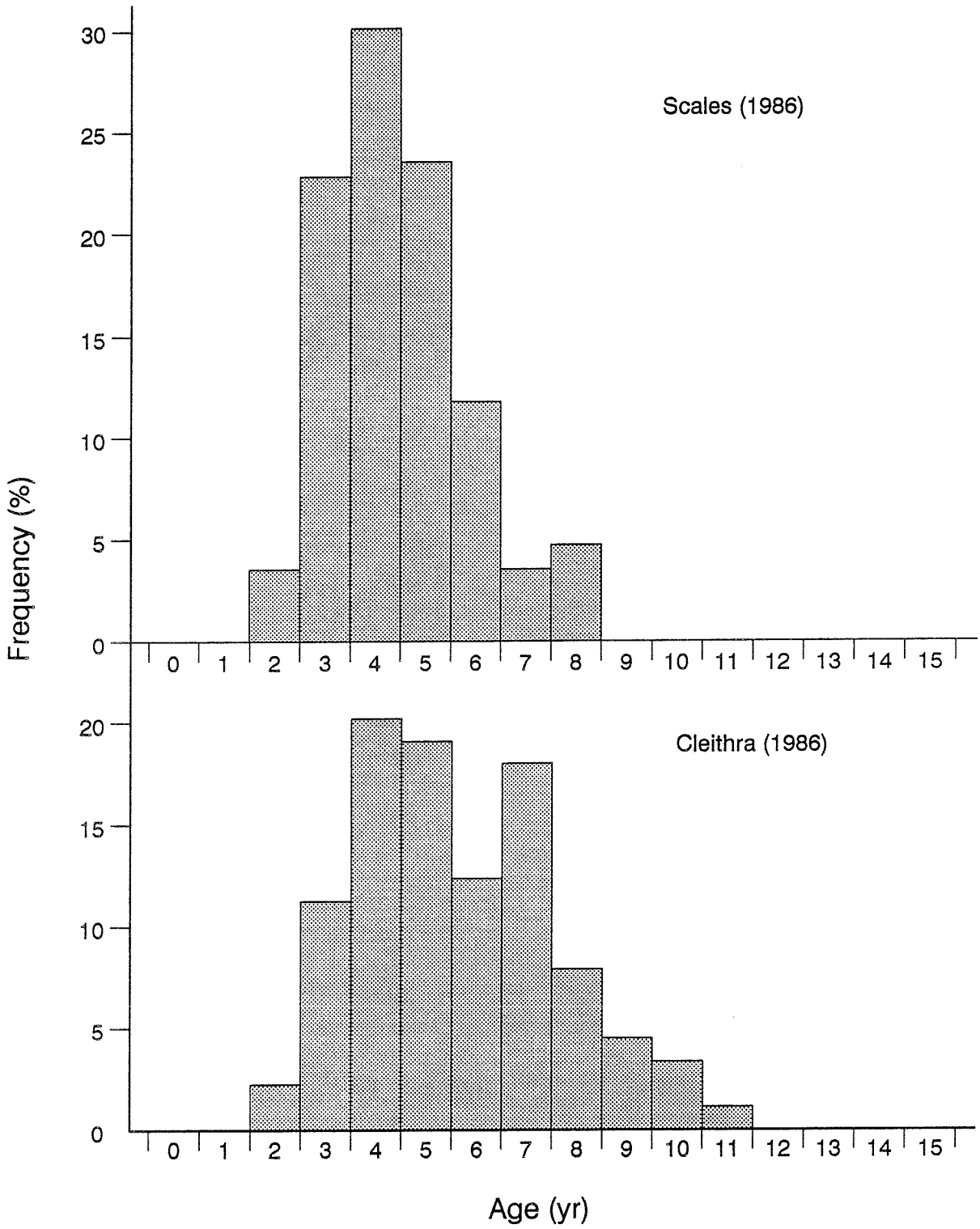


Fig. A1.3. Age frequency of the 1986 Wupaw Bay northern pike sample determined from both scales and cleithra.

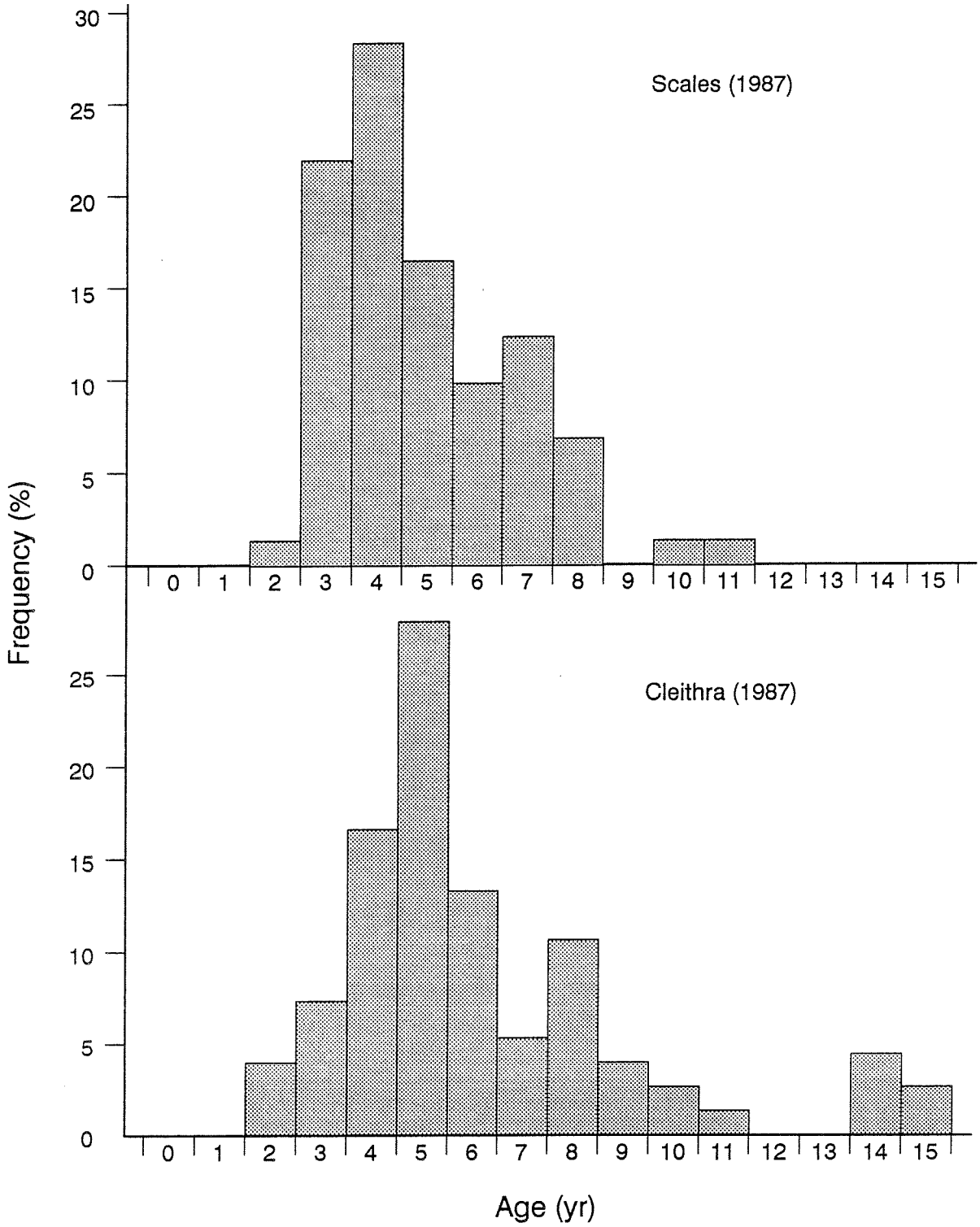


Fig. A1.4. Age frequency of the 1987 Wupaw Bay northern pike sample determined from both scales and cleithra.

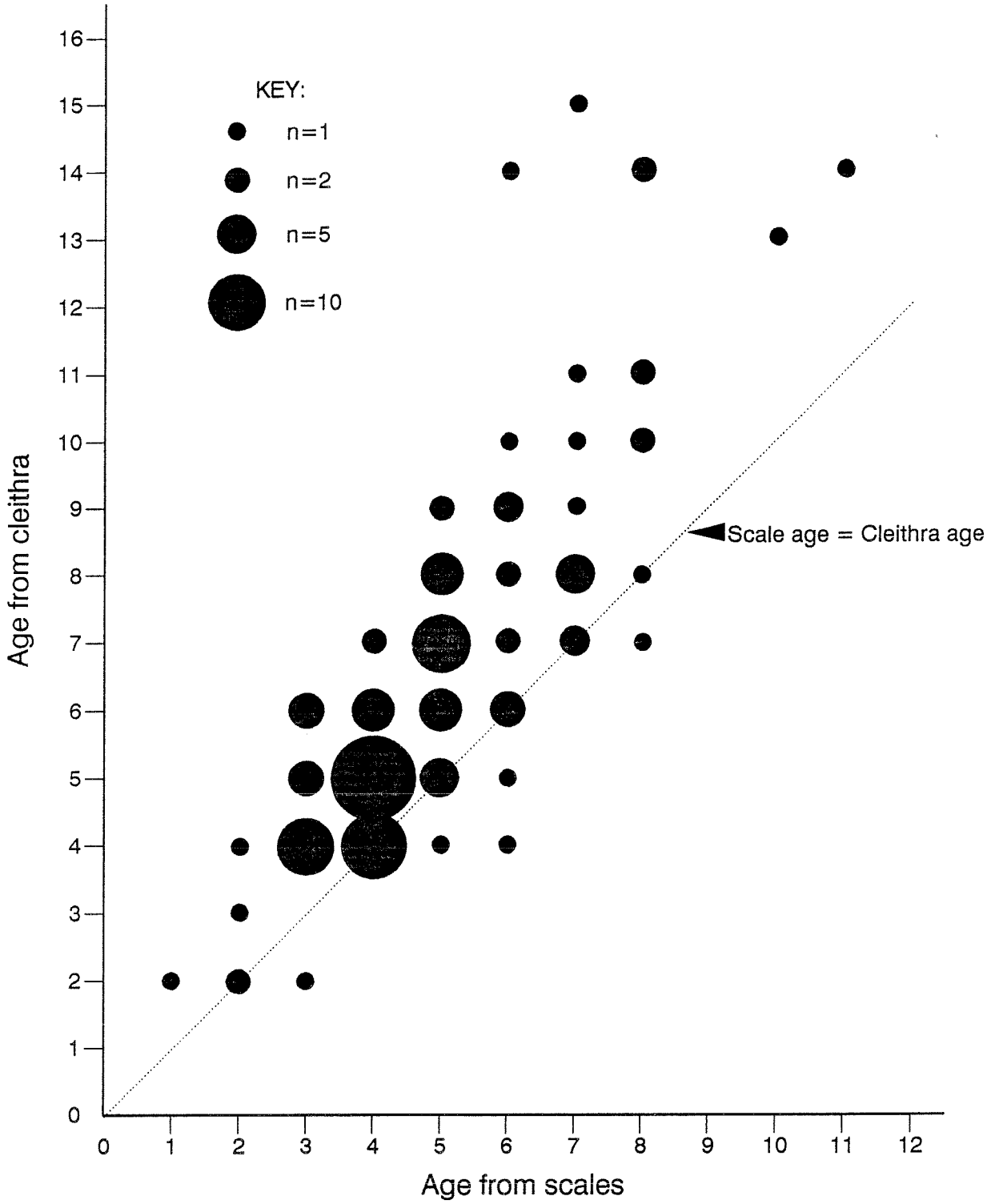


Fig. A1.5. Relationship between age from scales and age from cleithra for northern pike caught in gill nets in Wupaw Bay in 1986 and 1987. The size of data points is proportional to sample size.