

LARVAL AND JUVENILE ECOLOGY OF UPPER KLAMATH LAKE
SUCKERS: 1995-1998

FINAL REPORT

SUBMITTED TO

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SUMMARY

This report covers the time period of OSU/USBR contract 4-FC-20-11810 from 1994 through 1998, with data from 1991-1993 incorporated as needed. Nineteen ninety four was used primarily as a gear evaluation year, but some age 0 monitoring was conducted in summer and fall. We generally regarded our gear evaluation efforts as unsuccessful as age 0 suckers were scarce in 1994, and factors such as algae blooms clogging our nets made reasonable data interpretation nearly impossible. Gear evaluation did reveal that a larval fish trawl was an effective sampler of larval suckers and we subsequently incorporated this gear into our sampling program. Important points in this report:

- < Numbers of age 0 suckers in late summer/ fall have fluctuated over the period, 1995-1998. Numbers were relatively high in 1995 and 1996, but generally much lower in 1997 and 1998. Although data collection from 1991-1994 was not as intensive or comparable to 1995-1999, age 0 sucker numbers appeared relatively high in 1991 and 1993, but low in 1992 and 1994.
- < Median growth rates of juvenile suckers from 1991-1997 shifted from relatively high (>0.5 mm/day) prior to 1995 to relatively low (<0.5mm/day) from 1995-1997. The 1995 year class experienced the lowest median growth rate (0.43 mm /day).
- < The median hatchdate of juvenile survivors over the 1991-1997 period was May 21 (day 142) but annual differences exceeded one month. Median hatchdate was much earlier in 1995 (day 122, May 1) while it was much later in 1991 (day 154, June 1), 1993 (day 155, June 2), and 1996 (day 157, June 3). Median hatchdate patterns were similar between species but the range of hatchdates for Lost River suckers was usually greater.
- < Differences in hatchdates and growth rates between individuals resulted in fish reaching different sizes in September ranging from about 40 mm to over 100 mm. A year class's "strength" may be dependent on both its absolute size and the size of its individuals.
- < Patterns of sucker abundance in standardized surveys from 1995-1998 were mirrored in the near shore fish community as a whole with overall fish abundance and diversity higher in 1995-96 than 1997-98.
- < Patterns of sucker and other fish distributions in stratified random cast net surveys seem to reflect substrate

preference rather than water quality preferences. Most fish appear to be less densely distributed over fines and sand than larger substrates with suckers reaching highest densities on gravel and small mixed substrates. Water quality tended to be better over fines (lower pH) and sand (higher dissolved oxygen) and exotics were more often dominant on these substrates. Juvenile sucker distributions may reflect either avoidance of predators, parasites, or competitors on substrates with better water quality, or selection of preferred substrates.

- < Relationships between environmental variables of 23,767 daily growth increments of the 1994- and 1995-year classes showed positive relationships with temperature and pH and negative relationships with dissolved oxygen. Lake level was positively associated with growth increments early in the summer but negatively associated later in the year. The counter-intuitive relationships with dissolved oxygen (negative) and pH (positive) are consistent with distributional data showing that young suckers select substrates that are not associated with better water quality. The negative relationship with lake level later in the season coincides with periods when lake level is decreasing smoothly, suggesting the possibility of confounding with some other time-varying factor.
- < Lake-wide high ammonia concentrations in 1997 apparently had no negative sub-lethal growth effect. Fish collected from one of the most heavily impacted areas, Wocus Bay, did show an unexpected uncoupling of growth and temperature but a multiple regression analysis showed no effect of ammonia concentrations on growth ($p=0.5578$).

SECTION 1--Age 0 sucker year class assessment

INTRODUCTION AND OVERVIEW

The Klamath Basin's endangered suckers, *Chasmistes brevirostris* Cope, 1879 (shortnose sucker, SNS), and *Deltistes luxatus* (Cope, 1879) (Lost River sucker, LRS) were listed based, in part, on the perception that recruitment had failed for many years. Our fall cast net surveys supported the notion that recruitment failure was an important problem and indicated that the number of survivors in a year class can differ greatly. Because recruitment failure or variation in fishes can be caused by very small changes in mortality rates, growth rates, or stage durations in the early part of life (Houde 1987), we have expended our efforts on the first year of life of Upper Klamath Lake suckers.

Our survey methods and sampling designs evolved substantially from our initial work in 1991. Our initial year on Upper Klamath Lake, 1991, was spent sampling with beach seines, cast nets, and otter trawls throughout summer and early fall with an emphasis on testing the efficacy of these gears on age 0 suckers and developing a fixed site sampling strategy for future years. All three gears proved useful for sucker sampling, but only cast net sampling was conducted in 1992. No age 0 suckers were caught in late summer/fall cast net surveys in 1992, probably reflecting poor year class establishment. Although 1992 was probably a poor year class, as canal salvage data for that year corroborated our data, we realized the importance of sampling over the course of the growing season to pinpoint the timing of mortality events, if any. In 1993 we resumed summer beach seine and fall otter trawl sampling in addition to cast net sampling. Otter trawl catches were low in 1993, despite good catches with beach seines and cast nets, prompting us to switch to a larger trawl with a small mesh liner in 1994. An attempt at a comprehensive evaluation of our gears, plus a new larval fish trawl, was emphasized in 1994. This precluded year class monitoring, unfortunately, in another year when fall catches were very low and indicative of a poor year class. Gear evaluation did suggest there were fair numbers of young suckers in the lake up through July (at least near the Williamson River and in Goose Bay) but this sampling could not be logically compared to routine year class monitoring. Thus we did not make any conclusions on early season abundance in 1994. Late season abundance was low in both beach seine and cast net surveys, but higher in otter trawl surveys. Because of generally low numbers of suckers, and algae fouling our nets, gear evaluation was regarded as a failure. However, a larval fish trawl we tested did prove effective. Beginning in 1995 we made some major changes to our sampling design. We incorporated the larval fish trawl into

our suite of routine sampling gears and used it at our fixed site beach seine for five surveys sites prior to beach seining. Larval sampling was always initiated in early April prior to larval sucker emigration out the Williamson River. After larval sampling we then switched to beach seining as the fish grew larger. We also converted our fixed site cast net sampling to a habitat-based (substrate) stratified random design, and converted our otter trawl sampling to a random design. Final adjustments to our design were completed in 1996. We added spring random otter trawl sampling to catch age 1 suckers to evaluate overwinter survival. We extended larval sampling while at the same time began beach seining sampling earlier so the two gears overlap. This ensured we would remain effective on multiple cohorts and not miss them if they quickly grew beyond the selectivity of one gear. Our sampling strategy for 1996-1998 was as follows: larval surveys in early April, late April/early May, late May, mid June, late June/early July, and late July; beach seine surveys in mid June, late June/early July, late July, and mid August; stratified random cast net surveys in late August, mid September, and early October; and random otter trawl surveys in early April, late April/early May, late August, mid September, and early October. The only change during this time was the dropping of an early September beach seine survey in 1997 and replacing it with the late August otter trawl survey. We anticipate maintaining this design in future years.

METHODS

Larval sampling

After evaluating the effectiveness of a larval trawl in 1994, we implemented it into our sampling regime beginning in 1995. Each year, except 1995, larval trawl sampling began in the first full week of April and continued through late July, with samples collected every third week for a total of 6 sampling surveys. In 1995, 6 larval trawl surveys were completed, but sampling was more frequent with some surveys being every other week, and sampling ended in late June. The larval trawl has a 0.8 x 1.5 m opening with a 2.5 m Nitex net of 1000 micron bar mesh and is mounted on an aluminum frame with runners, similar to that described by LaBolle et al. (1985). Two samples were collected from each of ten fixed sites in Upper Klamath Lake and five fixed sites in Agency Lake (Figure 1.1). The larval trawl was set 1-14 m (avg. 6 m) offshore in water one meter deep and pulled to shore with ropes. If vegetated and nonvegetated habitats were available at a site, one sample was collected from each. Because of disturbance to

the area when setting the trawls, they were allowed to soak for a minimum of 10-15 minutes before being pulled to shore.

Juvenile sampling

Beach seine

Beach seine sampling was initiated in 1991 at ten fixed sites in Upper Klamath Lake and five fixed sites in Agency Lake (Figure 1.1) and was sporadic from 1991-1995. The 1991 sampling was initiated in late July and continued through early October, with the goal of evaluating the effectiveness of beach seine sampling and to collect specimens for taxonomic purposes. There was no beach seine sampling in 1992, a June and July survey in 1993, and an August survey in 1994. In 1995, three surveys were conducted every other week from mid July to mid August. In 1996, five surveys were conducted every third week from mid June through early September. In 1997 and 1998 four surveys were conducted every third week from mid June through mid August. From 1996 to 1998, the first three beach seine surveys were concurrent with the last three larval trawl surveys. Each sample was collected with one person remaining on shore and the other walking perpendicular into the water while unrolling the seine until the end of the seine was reached. The offshore person then pulled the net to shore in a ¼-circle arc with the shoreline person remaining stationary. Samples were normally collected from waters less than 1.5 m deep and over unvegetated or sparsely vegetated shorelines. Two samples were collected at each site. The beach seine was 6.1 m long with a 2x2x2 m bag, and 4.8 mm bar mesh.

Cast net

Cast net sampling began as a trial effort in summer 1991 to determine the effectiveness of this gear on young suckers. As we observed sucker catches decline in our beach seine samples, they were subsequently collected in cast net samples. We sampled the ten fixed sites in Upper Klamath Lake on a sporadic basis in 1991 from July to October. From 1992 to 1995 fixed site cast net surveys were conducted from late summer to early fall in Upper Klamath Lake (Figure 1.2). A March cast net survey was conducted in 1992, but no suckers and few other fish were captured and we dropped spring cast netting from further consideration. From our cast net sampling in 1991 and

1993, we observed that age 0 suckers in late summer and early fall were more abundant on small-particle rocky substrates such as gravel and cobble. In fall 1994, low lake levels allowed us to walk the perimeter of Upper Klamath Lake and, using a hand-held GPS unit, construct a linear map of the shoreline substrates. We reduced these data into eight substrate categories (Table 1.1), and established a stratified random sampling protocol to replace fixed site cast net sampling. Two stratified random cast net surveys were conducted late summer (September) and early fall (October) of 1995 and three surveys were conducted in 1996, 1997, and 1998: late August, mid September, and early October. The cast net used from 1991-1993 was a 5-m diameter monofilament net with 9.5-mm bar mesh, and the cast net used from 1994-1998 was a 5-m-diameter multifilament net with 6.3-mm bar mesh. Cast net samples were taken from the nearshore areas of the lake, within 10 m of the shoreline. Typical sampling depths were 0.5-1.0 m, and rarely exceeded 1.5 m.

Otter trawl

Late summer/fall

Otter trawl sampling began in 1991 as a means of assessing abundance and distribution of age 0 suckers in offshore regions of Upper Klamath Lake. Sampling in 1991 was sporadic and inconsistent as we were testing the effectiveness of this gear. Six fixed stations were established and used for surveys in October 1993 and 1994 (Figure 1.3). Starting in 1995 otter trawl sampling was randomized. Trawl locations and direction were randomly selected from a grid of coordinates at 1-km intervals covering Upper Klamath Lake. No site began within one km of the shoreline, and direction of the tow was changed in the field if the selected direction was not possible (e.g., running into water too deep or shallow to effectively trawl, or strong winds necessitating direction change). Random otter trawl surveys were conducted in early and mid October 1995, in September and October in 1996, and in August, September, and October in 1997 and 1998. Each survey consisted of 15 tows, each tow lasted 20 minutes, and exact distance of each tow was calculated using differentially corrected GPS data. In 1991 and 1993 a 3-m semi-balloon otter trawl with 13-mm bar mesh was used. From 1994-1998 a 5-m semi-balloon otter trawl with 16-mm bar mesh and a 6-mm bar mesh liner was used.

Spring

Randomized otter trawl sampling was conducted in early April and late April/early May 1996-1998 using a 5-m semi-balloon otter trawl with 16-mm bar mesh and a 6-mm bar mesh liner. Sampling was conducted in the exact same manner as the fall randomized sampling.

Diversity and species dominance

Simple fish community attributes were estimated for fixed beach seine, stratified random cast net, and random trawl surveys. Diversity estimates were number of fish per sample, number of species per sample, number of exotic species per sample, and number of zero catches. Community dominance was based on species rank per sample and expressed as the percent of all samples in which the species ranked first in abundance. Percent of positive catches of age 0 suckers was also calculated. For stratified random cast net surveys these analyses were broken down by substrate type.

Population estimates

The typical beach profile of Upper Klamath Lake is such that shoreline substrates extend outward a short distance and then become fines. We assumed 10 m as the width of the band of shoreline substrates for estimating the total area of each substrate category. Field observations suggest this is a reasonable assumption, but we recognize there are many areas where this distance is greater or smaller. The appropriate estimate of the mean number of suckers per cast for stratified random sampling was calculated using the formula:

$$\bar{y}_{st} = \left(\sum_{h=1}^L N_h \bar{y} \right) / N$$

where:

L = number of strata (8 here)

N = total number of units available for sampling (2595 here)

N_h = number of units in each stratum (h) available for sampling

n_h = number of units sampled in stratum h

y_{hi} = value obtained (number of fish) for the i^{th} unit in stratum h

and,

$$\bar{y}_h = \text{mean of the } n_h \text{ values in stratum } h = \left(\sum_{i=1}^{n_h} y_{hi} \right) / n_h$$

Density per square meter was calculated by dividing mean number per cast by 5 m² (the area sampled by the cast net). Shoreline abundance was then calculated by multiplying the resulting density by the total shoreline area. Confidence intervals for the population estimates were calculated using a bias corrected bootstrap resampling procedure, adjusting for the fact that the true mean is not the median of the distribution of bootstrap estimates (Manly 1997). Offshore abundance was estimated by expanding estimated densities from otter trawl sampling to total area of the lake, less the 10 m shorelines area, using 61,543 acres (249,058,366.7 m²) from Johnson et al. (1985) as the surface area of Upper Klamath Lake. Total population of age 0 suckers by survey was estimated by summing shoreline and offshore population estimates. Although our sampling design and population estimation techniques are valid, our estimates of abundance remain arbitrary since we only assumed a 10 meter wide band of shoreline substrates around the lake. Only by knowing the exact area of the shoreline substrates would we have a reliable estimate of population size.

RESULTS AND DISCUSSION

Larval sampling

Mean larval trawl catch rates of sucker larvae peaked in the mid-1990s, but decline subsequently (Figure 1.4). Catch rates in Upper Klamath and Agency lakes in 1998 were the lowest since the initiation of larval sampling in 1995. Although the catch rates in 1997 appeared similar to 1995 and 1996, this was heavily influenced by 2 large catches in Goose Bay that year in June (series 10, Figure 1.5). Without that influence, catches in 1997 were flat and very low, similar to 1998 (Figure 1.5). The proportion of positive catches (catches of >0 sucker larvae) were higher in 1995 (51%) and 1996 (53%) than in 1997 (44%) or 1998 (36%) (Table 1.2). Proportion of large catches (>100) were more common in 1995 (3.4%) and 1996 (7.1%) than in 1997 (1.7%) and 1998 (0%) (Table 1.2, Figure 1.6). Catches were generally highest near the mouth of the Williamson River (U6) and Goose Bay (U5) (Figures 1.7-1.10) in most years.

Other areas of high or moderate densities included sites near Hagelstein Park (U2), Wocus Bay (U9), and the two sites in the south end of Upper Klamath Lake (Cove Point (U1) and Stone House Ranch (U10)). Overall, densities were lowest lakewide in 1997 and 1998. Catches in Agency Lake were highest along the eastern shore and the northernmost site near the mouth of the Wood River (A3).

Beach seine

Beach seine catch rates in Upper Klamath Lake generally increased in the early 1990s and declined in the late 1990s, with the exception of the drought year of 1994 (Figure 1.4). In the other drought year, 1992, there was no beach seine sampling. Catch rates were lowest in 1991, 1994, and 1998, although sampling was not initiated in 1991 until the end of July (Figure 1.11), and may have missed the period when suckers were most vulnerable. Catch rates were highest in 1995 and 1996, in Upper Klamath Lake, but highest in 1993 in Agency Lake. From 1995-1998, the proportion of positive catches in July and August was higher in 1995 (52%) and 1996 (62%) than in 1997 (34%) or 1998 (32%) (Table 1.3). The proportion of large catches of suckers (>25 in a sample) was much greater in 1995 (20%) and 1996 (35%) than in 1997 (10%) or 1998 (8%) (Table 1.3, Figure 1.12). Catches were generally highest in Goose Bay (U5), which ranked #1 or #2 in mean catch rate in every year except 1993, when catches were highest at the Hagelstein Park site (U2). The Modoc Point boat launch site (U4) generally had high densities of suckers, and sites in Wocus Bay (U9) and near Stone House Ranch (U10) had high densities in some years (Figures 1.13-1.17). Similar to larval trawl samples, densities were lowest lakewide in 1997 and 1998. Catches in Agency Lake were highest along the eastern shore. Beach seine and larval trawl catch rates were moderately correlated ($r=0.80$).

Blue chub or fathead minnow usually dominated beach seine samples (Table 1.4) and dominance was often asynchronous between Upper Klamath Lake and Agency Lake. Over the 1995-98 period, blue chub were first in abundance in 53.9% of Upper Klamath Lake samples and fathead minnow were first in abundance in 50.0% of Agency lake samples. Fathead minnow dominance was lowest in 1995 in both Upper Klamath and Agency lakes, and Simon and Markle (1997) showed a general decline in fathead minnow abundance from 1991-1995. Since fathead minnow spawns upside down on the underside of habitat structures (Scott and Crossman 1973) and has a protracted spawning season as late as August (Scott and Crossman 1973), reduced shoreline habitat complexity during the

drought years of 1992 and 1994 might have reduced recruitment of this nonnative species. During 1996, age 0 suckers were the third most dominant taxon in both lakes. Over the 1995-98 period, positive catches of suckers and number of species per seine both declined. Samples from 1995-96 averaged over 50% positive catches of suckers and over 2.9 species per seine while samples from 1997-98 averaged less than 30% positive catches of suckers and 2.2 species per seine (Table 1.4).

Cast net

Fixed site cast net sampling showed age 0 suckers were more abundant in 1991, 1993, and 1995, but were considerably less abundant in 1994 and absent in 1992 (Figures 1.18, 1.19). Fixed site cast net samples could not be correlated with larval abundance because larval sampling was not initiated until 1995, but beach seine catch rates were moderately correlated with fixed cast net catch rates ($r=0.55$). August shoreline population estimates for age 0 SNS from stratified-random cast net sampling were highest in 1996 and 1998, intermediate in 1995, and low in 1997 (Figure 1.20). August shoreline population estimates for age 0 LRS were highest in 1998 and low in all other years (Figure 1.20). In 1998, however, a single large catch of suckers (1,168) extraordinarily skewed these data: this single catch was 15 times greater than the next highest catch (80) in any year. If considered an outlier and omitted from analysis, the shoreline estimates for August 1998 were similar to August 1997 (Figure 1.21). Thus, stratified-random catches would have peaked in 1996 and trended downward since, mirroring trends observed with larval trawl and beach seine catch rates. There was a higher percentage of zero catches of suckers in 1997 and 1998 than in 1995 or 1996 (Table 1.5), and a lower percentage of large catches (>5) in 1997 (0.1%) and 1998 (1.4%) than in 1995 (2.1%) and 1996 (3.3%). Patchy distribution of suckers resulted in wide confidence intervals about each estimate (Table 1.6) and thus poor precision. The effect on accuracy is unknown. Catch per unit effort was much higher on gravel and smallmix than other substrates (Table 1.7).

Low lake levels in 1992 and 1994 might have affected sucker catch rates if typical shoreline substrates were either left dry or reduced. Our data show that typical shoreline substrates were inundated at most sites at low lake levels during these years, but most certainly the area under water was less than years when lake levels were higher. This might affect sucker catch rates by either driving suckers offshore and thus not vulnerable to cast net sampling,

or concentrating suckers on the remaining shoreline substrates.

Blue chub and tui chub in 1995-96 and blue chub and fathead minnow in 1997-98 (Table 1.8) dominated stratified random cast net samples. Positive catches of shortnose suckers declined from about 10% of samples in 1995-96 to about 6.2% in 1997-98 and Lost River suckers showed a similar but smaller decline (Table 1.8). The number of fish per sample, number of exotics per sample and number of zero catches of fish all increased from 1995-96 to 1997-98.

Several physical and biological variables appeared related to substrate type. The eight substrates targeted tended to have similar temperatures and, with the exception of the intermediate mixed substrate, similar conductivity (Figure 1.22). Dissolved oxygen tended to be higher over sand and cobble substrates and pH tended to be lower over fine substrates (Figure 1.22). The total number of species and the total number of individuals caught per cast net tended to increase with substrate particle size (Figure 1.23) while the proportion of exotics and proportion of zero catches tended to decrease with substrate particle size (Figure 1.23). Substrates preferred by age 0 suckers, gravel and smallmix (Table 1.7) are not noteworthy for water quality or fish community parameters.

Otter trawl

fall

Because suckers in the offshore regions of Upper Klamath Lake appear randomly distributed (see below), we can make interannual comparisons of otter trawl catches from fixed site and random sampling by using mean catch per tow. Otter trawl catches were highest in the early 1990s, but have declined substantially in the late 1990s (Figure 1.24). Catch rates for age 0 LRS were over 1/tow in 1991, 1994, and 1995, but have never been over 0.20/tow since. Trends were similar for age 0 SNS, but SNS appear much less abundant offshore in most years. Although LRS otter trawl catches were high in 1994, the near-absence of suckers along the shoreline indicate this was probably a poor year class.

Offshore population estimates for age 0 LRS in late summer/early fall as calculated from random sampling were highest in 1995 at 35,155 suckers (Table 1.6, Figure 1.25). The highest estimate for age 0 SNS was 16,170 in 1996 (Table 1.6, Figure 1.25). Estimates in 1997 and 1998 were much lower. We have been concerned about the efficacy of

this gear because of the generally low catch rates, but sampling in August of 1999 captured 168 age 0 suckers in 15 samples, suggesting that numbers of suckers were high in 1999 and that the otter trawl is likely an effective sampler. There were no evident trends of trawl catches increasing over the sampling period (Figures 1.26, 1.27).

Blue chub and Klamath Lake sculpin (Table 1.9) dominated fall trawl samples. The proportion of positive catches of young of year shortnose sucker was high (>20%) in 1995-96 and of Lost River suckers was high (>40%) in 1994-95 (Table 1.9). Overall fish catch rates per trawl plummeted by more than 50% from 1994-96 to 1997-98 (Table 1.9).

spring

Spring catch rates of age 0 suckers were always less than those of the previous fall (Figure 1.28), ranging from a high of 0.10/ tow in the spring of 1996 to zero in 1998 and 1999. Spring catches showed decreasing trends throughout the late 1990s similar to fall catches. Spring catch rates were an order of magnitude less in the springs of 1996 and 1997 compared to their respective fall catch rates, suggesting substantial reductions in the number of age 0 suckers surviving overwinter. However, this speculation is based on small numbers of age 0 suckers caught in the spring—only 4 were caught in 120 tows from 1996-1999.

Blue chub and Klamath Lake sculpin (Table 1.10) also dominated spring trawl samples. The proportion of positive catches of young of year suckers was always low (Table 1.10). Overall fish catch rates per trawl were an order of magnitude lower than the previous fall while the number of species and number of exotics per trawl were similar between seasons (Tables 1.9 and 1.10).

Whole lake population estimates

Lakewide estimates of age 0 sucker abundance were estimated for each August, September, and October sample period by summing abundance estimates from stratified random cast netting and random trawling. The largest estimate of age 0 suckers (both species) was in August 1998 at 665,421 (Table 1.6, Figure 1.29), although this estimate might be overestimated by the influence, as mentioned above, of a single, large outlier. Omitting this catch from analysis resulted in an estimate of 105,174 and is more consistent with low larval fish trawl and beach seine

abundance during the year. After this consideration, population estimates were highest in 1995 and 1996, and lowest in 1997 and 1998, consistent with downward trends in larval trawl and beach seine CPUE in these latter two years. These apparent downward trends in age 0 sucker abundance from 1995 and 1996 to 1997 and 1998 might be attributed to a lower populations of adult spawners. Successive fish kills during 1995, 1996, and 1997 in Upper Klamath Lake has resulted in a steady decline in adult spawning indices from 1995-1998 (Perkins et al. 1998).

Seasonal trends in abundance

There are marked seasonal trends in abundance of age 0 suckers, some of which are logical interpretations of gear bias, and others that may have more serious long term implications for sucker year class success. Larval fish trawl sampling was initiated each year in the first week of April, when sucker larvae were rare (a single larva was caught in 1995, none in other years). Larval trawl catch rates increased in subsequent surveys as larval suckers entered the lake, and then decreased as suckers became large enough to avoid the gear and mortality reduced their number (Figure 1.5). Similar trends were seen in beach seine sampling, as catches increased when age 0 suckers were large enough to be recruited to the mesh size, and decreased as they grew large enough to avoid the gear and natural mortality reduced the number available. In both cases, age 0 suckers were readily captured with another gear; when larval trawl sucker catches declined, they were readily caught in beach seines, and when beach seine catches declined, they were caught in cast nets.

Temporal trends in fixed site cast net surveys were less clear. For example, catch rates during the sampling period remained fairly stable in 1991, increased in 1993, but declined in 1995 (Figure 1.19). Stratified random cast net survey catches have always been highest in the first survey, followed by sharp declines (Figure 1.20). There was little evidence that suckers moved offshore, as there were no consistent trends of increased trawl catches as shoreline catches declined. For example, in fixed site otter trawling in 1991 and 1994, catches tended to increase over time, particularly for LRS (Figure 1.26, 1.27). From random otter trawl sampling 1995-1998, catches decreased over time in 1995 and 1998, and increased in 1996 (Figure 1.25). However, the two trawl surveys in fall 1996 were concurrent with the last two cast net surveys, in which sucker catches also increased (Figure 1.20, Table 1.6).

The question remains unknown as to why age 0 sucker abundance becomes quite low in September and

October. Fish kills in August and September of 1995-1997 seemed selective for adult fish only, with no evidence of younger fish being affected. Further, catches declined throughout September and October in 1998 (and 1999) when there were no fish kills in Upper Klamath Lake. Thus, it is unlikely that fish kills were the cause of low catches in September and October. Associated with lower catches in September and October are cooling of water temperatures and lowering of lake elevations (Figure 1.30), which might cause fish to move offshore. We hypothesized this in 1991 when otter trawl catches increased in late summer and early fall, and a March 1992 cast net survey revealed few fish along the shoreline. However, trawl data since has not supported this hypothesis, unless offshore age 0 sucker densities are sufficiently low in some years to prevent detection of any offshore movement.

Recent work by Gutermuth et al. (1999) has shown that large numbers of young suckers are lost from Upper Klamath Lake via three canals located at the southern end of the lake: the A-Canal (irrigation canal), and Eastside and Westside hydropower canals alongside the Link River (Gutermuth et al. 1999). In 1997 an estimated 14,419 suckers, about 50% that were age 0, were lost to entrainment via the canals (Gutermuth et al. 1999, B. Gutermuth, pers. comm) from the time we began our cast net surveys in late August through the end of the year. Most of this entrainment was in August and September. If, as their data suggest, about 7,200 age 0 suckers are lost via the canals, that represented about 7% of the drop in our population estimate from August to September 1997. In 1998, an estimated 187,453 suckers were lost via the canals from the time we began our cast net surveys in late August through the end of the year, most of which were in August and September. Nearly all were age 0 (B. Gutermuth, pers. comm.). This represented 30% of the drop in our population estimate from August to September 1998. B. Gutermuth (pers. comm.) has indicated that results of efficiency tests on their netting will probably increase their estimates by up to 30% for the eastside and westside canals. Although these numbers do not entirely account for the drops in our population estimates from August to September/October in 1997 and 1998, they do suggest a substantial portion of age 0 suckers can be lost via canals.

Fall age 0 sucker distributions

Age 0 sucker distribution from fixed site larval trawl and beach seine sampling showed highest densities primarily along the eastern shore of Upper Klamath Lake from the mouth of the Williamson River (U6) to Hagelstein

Park (U2). However age 0 sucker distribution from stratified random cast net and random trawl sampling was markedly different. Stratified random cast net sampling showed three major areas of age 0 sucker concentration in Upper Klamath Lake: the south end of the lake, an area primarily south of Buck Island; the eastern shoreline from Modoc Point to Hagelstein Park; and the Shoalwater Bay/Ball Bay area (Figure 1.31). A fourth minor area of sucker concentration is Wocus Bay. These trends generally held true for each year of stratified random cast net sampling (Figures 1.32-1.35), except that no suckers were caught in the Shoalwater Bay/Ball Bay region in 1997. Of these areas of age 0 sucker concentration, the south end is the largest, both in terms of size and sucker abundance. These factors may partially explain why large numbers of suckers exit the lake in late summer and early fall via irrigation and power canals, also located in this area (Gutermuth et al. 1999, B. Gutermuth, pers. comm). Shoreline distribution did not appear different between age 0 LRS and SNS (Figures 1.36, 1.37). Age 0 sucker distribution from otter trawl sampling in late summer/fall and spring appeared random for both LRS and SNS (Figures 1.38, 1.39). Similar patterns were observed for adult suckers in fall (Figures 1.40, 1.41) and spring (Figures 1.42, 1.43). Insufficient age 0 suckers were caught in spring to determine distribution patterns.

The northern 1/3rd of the shoreline of Upper Klamath Lake appears practically devoid of age 0 suckers in late summer/fall, including the marshy shoreline of the Upper Klamath Lake National Wildlife Refuge. Suckers were not caught along the shorelines of several other marshes, including Squaw Point Marsh, Shoalwater Bay Marsh, and Hanks Marsh (Figure 1.31). Age 0 suckers were caught along Hagelstein Marsh (Figures 1.32, 1.33), but were not common. This pattern of few age 0 suckers caught near marshes was also evident in other species. Distribution maps of all fish (Figure 1.44) show heaviest abundance along the eastern shore, with low abundance along marshes. Fish, including suckers, were even more likely to be found along the shoreline in the water-quality-deficient Wocus Bay than along marshy shorelines in other areas of the lake.

These patterns of distribution are likely explained by substrate. Age 0 suckers and all fish had higher catch-per-unit-effort on substrates comprised mostly of rocks, such as gravel, cobble, etc (Table 1.7, 1.11). Catches were generally low on small particle substrates such as sand and fines. Shoreline substrates near the edge of marshes are heavy, unconsolidated, organic fines, or a compact peat substrate. Our cast net data suggest age 0 suckers and all fish generally avoid these substrates, and thus the marshes, along the shoreline, and inhabit rocky substrates as

preferred habitats. Although marshes may be important for improved water quality and larval fish rearing, our data have not suggested that these are important for juveniles later in the summer/fall.

One of the more difficult aspects of this research is interpretation of year class success. First, we assume that year class formation is largely set near the end of the first growing season, and thus, years where higher numbers of age 0 suckers are found in September will translate into higher numbers entering the spawning population several years later. Sporadic events such as fish kills can certainly alter this assumption, but there has been very little evidence that recent fish kills have affected immature suckers. Second, there is no historical context for which to compare our data. In this absence, there is no real way to postulate what might be a good year class. For example, a population estimate of 500,000 age 0 suckers in September might be good for the 8 years of research covered in this report, but might be insufficient to sustain a population long-term, and might be much less than would have been found prior to the decline of the suckers. What is evident from our sampling is that the number of age 0 suckers can vary widely among years. More troubling is that the numbers can also vary widely within a year, some of which is logically explained by gear bias and is expected. The drop in cast net catches from August to October is not readily explainable and makes year class formation assessments difficult. If the declines in our estimates are real, this then suggests that there are few age 0 suckers remaining in September or October than there were in August, losses that might be attributed to mortality or loss via canals. If fish moving offshore cause these declines, then our current offshore sampling is not sufficient to detect this shift in habitat use (because of low offshore density). We must then either discover new techniques to sample the offshore regions of Upper Klamath Lake, or accept our August estimates as a final assessment of year class strength

Section 2--Age and growth of juvenile Lost River and shortnose suckers

INTRODUCTION

Upper Klamath Lake suckers were listed as endangered in 1988 based on studies documenting that populations were declining in size and aging due to apparent recruitment failure since the early 1970s (Buettner and Scopettone, 1990). Hypotheses linking ongoing recruitment failure to fishing pressure, water-development projects, pollution, habitat reduction, hybridization, and introduction of exotic species have been proposed by several authors (Andreasen, 1975; Scopettone and Vinyard, 1991; U.S. Fish and Wildlife Service, 1993). Growth and mortality during the early life history stages of fishes are important components in understanding recruitment dynamics of populations. Tenfold or greater fluctuations in recruitment can be precipitated by a relatively small variation in mortality or growth rates (Houde, 1987). By understanding the processes that affect mortality and growth rates of larval and juvenile fishes, researchers may be able to determine both biological and environmental factors that impact recruitment variability.

Use of otolith data in fisheries research accelerated after Pannella (1971) first described daily otolith growth increments in some cold-temperate fishes. The deposition of daily and annual increments in fish otoliths has been validated by a number of researchers for several species (see review by Secor et al., 1991), including both shortnose and Lost River suckers (Hoff et al. 1997). In addition to obtaining key information such as population age structure and hatchdate distributions from increment counts, otoliths may also allow estimates of individual growth through the examination of increment widths (Gutiérrez and Morales-Nin, 1986; Eckmann and Rey, 1987; Karakiri and von Westernhagen, 1989; Molony and Choat, 1990; Williams and Lowe, 1997).

The use of otolith width data can be extremely valuable to the researcher if a positive relationship can be established between increment width and somatic growth (Secor and Dean, 1989). During stressful conditions, otolith growth and somatic growth can become uncoupled, with somatic growth slowing or stopping while metabolic-dependent otolith growth may continue or increase (Neilsen and Geen, 1985; Gutiérrez and Morales-Nin, 1986; Molony and Choat, 1990; Simon et al., 1996). Preliminary analyses by Simon et al. (1996) indicate that otolith and somatic growth are indeed coupled in shortnose and Lost River suckers.

Extremely high levels of unionized ammonia were recorded in several regions of Upper Klamath Lake in 1997,

especially the Wocus Bay region (J. Kann, unpubl. data). Because unionized ammonia is toxic to fish at relatively low concentrations (Tucker et al., 1984; Bellerud and Saiki, 1995; Rasmussen and Korsgaard, 1996), sublethal effects of exposure (in the form of reduced increment widths) may be present in the otoliths of suckers caught in areas with high unionized ammonia concentrations. The effects of stress and reduced growth may play important roles in recruitment variability of shortnose and Lost River suckers.

We are investigating otolith microstructure in order to provide an estimate of early health and growth of shortnose and Lost River suckers. This report also serves to describe general patterns in otolith growth, Julian hatchdate distributions, growth rates, and sublethal environmental effects on growth of shortnose and Lost River suckers from Upper Klamath Lake from 1991-1997.

METHODS

Otoliths were obtained from juvenile suckers caught during beach seine, cast net and trawl surveys that occurred from 1991 through 1997 in Upper Klamath and Agency Lakes. Suckers were preserved and stored in 95% ethanol, and otoliths were removed after a period of time ranging from months to years. The number of fishes chosen for otolith analyses varied among years due to differences in sample size and the subsampling techniques of multiple readers. For years 1993-1995, most fish captured in the castnet and trawl samples were aged and random subsamples from the beach seine samples were selected to represent the range of lengths captured (see Simon et al., 1996). No laboratory subsampling occurred for years 1991, 1996, or 1997.

Right lapilli were removed from suckers using a dissecting microscope and fine probes. Otoliths were cleaned in 10% bleach for 30 minutes, rinsed twice with deionized water, and given a final rinse of 95% ethanol to remove any moisture from the otoliths. Otoliths were placed in uncapped screw top scintillation vials and allowed to air dry for several days in a clean, dry environment. Once dry, the otoliths were weighed to the nearest 0.0001-mg using a Cahn 29 Electrobalance.

Each lapillus was mounted distal side up on a petrographic slide with Crystalbond thermoplastic resin. Otoliths were then ground by hand along the sagittal plane using 1500-grit wet/dry sandpaper to gain proximity to the core, and polished using a synthetic velvet cloth and 0.05 μm alumina powder. It was necessary to flip the otolith

several times during grinding and polishing in order to create a thin section with visible increments along the entire diameter of the otolith.

Hoff et al. (1997) previously validated daily lapillus increments for these species using known-age hatchery-raised larvae and alizarin complexone-marked wild-caught larvae and juveniles. For this study, daily increments were counted and measured to the nearest 0.0001 μm using a digital imaging system equipped with Optimas 5.0 (1995) software. A counting transect from core to edge along the leading growth axis was consistently used for counting and measuring otolith increments. All counts and measurements were made without information regarding fish length or catch date.

Large sample sizes, time constraints, and the desire to investigate sublethal effects of water quality on growth of surviving suckers precluded the use of all otoliths in subsequent analyses. Sample sizes were therefore reduced to include only those fish caught toward the end of the respective year's survey (catch dates later than Julian day 224). Fish ages were obtained from total ring counts, and Julian hatchdates were determined by subtracting fish age from capture date. Average growth rate was determined for each fish by dividing standard length by age. Eight-mm. was subtracted from standard length to compensate for average length at hatch (Buettner and Scopetone, 1990) before average daily growth rate estimates were calculated. Regressions of lapillus weight on age and standard length, standard length on age, and growth rate on Julian hatchdate were calculated by the method of least squares. Analyses of covariance (ANCOVA) were used to determine statistically significant differences between regression lines. Median hatchdates and growth rates (mm/day) were compared between species and years using Mann-Whitney U-tests and Kruskal-Wallis tests, respectively.

The effects of poor water quality on sucker growth were investigated using 12 fish captured in Wocus Bay in 1997, when unionized ammonia concentrations reached levels toxic to suckers (see Monda and Saiki, 1994). Water quality data were obtained from an open water site in Wocus Bay at approximate two-week intervals from mid-March through late September, 1997 (J. Kann, unpubl. data). We plotted mean increment width at age for all suckers (by species) from all years and used the relationships to establish a baseline to which mean increment width of 1997 Wocus Bay suckers could be compared (see Section 3--Associations of increment width with environmental variables, for detailed reasoning behind choosing this baseline). Departures from the baseline were related to

environmental parameters from Wocus Bay (unionized ammonia, temperature, dissolved oxygen, pH, and conductivity) using multiple regression.

RESULTS

General growth

Lapilli were examined from 353 shortnose and 230 Lost River suckers from years 1991, 1993-1997. General otolith shape and increment growth patterns were similar between species. Lapilli exhibited a thin, tapered posterior edge that was easily eroded by overgrinding. The anterior edge was relatively thicker, resulting in an otolith that was wedge-shaped dorsoventrally. Sagittal sections exhibited a core offset so far to the anterior edge that it was realistic to count and measure increments only along the posterior growth axis. A transition from relatively wide to narrow increments occurred anywhere between increments 8-14 (Figure 2.1). A change in growth plane was noted in lapilli for both species between increments 25-32 (Figure 2.2). This change of growth plane gave the otolith a slightly palmate shape. A “washout” area occurred on several (but not all) otoliths sometime after increment 42. This area was distinguished by difficult to read daily increments and the presence of sub-daily increments. The general pattern of average increment width over time was one of increasing increment widths (ages ~1-50, LRS; ages ~1-40, SNS) followed by a period where average increment width remained fairly constant (ages ~51-90, LRS; ages ~41-80, SNS), and then a period of decreasing average increment widths (ages >~90, LRS; ages >~80, SNS) (Figure 2.3).

Descriptive statistics

Standard length-at-age plots (by year) for juvenile Lost River and shortnose suckers are shown in Figure 2.4. Results of ANCOVA (Table 2.1) indicate no significant differences in slopes of the regression lines between species at the 90% or higher confidence level; however, there were statistically significant differences in the intercepts at the 99% confidence level for years 1991, 1993-1995. Relationships for 1996 and 1997 exhibited non-significant differences in intercepts ($P = 0.0637, 0.5826$, respectively). These non-significant differences may be a result of small sample size of Lost River suckers for those years ($n = 14, 4$, respectively). Plots for years 1991, 1993-1995 show obvious differences between species in standard length at age, with Lost River suckers exhibiting greater

standard length-at-age than shortnose suckers.

Regressions of lapillus weight on age and standard length for both Lost River and shortnose suckers from 1991, 1993-1996 were compared by ANCOVA (Tables 2.2 and 2.3, respectively.). Time constraints precluded weighing otoliths from fish caught in 1997. Regression slopes of otolith weight on age were not significantly different between species per year, but intercepts were significantly different between species for years 1994 and 1995. We pooled the data for years 1991, 1993, and 1996 prior to calculating regression equations (Figure 2.5). Age was not necessarily a good predictor of otolith weight, as r^2 values ranged from 0.29 in 1994 to 0.68 in 1996 for both species combined. Low r^2 values for both species in 1994 and 1995 may be a result of smaller sample sizes used to calculate the regression equations. Regression slopes of otolith weight on standard length were not significantly different between species per year, but intercepts were significantly different for every year, indicating that shortnose suckers had heavier lapilli-at-length than did Lost River suckers. Standard length explained most of the variation in lapillus weight, with r^2 values ranging from 0.59 in 1993 to 0.96 in 1994 (Figure 2.6).

Julian hatchdate distributions are shown in Figure 2.7, and summary statistics are presented in Table 2.4. The range of Julian hatchdates for a given year was consistently greater for Lost River suckers than for shortnose suckers, except for years 1996 and 1997, when sample sizes of Lost River suckers were low ($n = 14$ and 4 for 1996 and 1997, respectively). Median hatchdates also varied by year. Median hatchdates for 1994 and 1997 (138 and 139, respectively), occurred close to the median Julian hatchdate for all fish combined (142). By comparison, hatchdates occurred relatively later for years 1991, 1993, and 1996 (median Julian hatchdates of 154, 155, and 157, respectively), and much earlier for 1995 (122). Annual trends in Julian hatchdate patterns were similar between species—median Julian hatchdates between species were a maximum of three days apart for years 1991-1995. Mann-Whitney U-tests (Table 2.5) indicated significant differences among median Julian hatchdates between species for years 1991, 1996, and 1997, with shortnose suckers exhibiting later median Julian hatchdates than Lost River suckers. Low P values for 1996 and 1997 (0.0038 and 0.0215, respectively) are probably the result of small sample sizes. Kruskal-Wallis tests ($P = 0.0000$) indicated significant differences in median Julian hatchdates between years for both species. Multiple comparison tests (Table 2.6) and box-and-whisker plots (Figure 2.8) indicate significant differences between all combinations of years except between years 1991 and 1993 and between 1994 and 1997 for shortnose suckers, and

between 1991 and 1996, 1993 and 1996, 1994 and 1997, and 1995 and 1997 for Lost River suckers. Again, small sample sizes of Lost River suckers in years 1996 and 1997 probably influenced these results.

Growth rate distributions are shown in Figure 2.9, and summary statistics are presented in Table 2.7. Mann-Whitney U-tests (Table 2.8) indicated statistically significant differences among median growth rates between species for all years except 1997 ($P = 0.6993$). Lost River suckers consistently had higher median growth rates than shortnose suckers for all years except 1997. Small sample size for Lost River suckers in 1997 may influence the significance of the 1997 comparison. Kruskal-Wallis tests ($P = 0.0000$) indicated significant differences in median growth rates between years for both species. Multiple comparison tests (Table 2.9) and box-and-whisker plots (Figure 2.10) indicate significant differences between all combinations of years except between years 1991 and 1994 and 1996 and 1997 for shortnose suckers, and between years 1993 and 1996 and 1995 and 1997 for Lost River suckers. A general shift from higher median growth rates (> 0.5 mm/day) to lower median growth rates (< 0.5 mm/day) occurred after 1994, with 1995 fish exhibiting the lowest median growth rates for all years (0.43 mm/day). Although there were significant differences in growth rates between years for both species, growth rate data was pooled for each species and regressed on Julian hatchdate to determine if hatchdate exhibited any influence on growth rate (Figure 2.11). Slopes of both regression lines were positive and significantly different than zero ($P = 0.0000$), indicating that later-born fish had relatively higher growth rates than earlier-born fish.

Environmental effects on mean increment width

We plotted mean increment width (both species combined) vs. Julian day for each year separately to graphically determine if high unionized ammonia levels exhibited a sub-lethal effect on lapillus growth of juvenile suckers. By limiting Julian date to a 38-day window, we could delineate small changes in increment widths with changes in both temperature and unionized ammonia concentrations. For years 91-96, mean increment width exhibited a positive correlation with temperature—mean increment width generally increased and decreased as temperature increased and decreased (Figure 2.12). No correlation with unionized ammonia levels was noted (Figure 2.13). In 1997, however, it appeared as though mean increment width and temperature “uncoupled”. Lakewide, mean increment width decreased by more than four microns over a period of 27 days, and by more than four microns over a

week-long period in Wocus Bay, even though temperature remained fairly constant over that time period (21.50-21.90 °C). Mean increment widths appeared to be driven instead by relatively large spikes in unionized ammonia concentrations (lakewide average 0.954 mg/L, Julian day 212; Wocus Bay average 4.136 mg/L, Julian day 212).

The effects of water temperature, unionized ammonia concentration, pH, dissolved oxygen, and conductivity on residual increment widths of 1997 Wocus Bay suckers was determined statistically by multiple regression (Table 2.10). As expected, water temperature was positively associated with increment width residuals ($P = 0.0246$). However, neither conductivity, dissolved oxygen, unionized ammonia, nor pH had a significant association with increment width residuals ($P = 0.7669, 0.5618, 0.5578, 0.5793$, respectively).

DISCUSSION

General growth

The variation in otolith shape, size, and location among species is impressive. Many studies have reported morphological differences among sagittae, lapilli, and asterisci in the same species (Nolf, 1985; Fowler, 1989; David et al., 1993; Hoff et al., 1997). These morphological differences often dictate which otolith is easiest to extract and read for aging studies. For most species, the sagittae are the largest otolith present, and therefore the easiest to prepare and read. A key difference in otolith morphology between ostariophysean fishes and other teleosts is that the ostariophysean sagitta is highly modified from the typical teleost condition, being smaller, very elongate, and easily broken during removal (Jenkins, 1979a, b; Brothers, 1984). Hoff et al. (1997) determined that the lapillus was best suited for aging shortnose and Lost River suckers, based upon its large size, time of formation, readability, and ease of removal.

Accurate interpretation of otolith growth patterns requires knowledge of the factors that influence growth ring formation. Both physiological and environmental factors such as temperature, pH, dissolved oxygen, feeding, growth, photoperiod, and an endogenous circadian rhythm can potentially influence the rate of otolith deposition (Geen et al., 1985; Jones, 1985; Molony and Choat, 1990; Weisberg, 1993; Baltz et al., 1998; Gallego et al., 1999). The first transition from relatively wide to narrow increments (ages 8-14) occurs at a stage in larval development during yolk-sac absorption and the start of notochord flexion. The change in growth plane between the ages of 25-32 occurs coincident with ages when sucker larvae first reach the mouth of the Williamson River (Simon et al, 1996), and

the “washout” area (after age 42) occurs coincident with ages when suckers are entering the metalarval stage of development (see Kendall et al., 1984; Buettner and Scopettone, 1990). It is problematic that the “washout” area was not seen on all otoliths, and may simply be the result of poor sample preparation. It is invalid to assume cause and effect in the above-mentioned life-history stages without first performing detailed analyses of larval development; however, changes in otolith deposition rates could very well be affected by developmental stage and the environmental conditions at the time.

Descriptive statistics

We found that juvenile Lost River suckers attain greater lengths-at-age than do juvenile shortnose suckers. These results agree with data from Logan (1998), which reported greater lengths-at-age for October-caught Lost River suckers for years 1991, 1993, and 1995. Scopettone and Vinyard (1991) report that, in general, shortnose suckers attain a smaller body size than Lost River suckers, although their summary does not take into account the effect of age on standard length.

The regressions of lapillus weight on standard length indicate that shortnose suckers have heavier lapilli-at-length than do Lost River suckers. Templeman and Squire (1956) observed that otolith weight was consistently greater at a given length in slower growing populations of haddock *Melanogrammus aeglefinis* when compared to populations that exhibited higher growth rates. Several authors (Boehlert, 1985; Reznick et al., 1989; Logan, 1998) have reported similar results for other species, including shortnose suckers (Logan, 1998). Values of mean and median growth rates (measured in mm/day) for Lost River and shortnose suckers (Table 2.7) indicate both measures were consistently less for shortnose suckers than for Lost River suckers for all years except 1997. We believe that small sample size of Lost River suckers (4) skewed the results for that year. Although standard length explains most of the variation in lapillus weight, it is obvious that age is a factor as well. Older fish have heavier otoliths than younger fish because of the extra accretion of calcium carbonate and protein that is laid down on a daily basis.

Seasonal spawning patterns may best explain annual and species differences in Julian hatchdate statistics. For example, the greater range in Lost River sucker Julian hatchdates may be indicative of a protracted spawning season. Perkins et al. (1998) reported that the spawning migration of Lost River suckers may consist of an early run

of fish that spawn in the upper Sprague River, followed by a later run of fish that spawn in the Williamson River and the lower Sprague River. Data from 1987-1998 (Perkins et al., 1998) also indicate that Lost River suckers spawn at springs for up to a month longer than shortnose suckers. Julian hatchdate distributions correspond fairly well with spawning migration data of shortnose and Lost River sucker adults from 1995-1997 (Perkins et al., 1997). Catch per unit effort data from 1995 showed relatively large peaks (~5.0 mean CPUE) in sucker catches occurring in mid-March, earlier than in 1996 or 1997, and before the mid-April migrations reported for 1987 and 1988 (Bienz and Ziller, 1987; Buettner and Scopettone, 1990). Although time of spawning and larval development is highly variable between years, this early migration corresponds well with earlier hatchdates for juvenile suckers, and may be due to relatively high water temperatures. Perkins et al. (1998) noted that from 1995-1998, peaks in CPUE of Lost River and shortnose suckers in the lower Williamson almost always corresponded to peak water temperatures, usually at 10-15° C. Catch data for shortnose suckers in 1996 also exhibited a peak CPUE (~ 10.0) in early May that corresponds well with median Julian hatchdate (157) for that year. Low catches of Lost River suckers in 1996 and 1997, as well as low CPUE data for adults of both species in 1997 make any other correlation difficult. Unfortunately, spawning run data for years 1991, 1993, and 1994 are wanting.

Differences in median growth rates between species for each year correspond well with the length-at-age data. Because median growth rates were calculated by dividing standard length by age, it is intuitive that because Lost River suckers attain greater lengths-at-age than do shortnose suckers, they would exhibit higher growth rates. It is not easy, however, to determine what factors influence growth rate. Jones (1985) and Gallego et al. (1999) reported that later hatched fishes grew faster than fishes hatched earlier in the spawning season. However, median Julian hatchdates for both species in the same year are a maximum of three days apart, and both species encounter the same suite of environmental parameters over a lifetime. Growth rate, therefore, must be governed by physiological differences between species, such as an endogenous circadian rhythm, which is susceptible to modification by environmental parameters (Campana and Neilson, 1985). Such modifications can be seen when comparing growth rates between years. The lowest median growth rate (0.43 mm/day) occurred in 1995, when Julian hatchdates occurred up to 26 days earlier than any other year. Earlier spawning in 1995 occurred when water temperatures were cooler than in other years, and therefore corresponds to lower growth rates for fishes hatched in

1995. The mean annual lakewide water temperature (J. Kann, unpubl. data) for 1995 was also 1.6 degrees cooler than the mean annual water temperature for other years (15.9° C. compared to 17.5° C.). High growth rates for other years were not consistently related to high water temperatures, indicating that other factors or confounding variables may influence growth rate.

Environmental effects on mean increment width

The relationship between increment width residuals and environmental parameters were both expected and surprising. The fact that temperature is significantly positively correlated with otolith increment width has been documented in several studies (Townsend and Graham, 1981; Gutiérrez and Morales-Nin, 1986; Karakiri and Westernhagen, 1989, Bradford and Geen, 1992). Unfortunately, other studies exist that have found the effects of temperature on increment widths to be inconclusive (Ré, 1983; Bestgen and Bundy, 1998). Other studies have examined how otolith increment widths are affected by environmental parameters such as pH (Geen, et al., 1985), photoperiod (Campana, 1984; Campana and Neilson, 1985), and dissolved oxygen (Baltz et al., 1998). Most of these studies imply that confounding factors affect increment widths (e.g. increased water temperature is correlated with increased food availability, longer photoperiod, and decreased dissolved oxygen levels), while others give differing reports on the importance each component's affects has on growth. In the absence of laboratory studies, it is impossible to determine the separate effects temperature, food production, and photoperiod have on the growth of juvenile Lost River and shortnose suckers.

The fact that unionized ammonia proved non-significant in the multiple regression analysis was surprising. In 1997, Wocus Bay was characterized as having toxic unionized ammonia levels associated with seasonal blooms of *Aphanizomenon flos-aquae* (Tucker et al., 1984; Martin and Saiki, 1999). Several laboratory studies have been performed that examined the effects of unionized ammonia on growth and mortality of various species (Ball, 1967; Colt and Tchobanoglous, 1978; Tucker et al., 1984; Rasmussen and Korsgaard, 1996). These studies have shown that short-term exposure to increased unionized ammonia concentrations stressed fishes to the point of starvation, which resulted in reduced growth, and in some cases, mortality. In 1997, Wocus Bay average unionized ammonia concentrations greatly exceeded the median tolerance limits for juvenile Lost River (0.750 mg/L) and juvenile

shortnose (0.956 mg/L) suckers reported by Bellerud and Saiki (1995) for an approximate month-long period. Because water temperature never reached median tolerance limits (31.2° C., Bellerud and Saiki, 1995) for either species in 1997, we expected unionized ammonia concentrations to significantly relate to reduced mean increment widths.

There are several possible reasons for the apparent discrepancy between the graphical and statistical analyses. Because this was not a controlled study, suckers could have avoided areas of extreme unionized ammonia toxicity for most of their lives. Even though unionized ammonia levels were high lakewide, pockets of relatively good water quality may have existed in Upper Klamath Lake. The unionized ammonia data collection was sparse, having been collected at two week intervals, and did not address day/night variation. This may have resulted in the inability to detect statistical differences in spite of graphical associations that appeared to exist. Another unmeasured variable, such as food availability, or the confounding effects of unmeasured variables on the above-mentioned associations, may influence growth as well. Furthermore, the multiple regression analysis explores neither possible interactions among environmental variables, nor the possibility that a time lag exists between the onset of stress and physiological effects in fish. For example, Molony and Choat (1990) reported a 15-day time lag between starvation and reduced daily increment widths in glass fish, *Ambassis vachelli*, and Lehodey and Grandperrin (1996) report a time lag of several months between temperature fluctuations and annular increment widths in alfonsino, *Beryx splendens*. In a related study, Martin and Saiki (1999) reported that water temperatures and unionized ammonia levels in Upper Klamath Lake in 1996 were not directly responsible for instances of high fish mortality in caged suckers. However, unionized ammonia levels never reached median tolerance limits for suckers during the study period. Further, the study did not investigate any sub-lethal effects of unionized ammonia on fish health. Further controlled investigations into the effects environmental extremes have on sucker growth and mortality would lend insight on those factors, both biological and environmental, that play important roles in fish survival and recruitment.

METHODS

Growth data were gathered from age-0 fish captured throughout the summer. Otoliths were removed from specimens that were selected to be representative of the overall length frequency distribution of the population, and daily growth increments were counted and measured. Concurrent monitoring of environmental conditions allowed the calculation of lakewide averages of dissolved oxygen, pH, temperature, water level (expressed as the difference from 4141.8, the 1995 average), and redox potential. Lunar phase was coded as the minimum of the number of days since and the number of days to the new moon. The analyses presented here are based on 23,767 otolith increments from 263 fish collected in 1994 and 1995, with accompanying environmental data matched to the dates on which those increments were laid down.

Modeling the baseline growth curve

Our analysis strategy was to estimate a “baseline” growth curve--i.e., a trajectory of increment width vs. age that we expect would be followed by fish growing in identical, unchanging environments -- and then relate departures from that baseline to the environmental variables. In the absence of empirical information on the form of such a curve, we experimented with a variety of possible baselines, including:

1. A constant, age-independent increment width for each fish, estimated as the mean width of that fish's increment measurements;
2. A trajectory for each fish that is parallel to a plot of average increment width vs. age obtained by aggregating data from specimens of that species collected in 1991 and 1993--1997 (343 shortnose and 230 Lost River suckers); and
3. A trajectory obtained by applying a nonparametric scatterplot smoother available in the S-PLUS language (Cleveland 1979, MathSoft 1996) to each fish's width-vs.-age data.

Statistical analysis

Our general model for the increment width of fish i at age t_j (in days) is:

$$y_{ij} = f(t_j) + \eta_i + x_j\beta + \varepsilon_{ij}, \quad (1)$$

where $f(\cdot)$ is the possibly nonlinear function of time that we have chosen as our baseline growth curve; η_i is a random effect due to fish i , x_j is a row vector of the environmental variables recorded on the date that this fish was age j ; β is a vector of regression parameters; and $\varepsilon_{i1}, \varepsilon_{i2}, \dots, \varepsilon_{imi}$ are sequential errors for fish i , assumed to represent a first-order autoregressive process, abbreviated AR(1). That is, increment width is the sum of a baseline value, a random effect due to the individual fish (which will be close to zero for baselines 1 and 3), “effects” of the environmental variables, and a random error. The AR(1) structure implies that the correlation of the errors from an individual fish on days i and j is $\mathbf{r}^{|i-j|}$, where \mathbf{r} is the autoregression coefficient ($-1 < \mathbf{r} < 1$).

Because of the different forms of the three baseline growth curves, our strategy was to estimate the baseline, subtract it from the observed increment width, and then model the difference as

$$z_{ij} \equiv y_{ij} - f(t_j) = \eta_i + x_j\beta + \varepsilon_{ij}. \quad (2)$$

This is a linear mixed-effects model (Laird and Ware, 1982; Diggle et al. 1994) with serial autocorrelation of the random errors within fish. We fit the model using the S-PLUS function `lme`, choosing restricted maximum likelihood as the method of parameter estimation (e.g., see Venables and Ripley, 1997).

We also explored a method of inference based on individual estimates, as discussed by Davidian and Giltinan (1995). For each fish, we regressed the width residuals against the environmental predictors, adjusting for first-order serial correlation. Results for the entire sample of n fish were summarized as sets of n regression coefficients for each predictor, and statistical inference was based on these independent estimates. The computations in our implementation of this approach were more time-consuming than those for the “pooled” approach described above, and the resulting variance estimates tended to be larger, so we have chosen to emphasize the first method in our presentation.

RESULTS AND DISCUSSION

The baseline growth curve

Figure 3.1 shows average increment width vs. age for the two species, along with the nonparametric smoothed fits that were used for baseline 2 (see above). The increased vertical scatter for older fish is due to the smaller number of specimens contributing data for those ages.

For each fish, baseline 1 was obtained by simply averaging the increment widths for that fish, and baseline 3 is a nonparametric smoothed fit to that fish's trajectory of increment width vs. age (from the S-PLUS function *lowess*). Figure 3.2 shows examples of the three baseline curves fit to the data from an individual Lost River sucker.

In the absence of empirical information on the “true” form of the baseline growth curve, the choice of which one to use in our analyses was problematic. The age independence of baseline 1 seems biologically unreasonable. It tends to create runs of negative and positive residuals that might be interpreted as environmental effects, when in fact it is quite plausible that they represent ontogenetic changes in the growth rate of the otolith. On the other extreme, the fish-specific, nonparametric smoothed curves (baseline 3) seem too closely tied to individuals' growth trajectories, and they may be “adjusting out” important environmental influences on growth rate. After much exploration of the consequences of using these different baselines, we chose to adopt baseline 2 as a “best guess” compromise between the extremes represented by the other two baselines. Even though the horizontal axes in Figure 3.1 represent age, not calendar date, there is a general tendency for points on the left to come from earlier in the season than points on the right. Consequently, there remains a real potential for confounding of ontogenetic and environmental influences on growth rate.

Correlations with environmental variables

Analyses by year

Figure 3.3 shows average values of the residuals from baseline 2, and values of the lakewide averages of the environmental variables, as a function of Julian day in 1995. If the baseline curve is appropriate, the residuals

suggest that environmental factors might be hastening otolith growth through most of the summer, and then causing a decrease in growth rate at the end of the season.

Tables 3.1 and 3.2 show results of applying the linear mixed-effects model (Equation 2) to the residuals from baseline 2. In Table 3.1, all six environmental variables were included in the fits; in Table 3.2, backwards stepwise variable selection was used, starting with a model containing all predictors and then eliminating those not having statistically significant associations with the response.

As expected, temperature has a positive association with increment width, but the associations of the width residuals with the other environmental variables are harder to understand. Dissolved oxygen is negatively associated, and pH positively associated, with increment width--exactly the opposite of what might have been expected, since low oxygen and high pH are known to cause physiological stress for fish larvae. Since high values of dissolved oxygen and pH are associated with high levels of primary (and presumably secondary) production, it may be that these variables act as surrogates for food supply, an unmeasured but undoubtedly important influence on growth rate.

According to Tables 3.1 and 3.2, lake level has a consistently negative association with increment width. Again, this seems counterintuitive, since an increasing lake level would expand the area of productive littoral habitat available to larval suckers. However, the very smooth trajectory of lake level over time, as seen in Figure 3.3 for 1995, means that there is a strong potential for confounding of lake level with other factors that vary smoothly with time, so that its regression coefficients should be interpreted cautiously.

Analyses by age and time intervals

To look for evidence of confounding with other temporally varying factors, we did separate analyses of the data from particular intervals of age (Table 3.3) and calendar time (Table 3.4). In general, the regression coefficients from the interval analyses--especially the statistically significant coefficients—are similar to those from the full-year analyses in Tables 3.1 and 3.2. One exception is redox potential, which shows some relatively large-magnitude coefficients, both positive and negative, in the interval analyses. Another interesting exception is lake level, which in the full-year analyses (Tables 3.1 and 3.2), is negatively associated with increment width. In the analyses by date

intervals (Table 3.4), lake level tends to be *positively* associated with increment width, sometimes strongly so, early in the season, while later on the association tends to be negative. The negative coefficients tend to coincide with periods when level is decreasing smoothly (e.g., see Figure 3.3), suggesting the possibility of confounding with some other time-varying factor.

Caveats

The most important caution here is one that applies to all observational studies: there is no way to be sure that an observed association of a response and a predictor is not caused by confounding with some other, unmeasured variable.

Care in interpreting regression coefficients is also called for when, as in these data sets, some of the predictors are strongly correlated. The magnitude of a coefficient for one variable may change dramatically, depending on whether or not a correlated predictor is also in the model.

The results presented here should be considered preliminary, as we have just begun to explore (i) possible interactions among the environmental variables (early results suggest a lake level/temperature interaction for the 1995 Lost River suckers and a dissolved oxygen/pH interaction for the 1995 short-nosed suckers), and (ii) time lags in the influences of the environmental variables on increment width.

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Table 1.1. Particle size for each substrate group mapped in Upper Klamath Lake. Mixed substrates show percent of particle sizes in each group required to be classified in that group.

Substrate group	Particle size (mm)
finer	<0.06
sand	0.06 – 2
gravel	2 – 64
cobble	64 – 250
boulder	250 - 4000
smallmix	>75% <64
intermix	0% - 100%
largemix	>75% >64

Table 1.2. Distribution of the catch of larval suckers captured during fixed site larval sampling in Upper Klamath Lake, 1995-1998.

Number in a Catch	<u>Observed in:</u>			
	1995	1996	1997	1998
0	58 (49%)	53 (47%)	67 (56%)	77 (64%)
1	18	14	13	13
2	3	4	8	2
3	6	5	6	5
4	6	3	3	2
5	0	3	2	1
6-10	8	10	6	6
11-15	5	4	2	6
16-20	3	2	2	2
21-25	1	0	2	1
26-50	4	3	3	3
51-100	2	3	4	2
101-200	2	5	0	0
201-300	1	2	0	0
301-500	1	1	1	0
500-1000	0	0	0	0
>1000	0	0	1	0
	118	112	120	120

Table 1.3. Distribution of the catch of juvenile suckers captured during fixed site beach seine sampling in Upper Klamath Lake, 1995-1998.

Number in a Catch	<u>Observed in:</u>			
	1995	1996	1997	1998
0	29 (48%)	23 (38%)	38 (66%)	41 (68%)
1	7	6	8	3
2	5	3	2	2
3	0	0	0	2
4	1	1	0	0
5	0	0	0	0
6-10	2	1	2	3
11-15	0	2	1	3
16-20	2	1	0	0
21-25	2	2	1	1
26-50	5	6	2	3
51-100	2	5	1	1
101-200	2	4	1	1
201-300	2	1	1	0
301-500	1	2	0	0
501-1000	0	1	1	0
>1000	0	2	0	0
	60	60	58	60

Table 1.4. Species dominance expressed as percent of samples in which the species was first in abundance from beach seine sampling in Upper Klamath and Agency lakes, 1995-1998. Numbers in boldface are greater than the four-year average. CPUE = catch per unit effort. N = sample size.

Species	Upper Klamath Lake					Agency Lake				
	1995-98	1995	1996	1997	1998	1995-98	1995	1996	1997	1998
blue chub	53.9	67.8	44.3	60.0	49.3	35.6	70.8	31.8	29.0	21.2
fathead minnow	17.6	3.6	27.3	11.7	21.7	50.0	29.2	56.8	48.4	57.8
yellow perch	3.3		2.3	1.7	8.7	7.6			12.9	18.2
young of year sucker	12.5	8.9	20.4	11.7	5.8	2.3		6.8		
tui chub	7.0	14.3	2.3	5.0	8.7	1.5			6.4	
marbled sculpin	4.8	1.8	2.3	10.0	5.8	0.8			3.2	
Klamath Lake sculpin	0.7	3.6								
others	0.4		1.1			2.3		4.6		3.0
Positive catch/ young of year suckers (%)	40.6	51.7	53.6	32.9	23.7	20.0	26.7	30.0	17.5	5.0
CPUE (fish/seine)	229.2	221.2	372.0	124.7	161.4	624	257.9	392.9	183.7	1627.9
CPUE (species/seine)	2.58	3.07	2.87	2.22	2.22	2.13	2.30	2.60	1.92	1.60
CPUE (exotic species/ seine)	0.69	0.68	0.80	0.53	0.73	0.84	0.73	0.86	0.85	0.90
Zero catches (%)	12.8	6.7	9.3	21.0	13.8	17.5	20.0	12.0	22.5	17.5
N	313	60	97	76	80	160	30	50	40	40

Table 1.5. Distribution of the catch of juvenile suckers captured during stratified random cast net sampling in Upper Klamath Lake, 1995-1998.

Number in a Catch	<u>Observed in:</u>			
	1995	1996	1997	1998
0	213 (89%)	369 (88%)	397 (94%)	383 (91%)
1	11	17	8	24
2	4	4	6	2
3	1	6	3	3
4	4	6	1	1
5	0	3	1	1
6-10	1	3	2	2
11-15	1	2	2	1
16-20	0	5	0	2
21-25	0	1	0	0
26-30	0	1	0	0
31-40	1	1	0	0
41-50	0	0	0	0
51-60	0	0	0	0
>60	2 (67, 84)	1 (70)	0	1 (1,168)
	238	419	420	420

Table 1.6. Population estimates, 95% lower confidence limits (LCL), 95% upper confidence limits, and total population estimates by year, month, and gear type of age 0 Lost River and shortnose suckers in Upper Klamath Lake.

		LRS			SNS			
		LCL	Estimate	UCL	LCL	Estimate	UCL	
1995								
Sept.	castnet	10,139	33,003	72,629	71,907	209,454	461,547	
	trawl	14,315	35,155	58,202	1,907	8,764	16,049	
	total		68,158			218,218		286,376
Oct.	castnet	0	7,329	25,878	0	3,157	15,789	
	trawl	9,982	30,954	56,498	0	6,106	12,395	
	total		38,283			9,263		47,546
1996								
Aug.	castnet	16,947	40,061	71,426	188,432	380,328	676,444	
	trawl	-	-	-	-	-	-	
	total		40,061			380,328		420,389
Sept.	castnet	0	0	0	1,752	7,125	18,121	
	trawl	0	0	0	0	4,813	12,145	
	total		0			11,938		11,938
Oct.	castnet	0	5,690	19,550	10,088	58,072	146,079	
	trawl	0	5,452	13,626	7,104	16,170	26,822	
	total		11,142			74,242		85,384
1997								
Aug.	castnet	707	2,298	6,357	34,597	80,179	145,611	
	trawl	0	0	0	0	0	0	
	total		2,298			80,179		82,477
Sept.	castnet	0	0	0	0	401	2,406	
	trawl	0	2,256	7,035	0	0	0	
	total		2,256			401		2,657
Oct.	castnet	0	0	0	0	1,467	7,329	
	trawl	0	0	0	0	0	0	
	total		0			1,467		1,467

Table 1.6. Con't

		LRS			SNS		
		LCL	Estimate	UCL	LCL	Estimate	UCL
1998							
Aug.	castnet	20,193	297,403	1,079,036	30,532	349,582	1,250,879
	trawl	1,798	12,229	25,172	0	6,207	13,096
	total		309,632			355,789	665,421
Sept.	castnet	363	729	2,551	8,328	25,547	53,803
	trawl	0	7,542	19,898	0	0	0
	total		8,271			25,547	33,818
Oct.	castnet	0	5,162	25,808	0	11,746	44,142
	trawl	0	0	0	0	0	0
	total		5,162			11,746	16,908

Table 1.7. Substrate, number of samples on that substrate (N), mean catch-per-unit-effort (CPUE), and number of positive catches on each substrate from stratified-random cast net sampling, for age 0 LRS and SNS, 1995-1998. A unit of effort was one cast net sample. Proportion of positive catches is in parentheses expressed as a percent of N. N is the same for both species. One large catch of 1,168 omitted.

		LRS		SNS		
Substrate	N	CPUE	Positive catches	Substrate	CPUE	Positive catches (%)
finer	320	0.022	7 (2.19)	finer	0.063	8 (2.50)
sand	160	0.031	4 (2.50)	sand	0.206	7 (4.38)
gravel	196	0.193	8 (4.08)	gravel	0.923	21 (10.71)
cobble	204	0.039	6 (2.94)	cobble	0.333	17 (8.33)
boulders	54	0.000	0 (0.00)	boulders	0.222	2 (3.70)
smallmix	291	0.134	17 (5.84)	smallmix	0.966	36 (12.37)
intermix	187	0.069	5 (2.67)	intermix	0.310	19 (10.16)
largemix	83	0.036	2 (2.41)	largemix	0.566	10 (12.05)
	1495		49 (3.28)			120 (8.03)

Table 1.8. Species dominance expressed as percent of samples in which the species was first in abundance from stratified random cast net sampling in Upper Klamath Lake 1995-1998. Numbers in boldface are greater than the four-year average. CPUE = catch per unit effort. N = sample size.

Species	1995-98	1995	1996	1997	1998
blue chub	71.0	76.6	67.7	77.8	63.6
fathead minnow	12.2		10.0	9.3	26.5
tui chub	9.5	15.0	10.6	8.6	5.3
marbled sculpin	2.7	3.7	2.9	1.9	2.7
shortnose sucker	1.7	1.9	4.7		
Klamath Lake sculpin	1.2	1.9	2.4		0.7
yellow perch	1.0		0.6	1.9	1.3
Lost River sucker	0.3	0.9	0.6		
rainbow trout	0.2			0.6	
slender sculpin	0.2		0.6		
Positive catch/ young of year shortnose sucker, %	8.1	9.2	11.2	5.5	6.9
Positive catch/young of year Lost River sucker,%	3.3	5.0	4.3	1.0	3.8
CPUE (fish/cast)	39.2	23.3	16.9	76.1	33.6
CPUE (species/cast)	0.81	0.85	0.92	0.85	0.65
CPUE (exotic species/cast)	0.17	0.05	0.16	0.21	0.21
Zero catches (%)	60.4	55.0	59.4	61.4	63.6
N	1497	238	419	420	420

Table 1.9. Species dominance expressed as percent of samples in which the species was first in abundance from late summer/fall otter trawl sampling in Upper Klamath Lake 1993-1998. Numbers in boldface are greater than the six-year average. CPUE = catch per unit effort. N = sample size.

Species	1993-98	1993	1994	1995	1996	1997	1998
blue chub	55.3	5.9	97.0	73.3	33.3	60.0	35.6
Klamath Lake sculpin	42.2	76.5	3.0	26.7	63.3	37.8	64.4
Lost River sucker	9.7	11.8					
marbled sculpin	4.9					2.2	
tui chub	4.9				3.3		
yellow perch	4.9	5.9					
Positive catch/ young of year shortnose sucker, %	9.7	0	3.0	23.3	26.7	0	6.7
Positive catch/young of year Lost River sucker,%	14.3	11.1	72.3	43.3	6.7	2.2	13.3
CPUE (fish/trawl)	213.5	18.0	335.4	470.1	251.3	121.2	98.4
CPUE (species/trawl)	3.05	1.67	4.24	3.30	2.87	3.16	2.58
CPUE (exotic species/ trawl)	0.50	0.11	0.85	0.17	0.27	0.71	0.58
Zero catches (%)	1.9	5.6	0	7.7	0	0	0
N	201	18	33	30	30	45	45

Table 1.10. Species dominance expressed as percent of samples in which the species was first in abundance from spring otter trawl sampling, April- May, 1992 and 1996-1998, in Upper Klamath Lake. Numbers in boldface are greater than the four-year average. CPUE = catch per unit effort. N = sample size.

Species	1992-98	1992	1996	1997	1998
blue chub	53.3	28.6	43.3	46.4	77.8
Klamath Lake sculpin	42.4	42.9	56.7	50.0	18.5
Lost River sucker	1.1			3.4	
shortnose sucker	1.1				3.7
fathead minnow	1.1	14.3			
yellow perch	1.1	14.3			
Positive catch/ young of year shortnose sucker, %	1.0	0	0	3.3	0
Positive catch/young of year Lost River sucker,%	2.9	0	10.0	0	0
CPUE (fish/trawl)	15.2	1.2	29.9	10.4	11.3
CPUE (species/trawl)	2.19	0.77	2.77	2.10	2.33
CPUE (exotic species/ trawl)	0.33	0.23	0.23	0.30	0.50
Zero catches (%)	10.7	46.2	0	6.7	10.0
N	103	13	30	30	30

Table 1.11. Substrate, number of samples on that substrate (N), mean catch-per-unit-effort (CPUE), and number of positive catches (>1 fish) on each substrate from stratified-random cast net sampling for all fish, 1995-1998. A unit of effort was one cast net sample. Proportion of positive catches is in parentheses expressed as a percent of N.

Substrate	N	CPUE	Positive catches (%)
gravel	197	100.6	79 (40.10)
boulders	54	67.1	29 (53.70)
cobble	204	57.7	89 (43.62)
smallmix	291	41.3	136 (46.73)
largemix	83	38.5	50 (60.24)
intermix	187	26.1	83 (44.38)
sand	160	10.6	46 (28.75)
fines	320	5.1	79 (24.68)
	1496		591 (39.50)

Table 2.1. Results of analysis of covariance on regressions of standard length on age for Lost River and shortnose suckers. Values in **boldface** are statistically significant at the 99% level.

Year	Comparison	<i>P</i> slopes	<i>P</i> intercepts
1991	LRS vs. SNS	0.1414	0.0000
1993	LRS vs. SNS	0.5277	0.0000
1994	LRS vs. SNS	0.1054	0.0000
1995	LRS vs. SNS	0.5495	0.0000
1996	LRS vs. SNS	0.2218	0.0637
1997	LRS vs. SNS	0.8642	0.5826

Table 2.2. Results of analysis of covariance on regressions of lapillus weight on age for Lost River and shortnose suckers. Values in **boldface** are statistically significant at the 95% level or higher.

Year	Comparison	<i>P</i> slopes	<i>P</i> intercepts
1991	LRS vs. SNS	0.4114	0.0500
1993	LRS vs. SNS	0.7701	0.4774
1994	LRS vs. SNS	0.1389	0.0009
1995	LRS vs. SNS	0.7113	0.0136
1996	LRS vs. SNS	0.5790	0.1593

Table 2.3. Results of analysis of covariance on regressions of lapillus weight on standard length for Lost River and shortnose suckers. Values in **boldface** are statistically significant at the 95% level or higher.

Year	Comparison	<i>P</i> slopes	<i>P</i> intercepts
1991	LRS vs. SNS	0.9580	0.0000
1993	LRS vs. SNS	0.7370	0.0000
1994	LRS vs. SNS	0.3052	0.0235
1995	LRS vs. SNS	0.9359	0.0231
1996	LRS vs. SNS	0.1179	0.0001

Table 2.4. Julian hatchdate statistics for Lost River and shortnose suckers: 1991, 1993-1997.

Year	Species	Mean	Std. error	Median	Std. deviation	Minimum	Maximum
1991	LRS	152.4	0.6496	153.0	9.787	107.0	186.0
1991	SNS	155.8	0.5641	155.0	7.135	143.0	174.0
1991	BOTH	153.8	0.4539	154.0	8.929	107.0	186.0
1993	LRS	154.8	0.7781	155.0	14.11	120.0	191.0
1993	SNS	153.3	0.8363	154.0	12.06	129.0	178.0
1993	BOTH	154.2	0.5767	155.0	13.36	120.0	191.0
1994	LRS	139.2	2.905	136.0	17.43	112.0	176.0
1994	SNS	140.8	2.736	139.0	12.54	114.0	161.0
1994	BOTH	139.8	2.080	138.0	15.70	112.0	176.0
1995	LRS	120.4	1.441	123.0	14.41	81.0	149.0
1995	SNS	120.3	1.024	121.0	13.55	94.0	156.0
1995	BOTH	120.3	0.8347	122.0	13.84	81.0	156.0
1996	LRS	151.2	2.608	149.0	11.95	135.0	179.0
1996	SNS	159.2	0.8106	157.0	11.23	128.0	193.0
1996	BOTH	158.4	0.7896	157.0	11.52	128.0	193.0
1997	LRS	128.5	3.202	126.0	6.403	124.0	138.0
1997	SNS	140.0	1.178	139.0	10.86	122.0	173.0
1997	BOTH	139.4	1.160	139.0	10.94	122.0	173.0

Table 2.5. Results of Mann-Whitney U-tests of Julian hatchdate distributions between Lost River and shortnose suckers. Values in **boldface** are statistically significant at the 95% level or higher.

Year	Comparison	<i>P</i>
1991	LRS vs. SNS	0.0003
1993	LRS vs. SNS	0.4456
1994	LRS vs. SNS	0.5293
1995	LRS vs. SNS	0.2789
1996	LRS vs. SNS	0.0038
1997	LRS vs. SNS	0.0215

Table 2.6. Results of multiple comparison tests for Julian hatchdate distributions for Lost River and shortnose suckers: 1991, 1993-1997. Values in **boldface** are statistically significant at the 95% level or higher.

Comparison	<i>P</i> (LRS)	<i>P</i> (SNS)
1991-1993	0.0268	0.1252
1991-1994	0.0000	0.0000
1991-1995	0.0000	0.0000
1991-1996	0.3940	0.0006
1991-1997	0.0008	0.0000
1993-1994	0.0000	0.0001
1993-1995	0.0000	0.0000
1993-1996	0.1539	0.0000
1993-1997	0.0016	0.0000
1994-1995	0.0000	0.0000
1994-1996	0.0027	0.0000
1994-1997	0.2405	0.6398
1995-1996	0.0000	0.0000
1995-1997	0.2672	0.0000
1996-1997	0.0032	0.0000

Table 2.7. Growth rate statistics (mm/day) for Lost River and shortnose suckers: 1991, 1993-1997.

Year	Species	Mean	Std. error	Median	Std. deviation	Minimum	Maximum
1991	LRS	0.6553	0.0042	0.6417	0.0630	0.5575	0.8413
1991	SNS	0.5369	0.0043	0.5283	0.0536	0.3597	0.6410
1991	BOTH	0.6070	0.0042	0.6047	0.0831	0.3597	0.8413
1993	LRS	0.5305	0.0027	0.5333	0.0493	0.4352	0.6438
1993	SNS	0.4717	0.0036	0.4645	0.0512	0.3719	0.5653
1993	BOTH	0.5078	0.0025	0.5104	0.0577	0.3719	0.6438
1994	LRS	0.6384	0.0191	0.5976	0.1148	0.4898	0.8810
1994	SNS	0.5193	0.0164	0.5277	0.0751	0.3785	0.6466
1994	BOTH	0.5945	0.0155	0.5756	0.1167	0.3785	0.8810
1995	LRS	0.4482	0.0049	0.4471	0.0494	0.3570	0.5603
1995	SNS	0.4164	0.0030	0.4074	0.0401	0.3368	0.5043
1995	BOTH	0.4279	0.0028	0.4300	0.0462	0.3368	0.5603
1996	LRS	0.5339	0.0162	0.5602	0.0744	0.3946	0.6971
1996	SNS	0.4567	0.0051	0.4389	0.0711	0.3328	0.7034
1996	BOTH	0.4643	0.0051	0.4568	0.0749	0.3328	0.7034
1997	LRS	0.4382	0.0136	0.4397	0.0272	0.4053	0.4681
1997	SNS	0.4440	0.0065	0.4469	0.0598	0.2787	0.6172
1997	BOTH	0.4437	0.0062	0.4469	0.0586	0.2787	0.6172

Table 2.8. Results of Mann-Whitney U-tests of growth rate distributions for Lost River and shortnose suckers. Values in **boldface** are statistically significant at the 95% level and higher.

Year	Comparison	P
1991	LRS vs. SNS	0.0000
1993	LRS vs. SNS	0.0000
1994	LRS vs. SNS	0.0000
1995	LRS vs. SNS	0.0000
1996	LRS vs. SNS	0.0000
1997	LRS vs. SNS	0.6993

Table 2.9. Results of multiple comparison tests for growth rate distributions for Lost River and shortnose suckers: 1991, 1993-1997. Values in boldface are statistically significant at the 95% level or higher.

Comparison	P (LRS)	P (SNS)
1991-1993	0.0000	0.0000
1991-1994	0.0188	0.1895
1991-1995	0.0000	0.0000
1991-1996	0.0000	0.0000
1991-1997	0.0006	0.0000
1993-1994	0.0000	0.0022
1993-1995	0.0000	0.0000
1993-1996	0.6598	0.0051
1993-1997	0.0016	0.0011
1994-1995	0.0000	0.0000
1994-1996	0.0023	0.0004
1994-1997	0.0012	0.0000
1995-1996	0.0000	0.0000
1995-1997	0.5148	0.0000
1996-1997	0.0232	0.3455

Table 2.10. Variables from multiple regression analysis of environmental effects on increment width residuals. Values in **boldface** are statistically significant at the 95% level or higher.

Variable	Regression coefficient	Std. error	t value	Pr (> t)
Conductivity	-0.0133	0.0446	-0.2980	0.7669
D.O.	-0.1102	0.1887	-0.5840	0.5618
Unionized ammonia	-0.0002	0.0003	-0.5900	0.5578
pH	0.3907	0.7004	0.5579	0.5793
Temperature	0.2269	0.0979	2.3167	0.0246

Table 3.1. Regression coefficients from the linear mixed-effects model (Equation 2) applied to the residuals from baseline 2. Entries in **boldface** are statistically significant ($P < 0.05$).

Year	Species	D.O.	Level	Lunar phase	pH	Redox x10 ⁴	Temp.
1994	LRS	-0.0053	-0.316	-0.0028	0.104	-0.542	0.017
1994	SNS	-0.0124	-0.271	0.0150	0.088	1.906	0.048
1995	LRS	-0.0471	-0.241	-0.0072	0.248	0.719	0.042
1995	SNS	-0.0530	-0.242	-0.0056	0.490	-1.245	0.060

Table 3.2. Regression coefficients from the linear mixed-effects model applied to the residuals from baseline 2, with backwards stepwise variable selection. All tabled entries are significant at the 0.05 level.

Year	Species	D.O.	Level	Lunar phase	pH	Redox x 10 ⁴	Temp.
1994	LRS	--	-0.328	--	0.160	--	--
1994	SNS	--	-0.273	0.0145	--	--	0.056
1995	LRS	-0.0470	-0.241	--	0.218	--	0.047
1995	SNS	-0.0526	-0.242	--	0.493	--	0.062

Table 3.3. Regression coefficients from the linear mixed-effects model applied to the residuals from baseline 2, for three age intervals: 1-40 days (1), 41-80 days (2), and greater than 80 days (3). Entries in **boldface** are statistically significant ($P < 0.05$).

Year	Species	Age group	D.O.	Level	Lunar phase	pH	Redox x10 ⁴	Temp.
1994	LRS	1	0.0375	-0.351	0.0009	0.067	-1.838	-0.008
1994	LRS	2	-0.0002	-0.406	0.0052	0.139	-4.852	0.019
1994	LRS	3	-0.0176	-0.260	-0.0172	0.082	6.255	0.015
1994	SNS	1	0.0027	-0.746	-0.0109	-0.219	1.484	0.043
1994	SNS	2	-0.0557	0.087	0.0286	0.291	10.349	0.099
1994	SNS	3	0.0268	-0.113	0.0096	-0.114	7.287	0.063
1995	LRS	1	0.0315	0.589	-0.0262	-0.010	2.171	0.036
1995	LRS	2	-0.0425	-0.065	-0.0166	0.090	-1.333	0.019
1995	LRS	3	-0.0438	-0.240	0.0104	0.151	-7.642	0.073
1995	SNS	1	-0.0462	-0.287	-0.0104	0.323	-1.887	0.033
1995	SNS	2	-0.0320	-0.111	-0.0160	0.546	1.155	0.054
1995	SNS	3	-0.0476	-0.141	-0.0005	0.314	-9.045	0.023

Table 3.4. Regression coefficients from the linear mixed-effects model applied to the residuals from baseline 2, for three intervals of Julian days: before day 151 (1), days 151 to 200 (2), and after day 200 (3). Entries in **boldface** are statistically significant ($P < 0.05$).

Year	Species	Date interval	D.O.	Level	Lunar phase	pH	Redox $\times 10^4$	Temp.
1994	LRS	1	0.0543	2.365	-0.0091	0.384	-13.90	-0.050
1994	LRS	2	-0.0290	-0.114	-0.0037	0.117	6.153	0.065
1994	LRS	3	0.0029	0.239	-0.0149	-0.059	2.294	-0.048
1994	SNS	1	0.0465	2.042	-0.0202	0.365	-7.675	-0.030
1994	SNS	2	-0.0347	-0.390	0.0109	0.074	10.47	0.071
1994	SNS	3	-0.0046	0.072	0.0345	-0.003	6.671	0.010
1995	LRS	1	0.0846	0.780	-0.0158	-0.462	0.152	0.056
1995	LRS	2	-0.0176	-1.195	-0.0430	0.122	-2.213	-0.018
1995	LRS	3	-0.0535	-0.261	0.0125	0.212	-9.698	0.070
1995	SNS	1	0.1339	0.343	-0.0107	-0.534	-3.777	0.055
1995	SNS	2	-0.0277	-1.277	-0.0436	0.645	-3.258	0.011
1995	SNS	3	-0.0395	-0.067	0.0024	0.339	-2.439	0.005

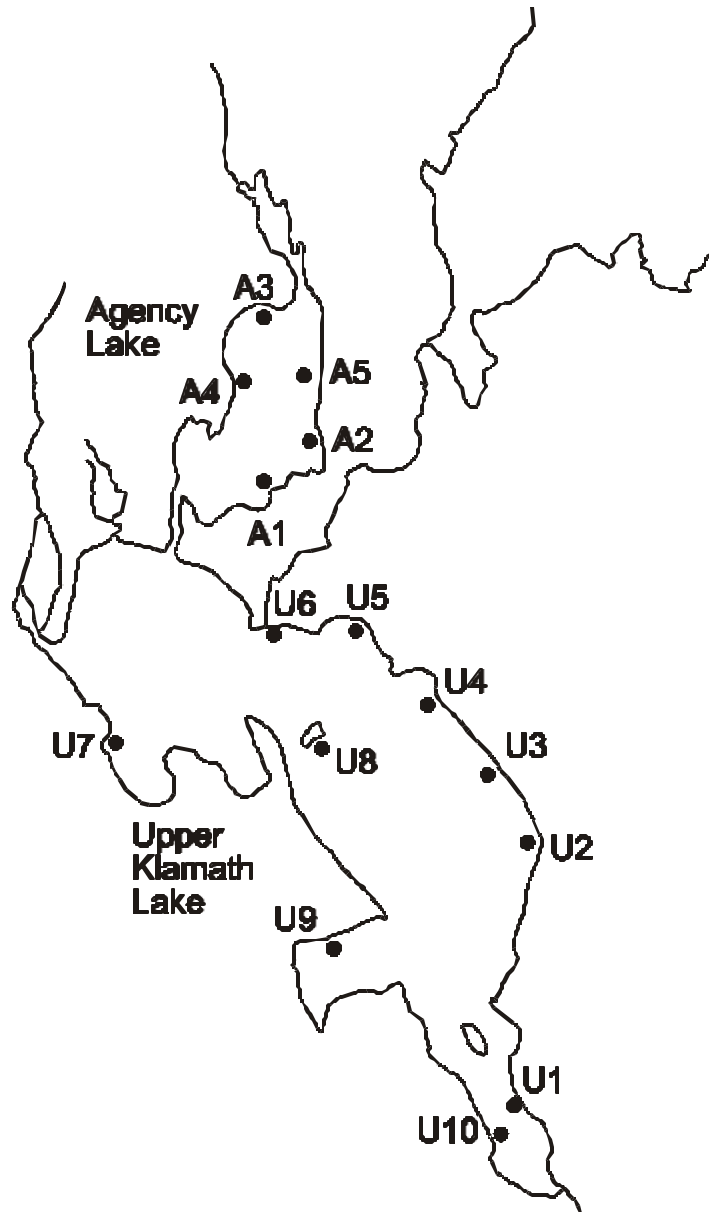


Figure 1.1. Fixed larval trawl and beach seine sites in Upper Klamath and Agency lakes.

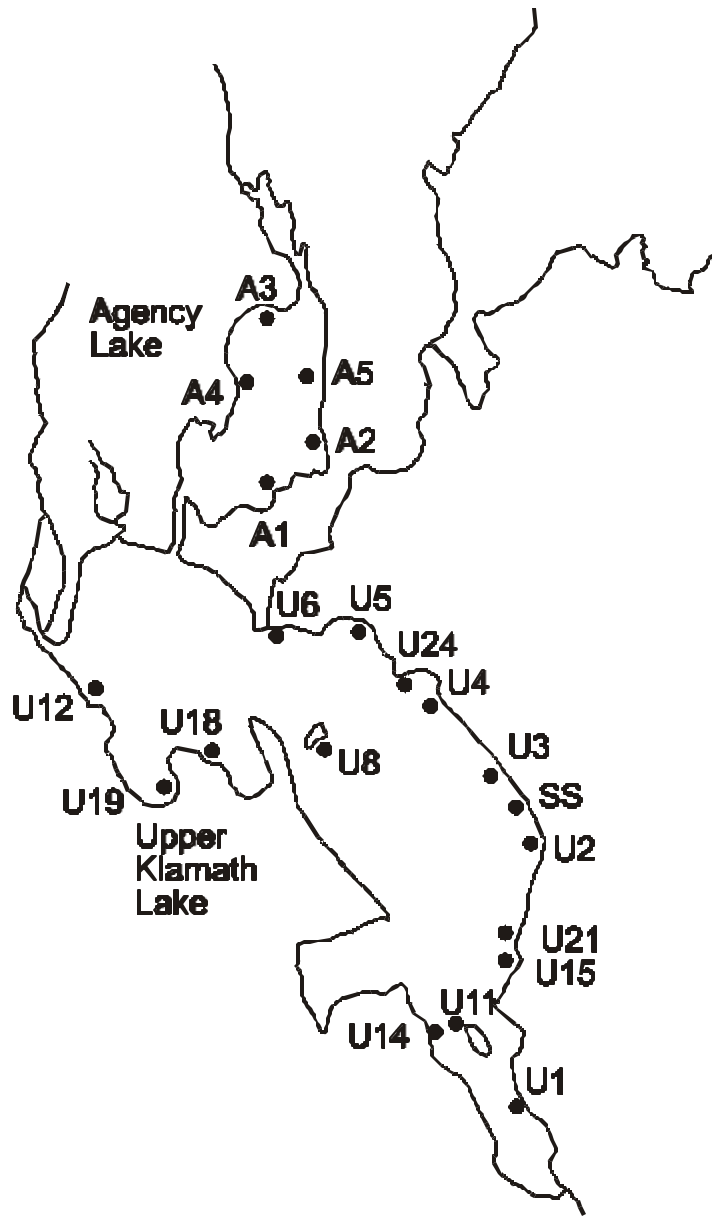


Figure 1.2. Fixed cast net sites in Upper Klamath and Agency lakes.

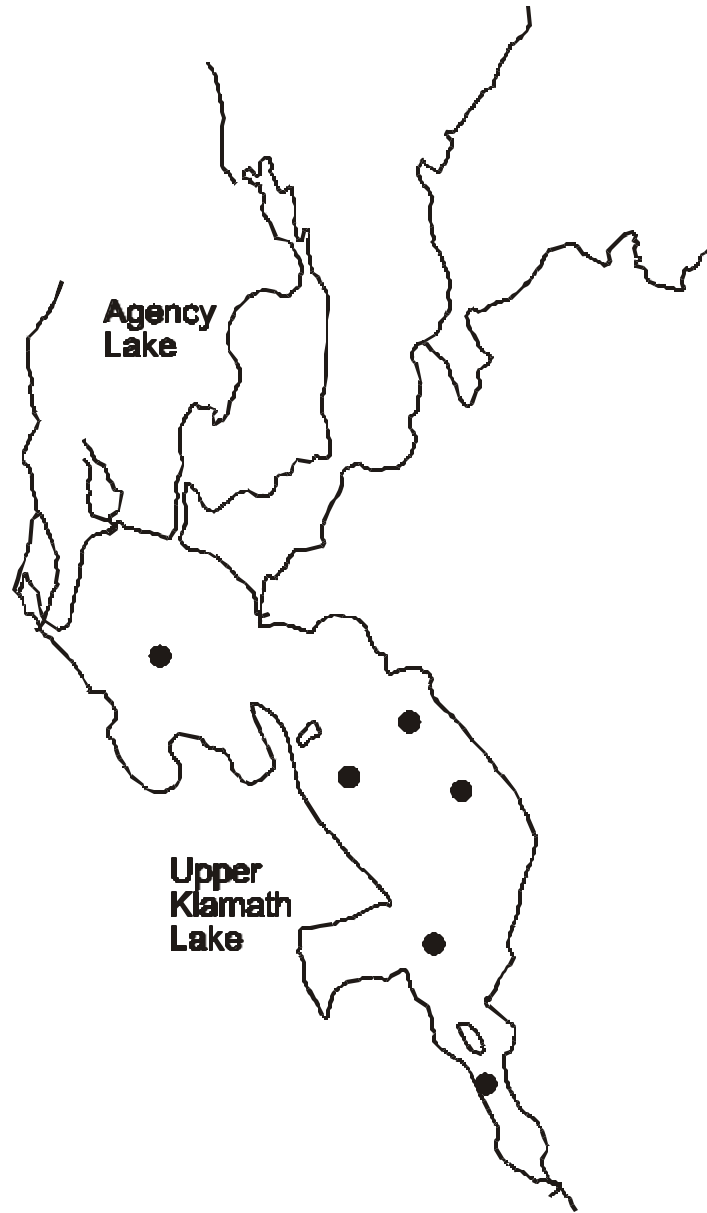


Figure 1.3. Fixed otter trawl sites in Upper Klamath and Agency lakes.

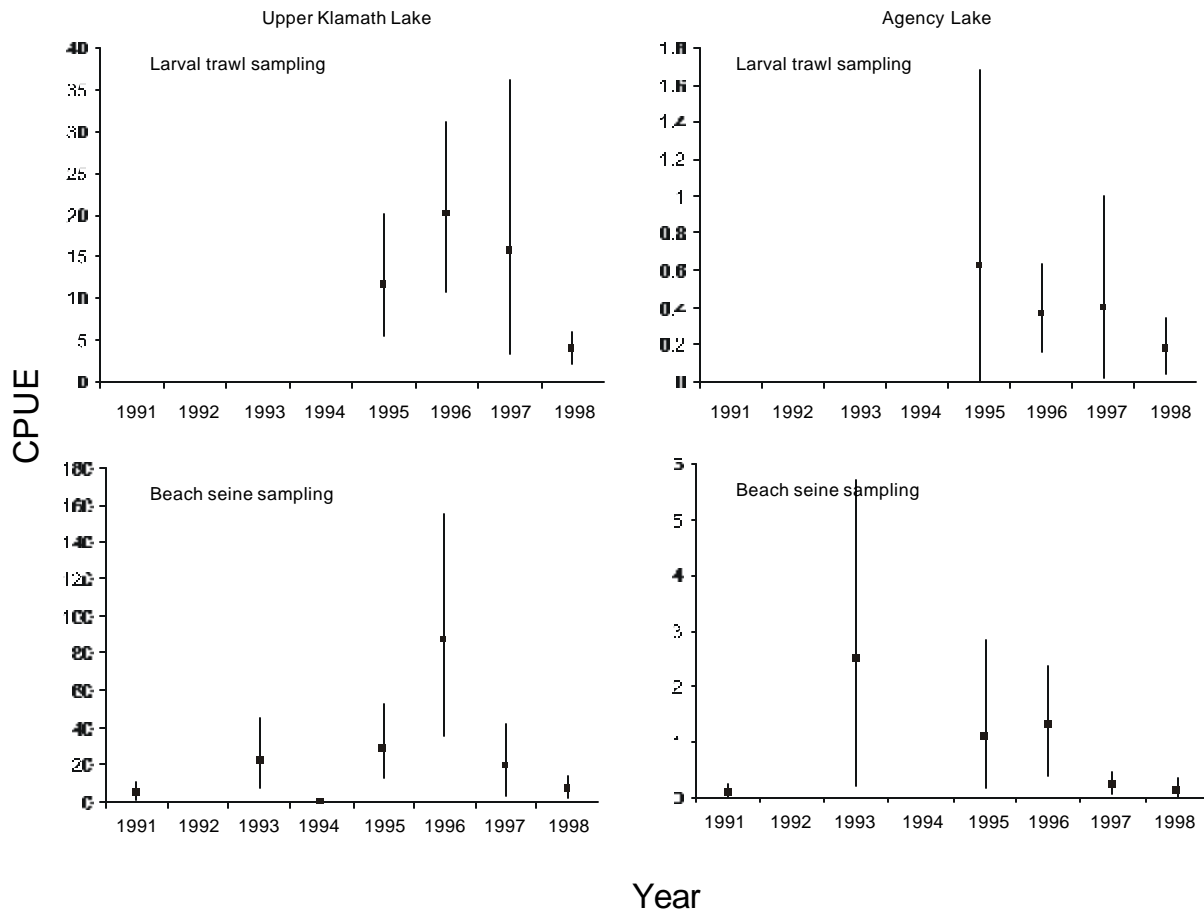


Figure 1.4. Larval trawl and beach seine catch-per-unit-effort by year in Upper Klamath and Agency lakes, 1991-1998. A unit of effort was a single larval trawl or beach seine haul.

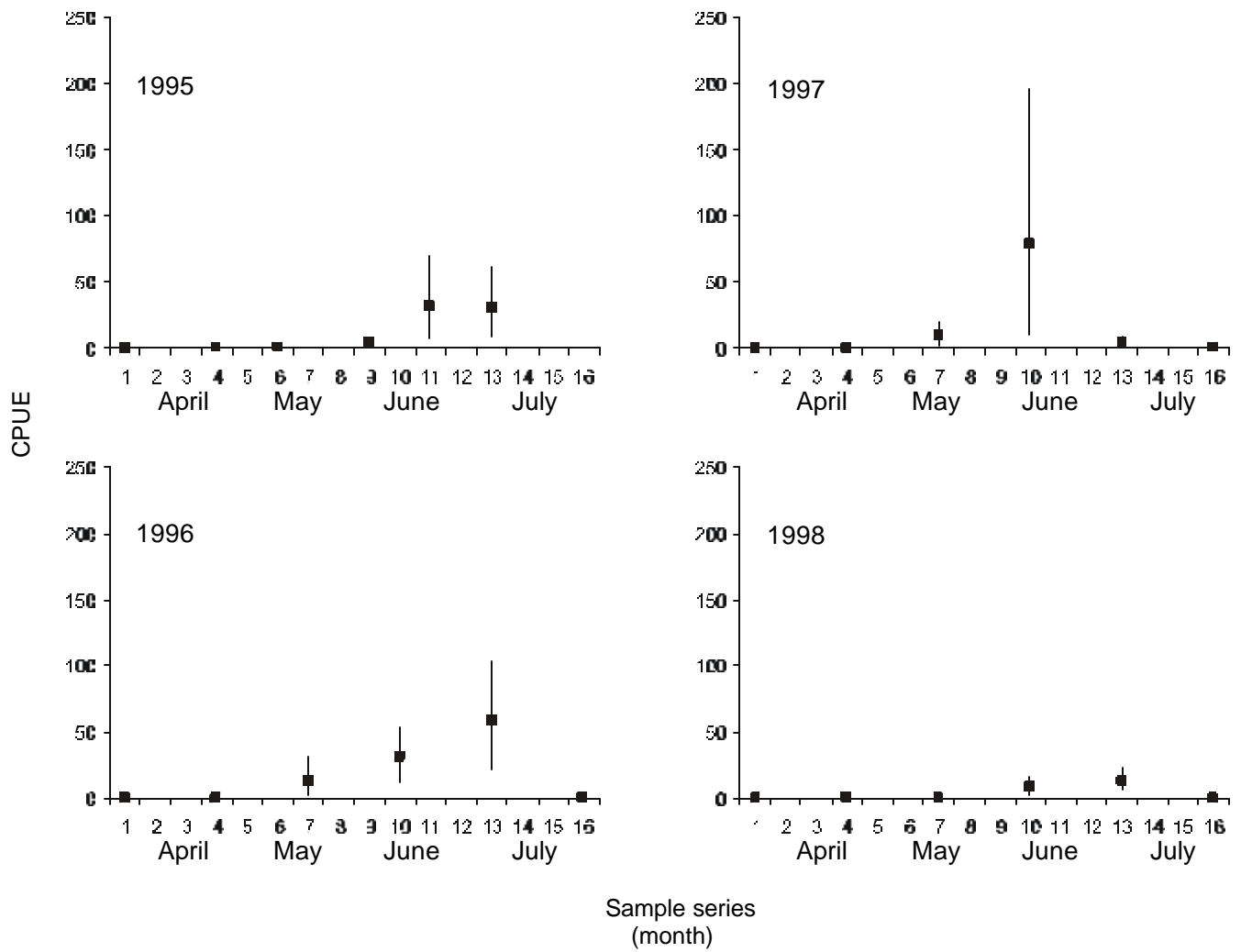


Figure 1.5. Larval trawl catch-per-unit-effort by sample series in Upper Klamath Lake, 1995-1998. A unit of effort was a single larval trawl. Series 1 is first week in April.

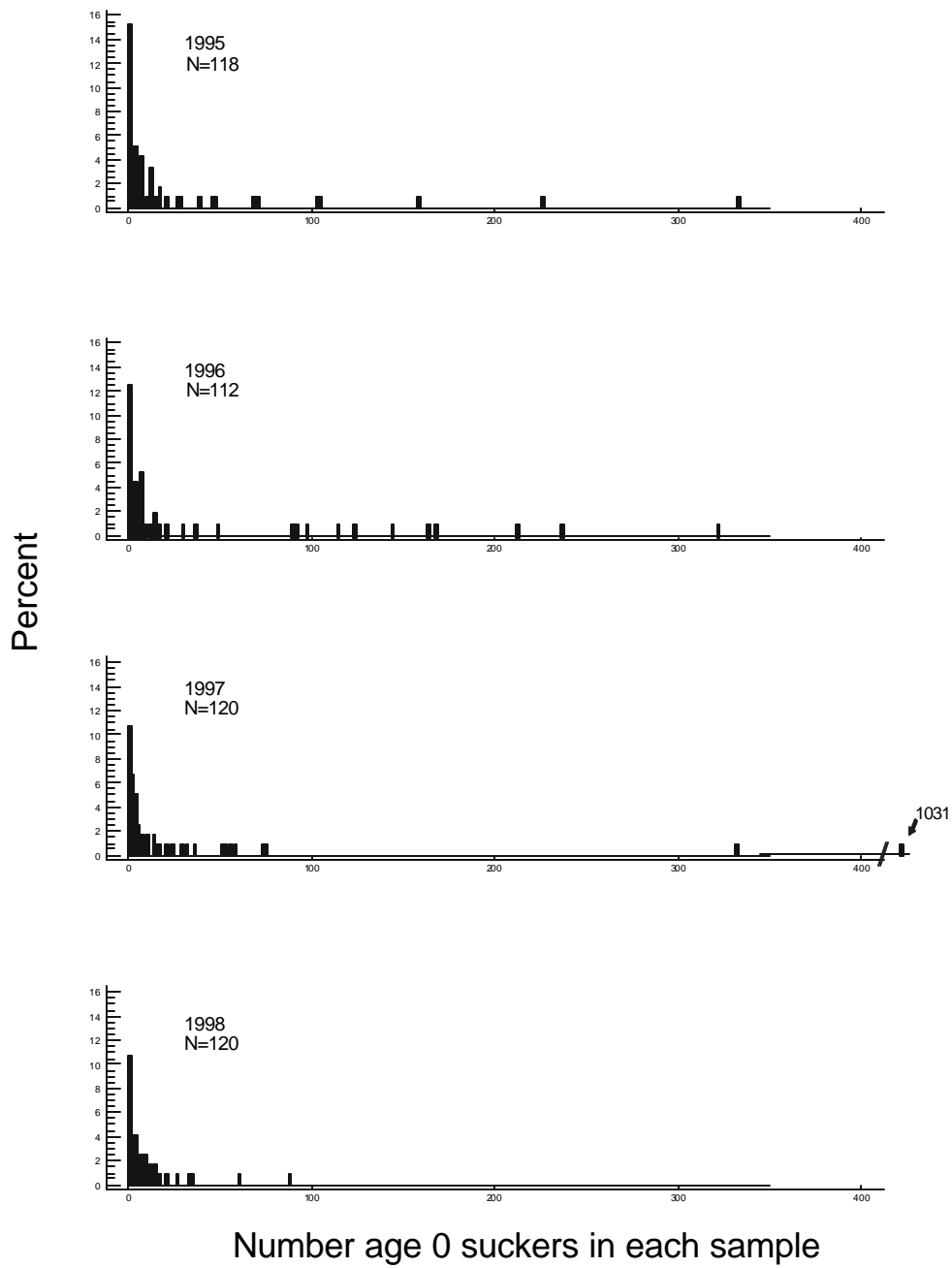


Figure 1.6. Frequency distribution of larval trawl catches in Upper Klamath Lake, 1995-1998.

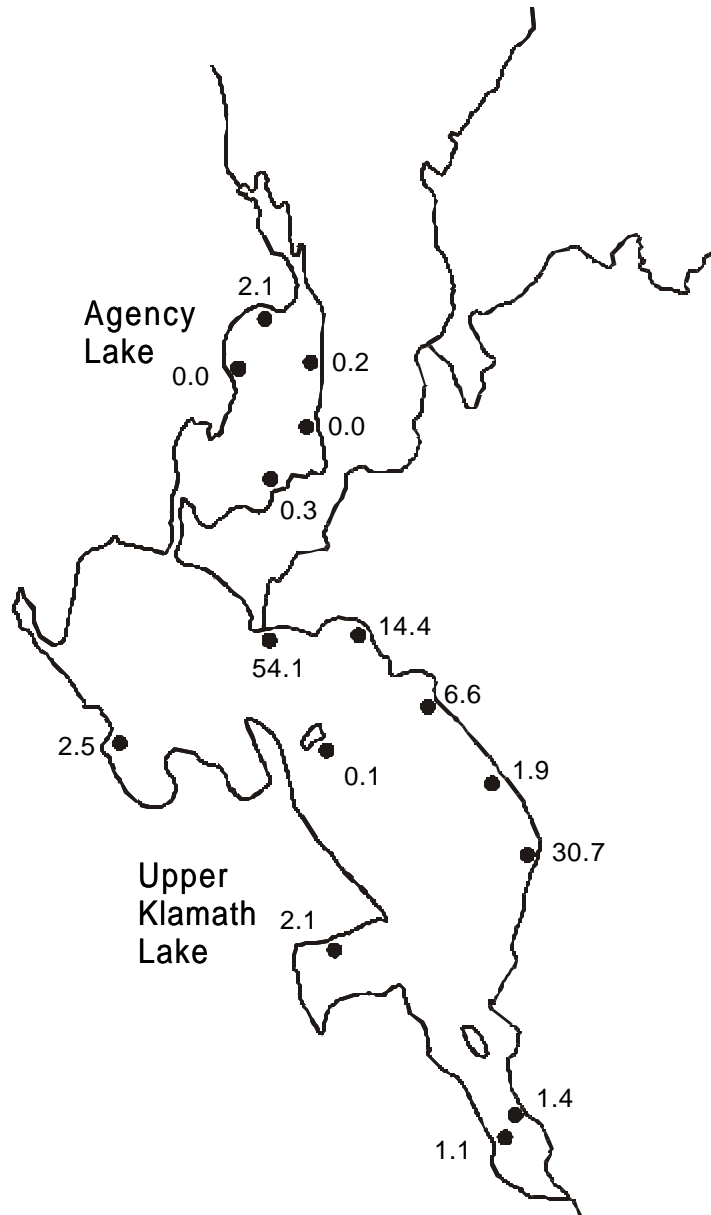


Figure 1.7. Larval trawl catch-per-unit-effort by site in Upper Klamath and Agency lakes, 1995. A unit of effort was a single larval trawl.

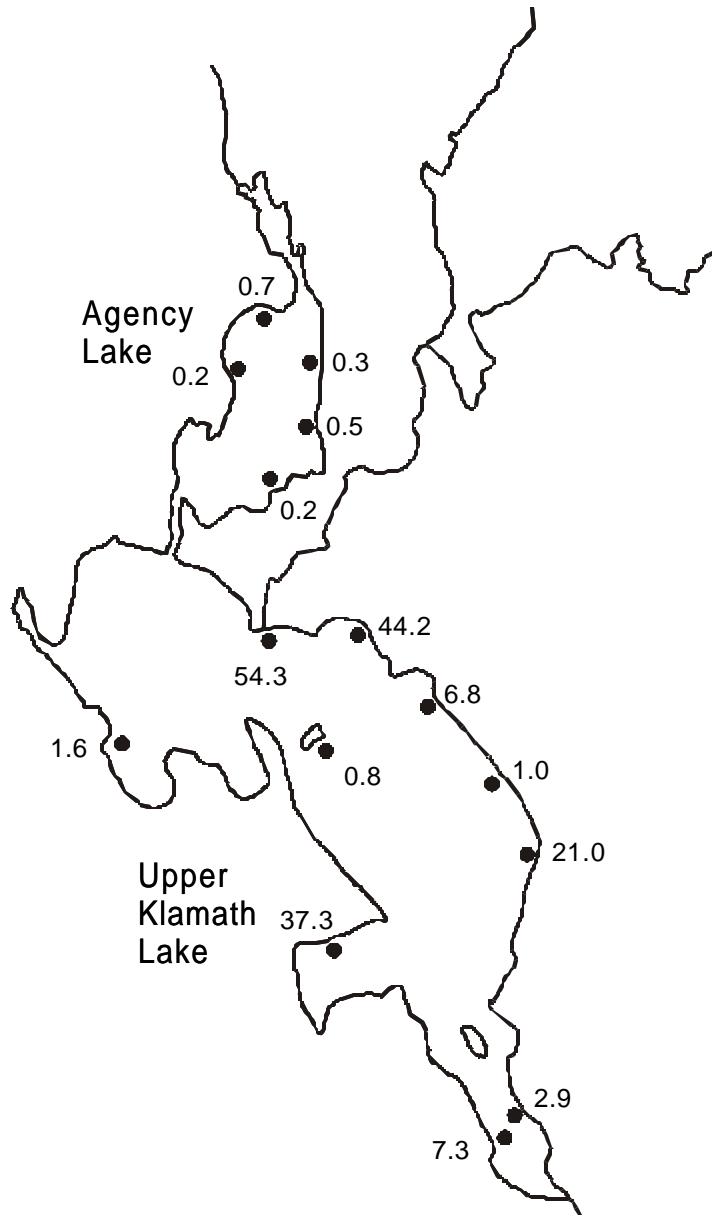


Figure 1.8. Larval trawl catch-per-unit-effort by site in Upper Klamath and Agency lakes, 1996. A unit of effort was a single larval trawl.

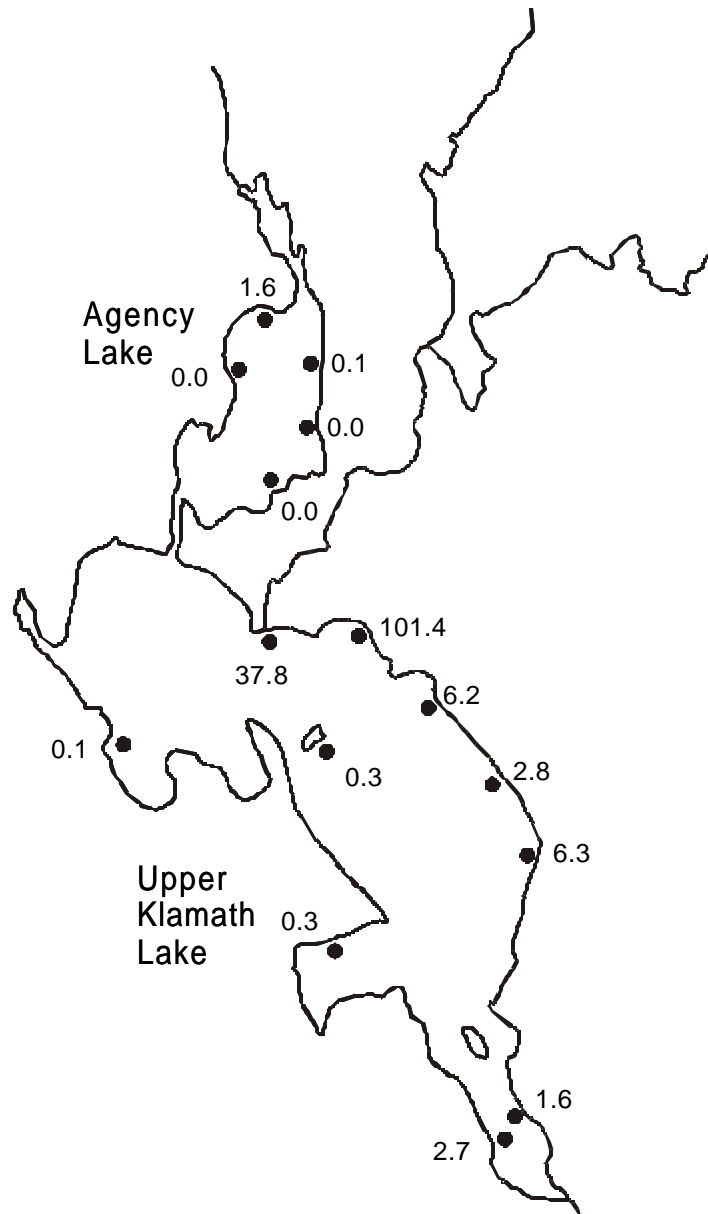


Figure 1.9. Larval trawl catch-per-unit-effort by site in Upper Klamath and Agency lakes, 1997. A unit of effort was a single larval trawl.

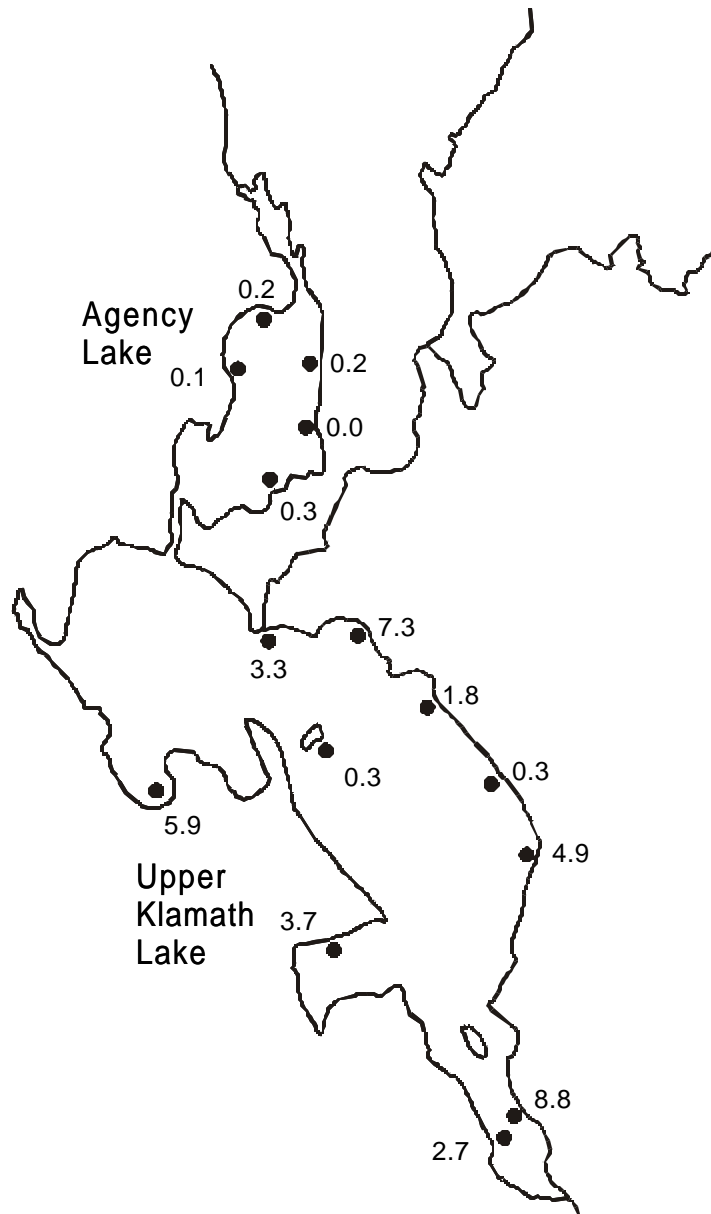


Figure 1.10. Larval trawl catch-per-unit-effort by site in Upper Klamath and Agency lakes, 1998. A unit of effort was a single larval trawl.

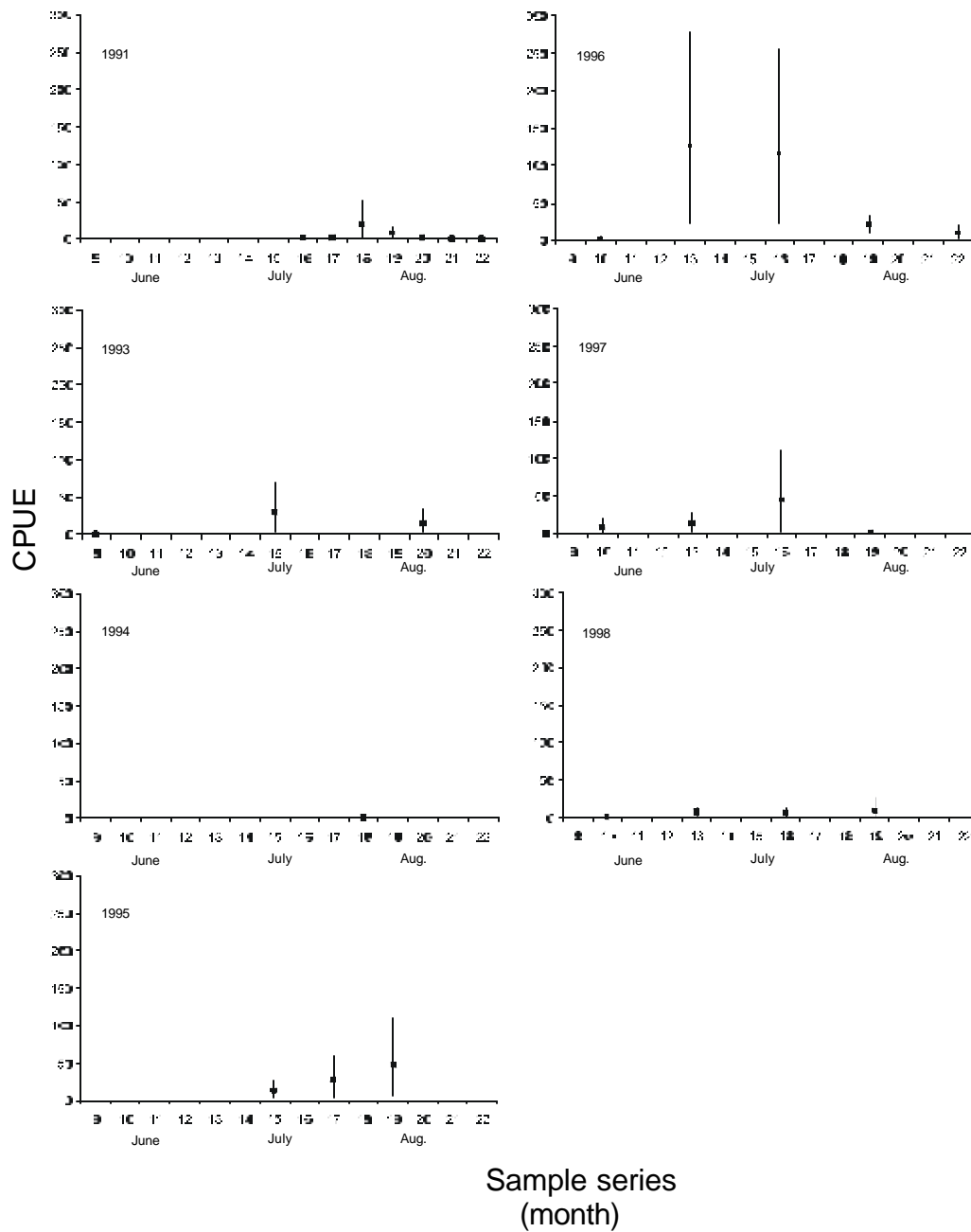


Figure 1.11. Beach seine catch-per-unit-effort by sample series in Upper Klamath Lakes, 1991-1998. A unit of effort was a single beach seine haul. Series 10 is approx. June 10th.

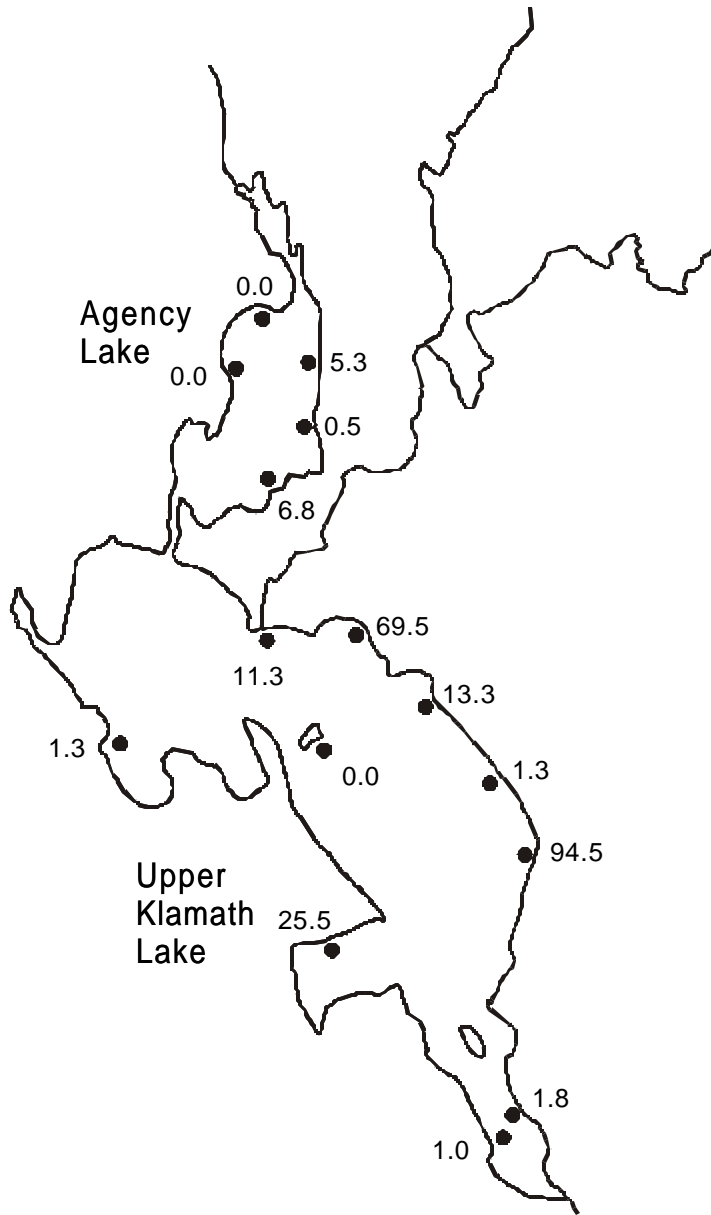


Figure 1.13. Beach seine catch-per-unit-effort by site in Upper Klamath and Agency lakes, 1993. A unit of effort was a single beach seine haul.

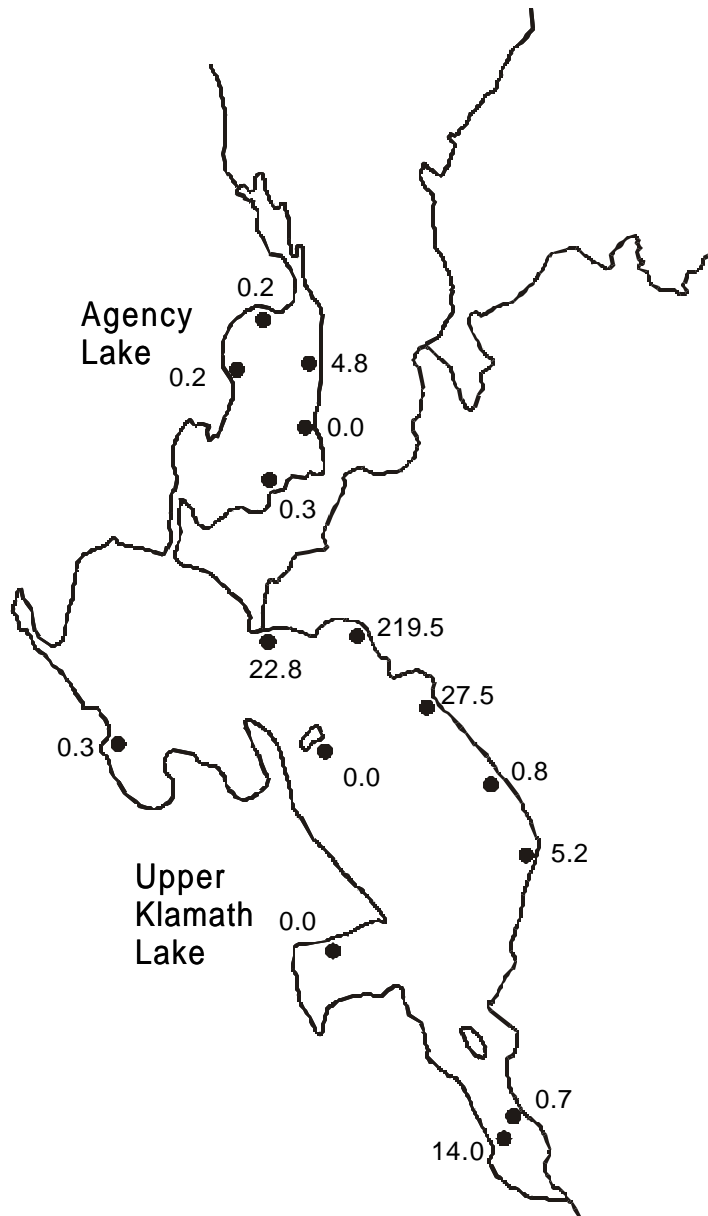


Figure 1.14. Beach seine catch-per-unit-effort by site in Upper Klamath and Agency lakes, 1995. A unit of effort was a single beach seine haul.

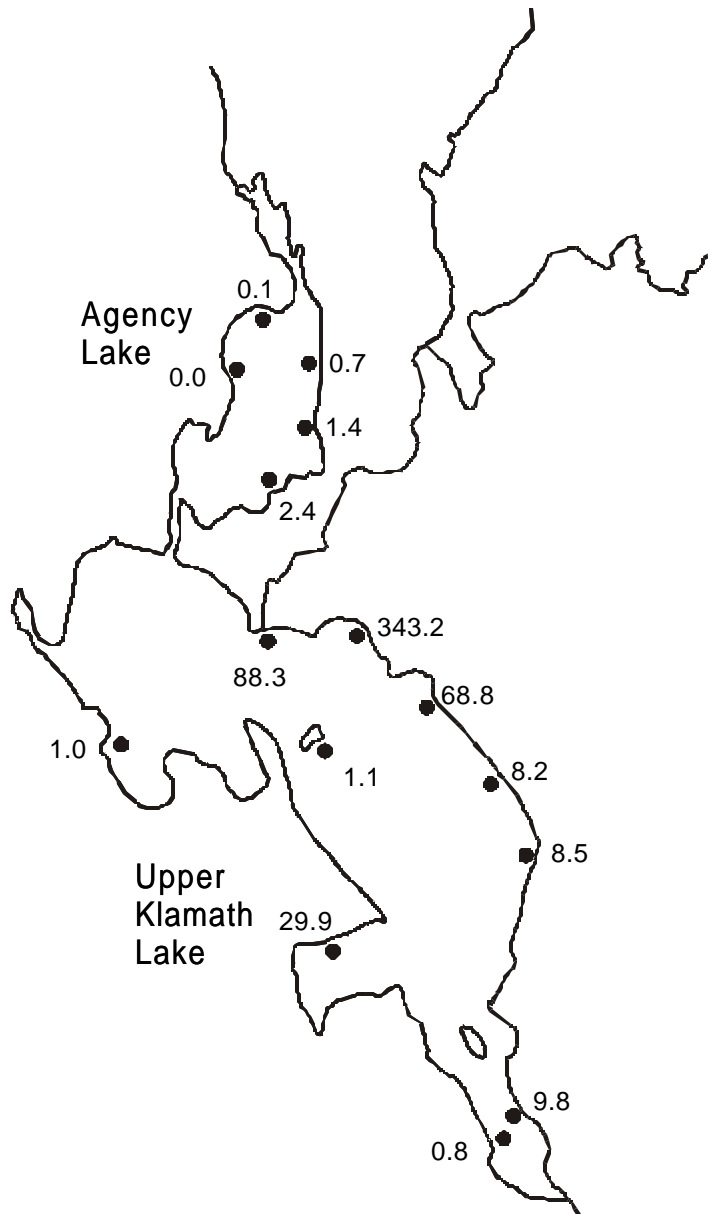


Figure 1.15. Beach seine catch-per-unit-effort by site in Upper Klamath and Agency lakes, 1996. A unit of effort was a single beach seine haul.

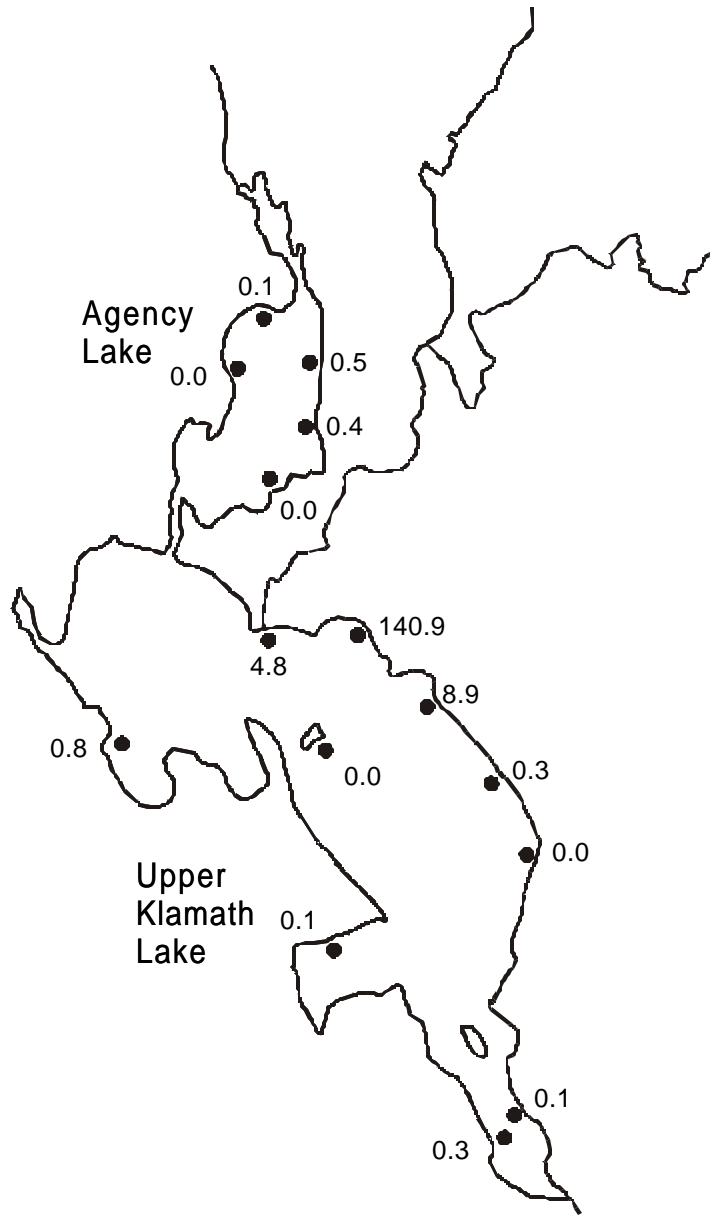


Figure 1.16. Beach seine catch-per-unit-effort by site in Upper Klamath and Agency lakes, 1997. A unit of effort was a single beach seine haul.

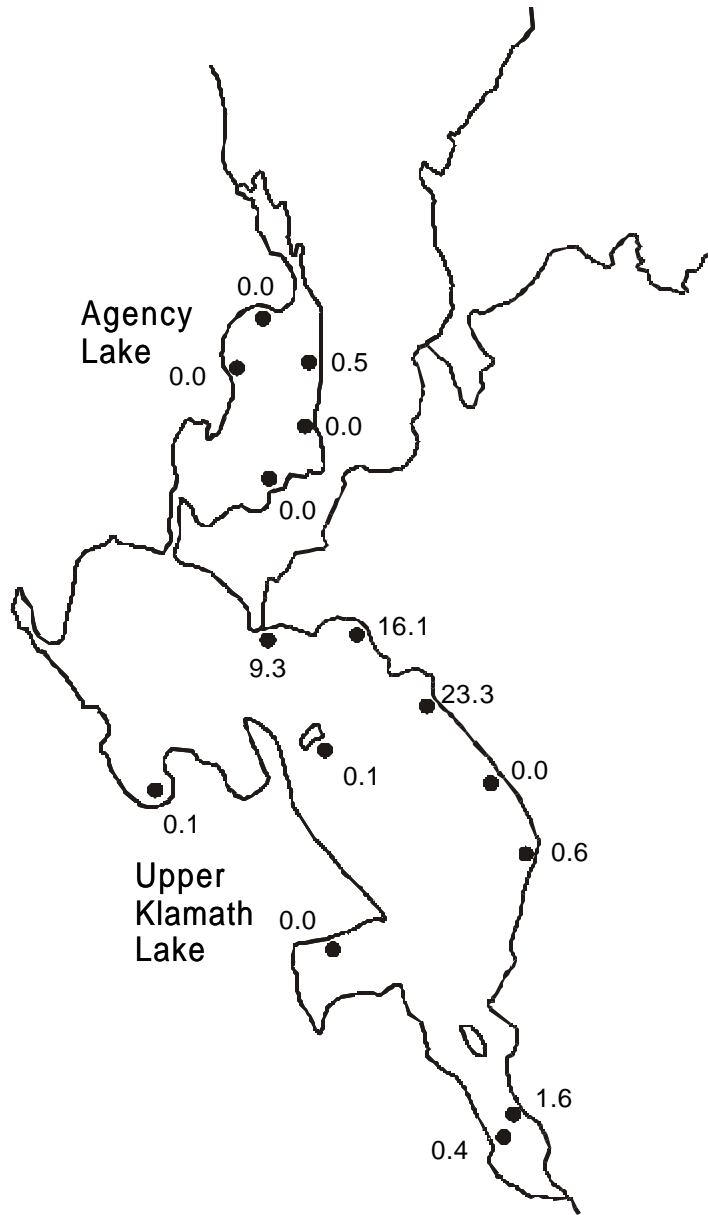


Figure 1.17. Beach seine catch-per-unit-effort by site in Upper Klamath and Agency lakes, 1998. A unit of effort was a single beach seine haul.

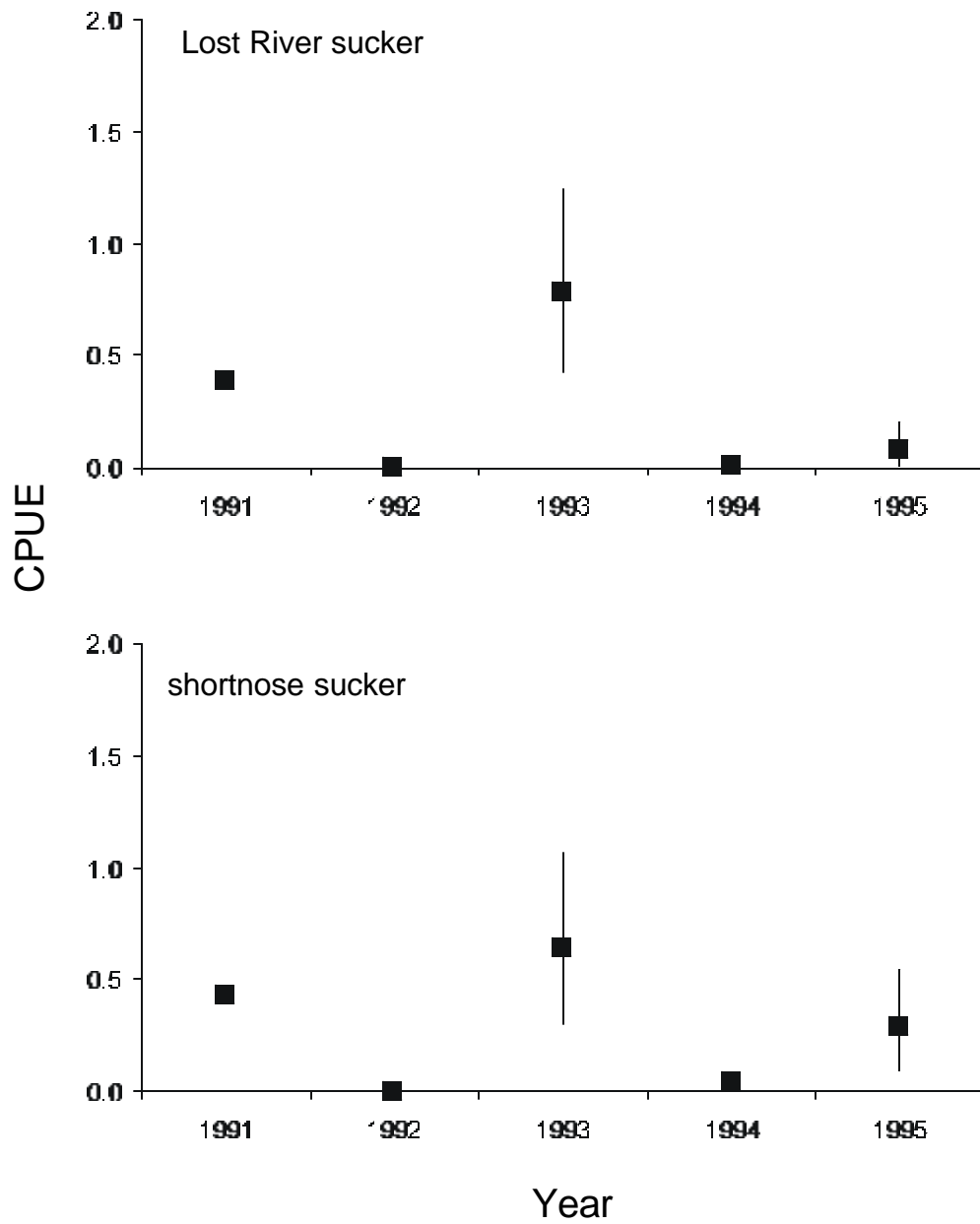


Figure 1.18. Fixed site cast net catch-per-unit-effort by year in Upper Klamath Lake, 1991-1995. A unit of effort was a single cast net sample.

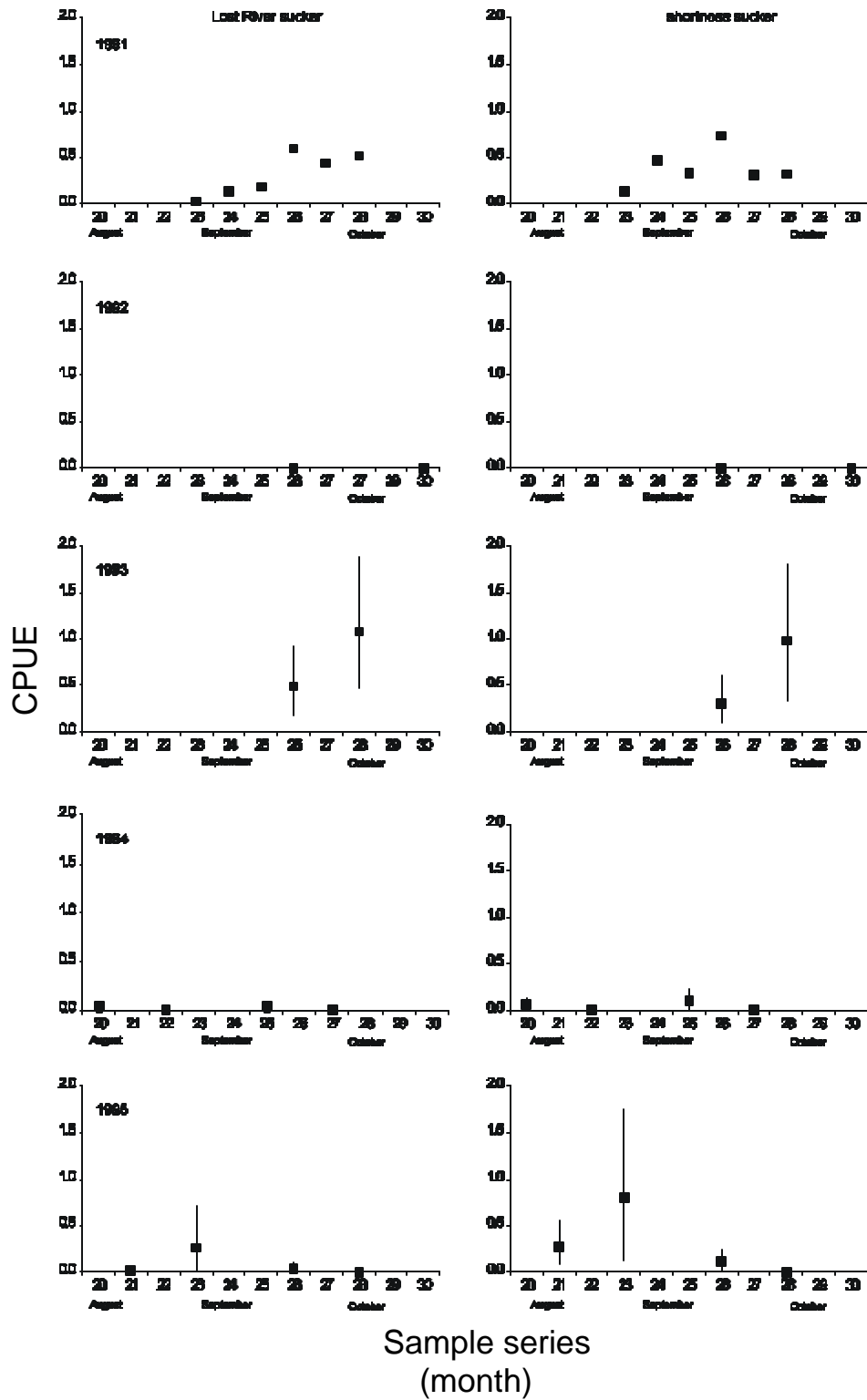


Figure 1.19. Fixed cast net catch-per-unit-effort by sample series in Upper Klamath Lake, 1991-1995. A unit of effort was a cast net sample. Sample series 20 was approx. August 21.

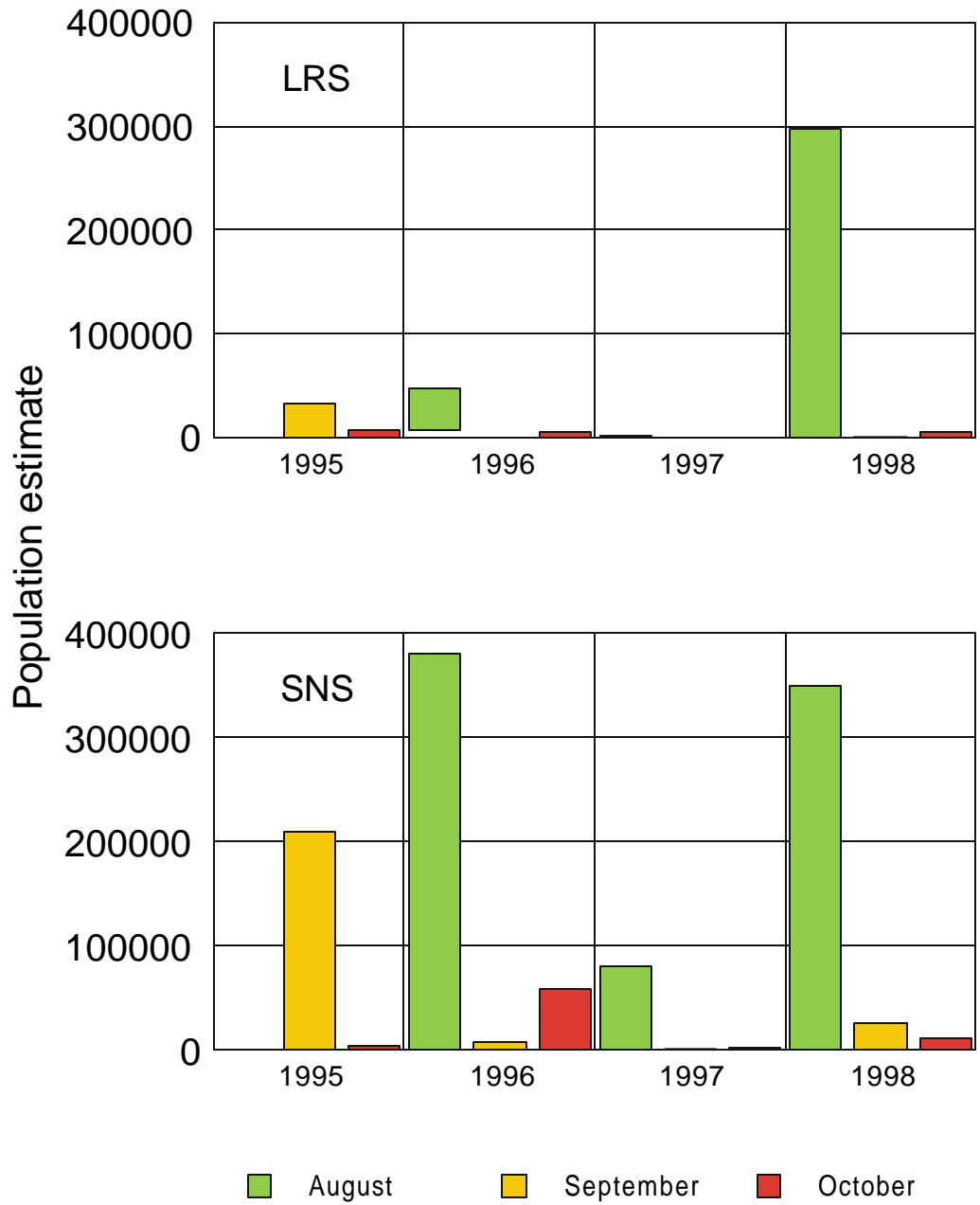


Figure 1.20. Shoreline population estimates by month of age 0 LRS and SNS, 1995-1998.

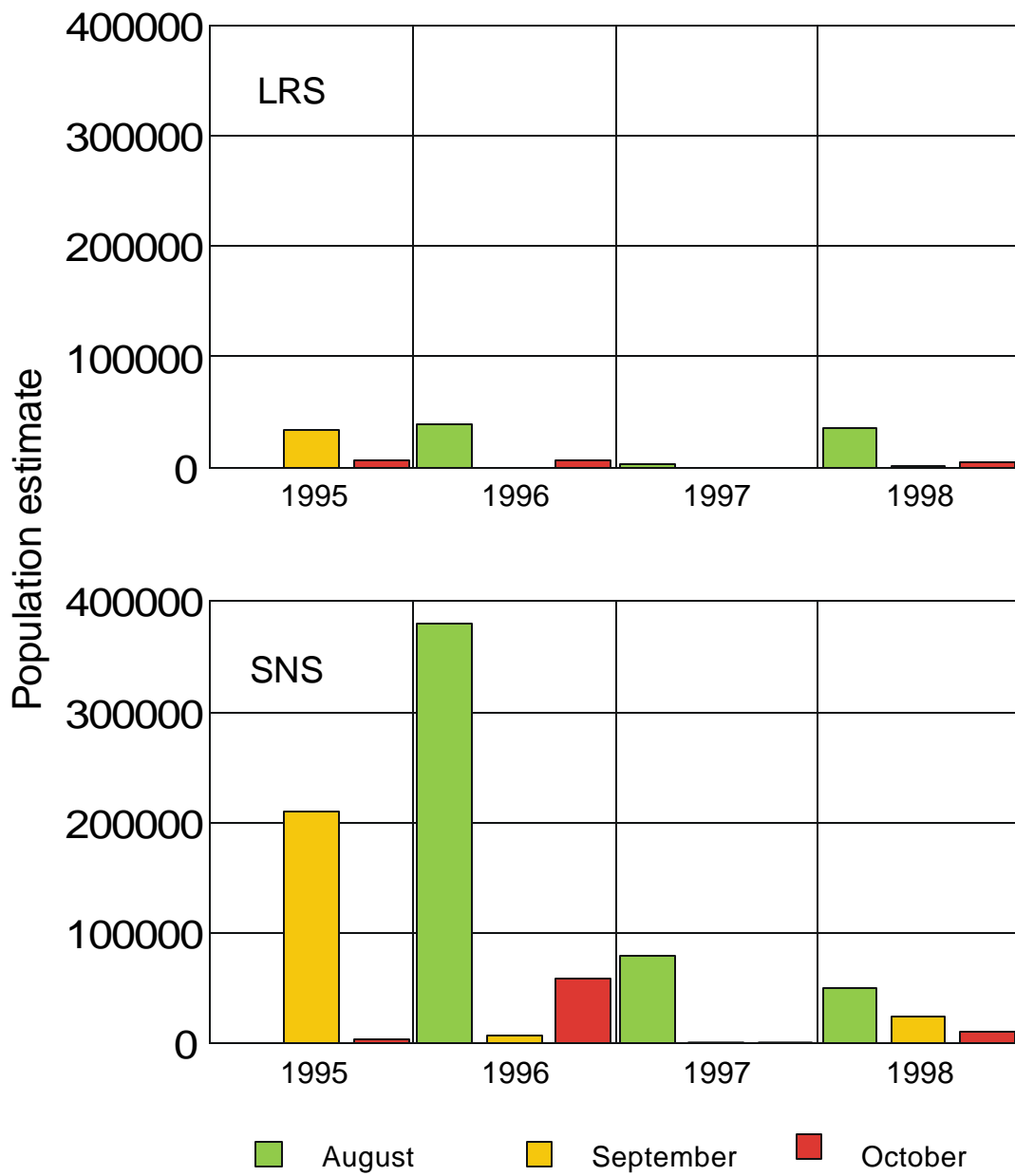


Figure 1.21. Shoreline population estimates by month of age 0 LRS and SNS, 1995-1998. Outlier sample excluded.

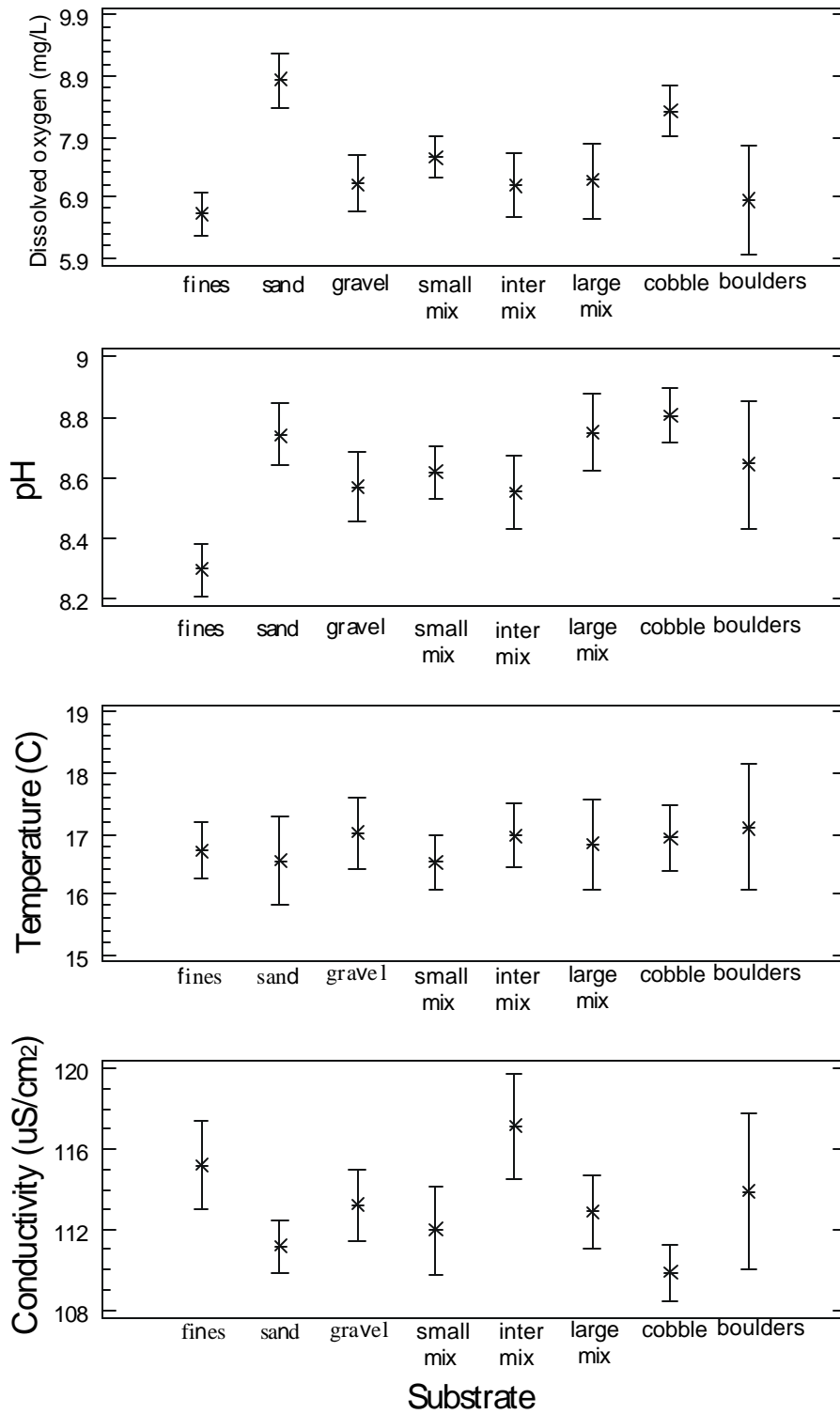


Figure 1.22. Associations between selected water quality variables and substrate type from stratified random cast net surveys, 1995-1998.

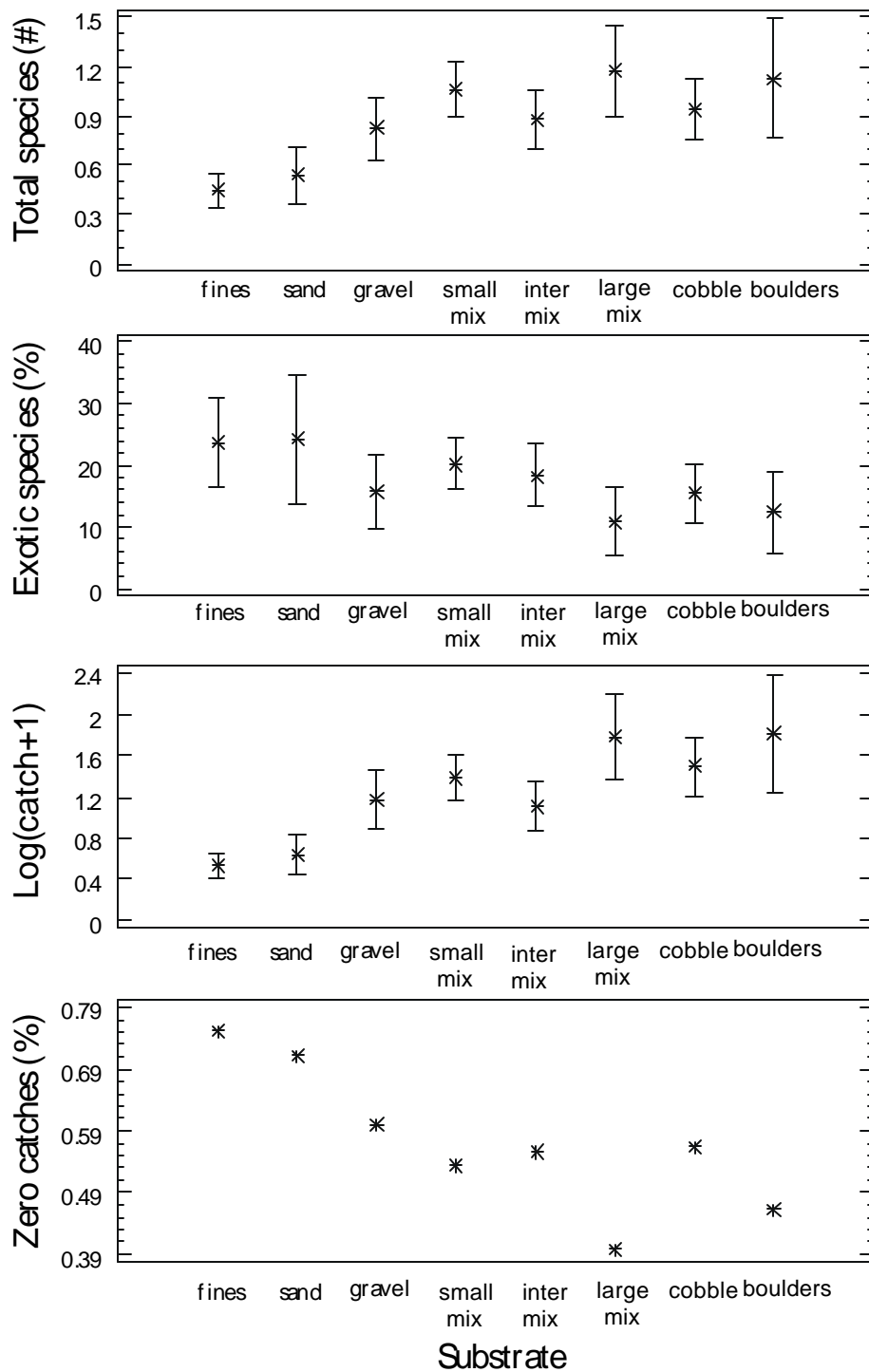


Figure 1.23. Associations between selected fish variables and substrate type from stratified random cast net surveys, 1995-1998.

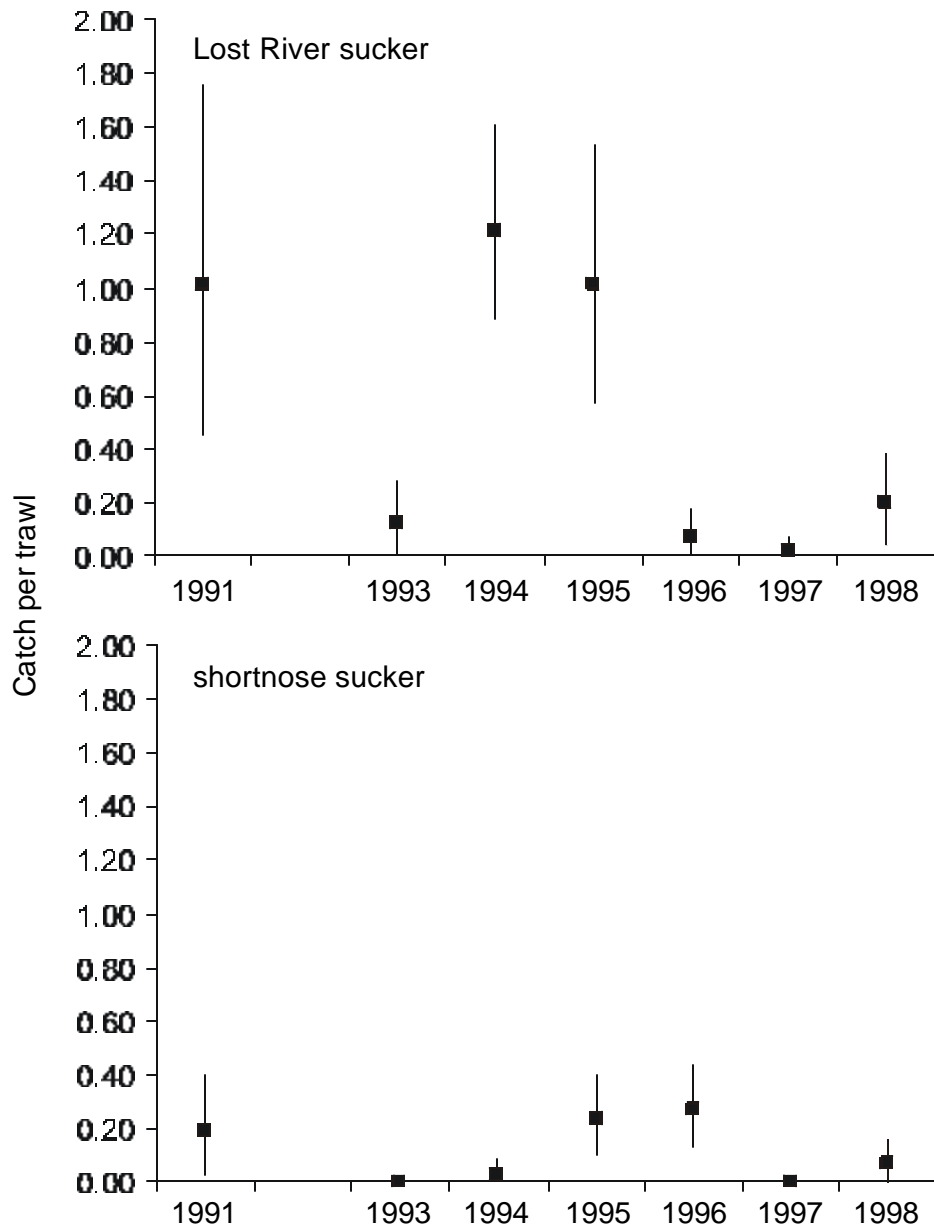


Figure 1.24. Otter trawl catch-per-unit-effort from late summer/fall sampling, Upper Klamath Lake, 1991-1998. A unit of effort was a single tow.

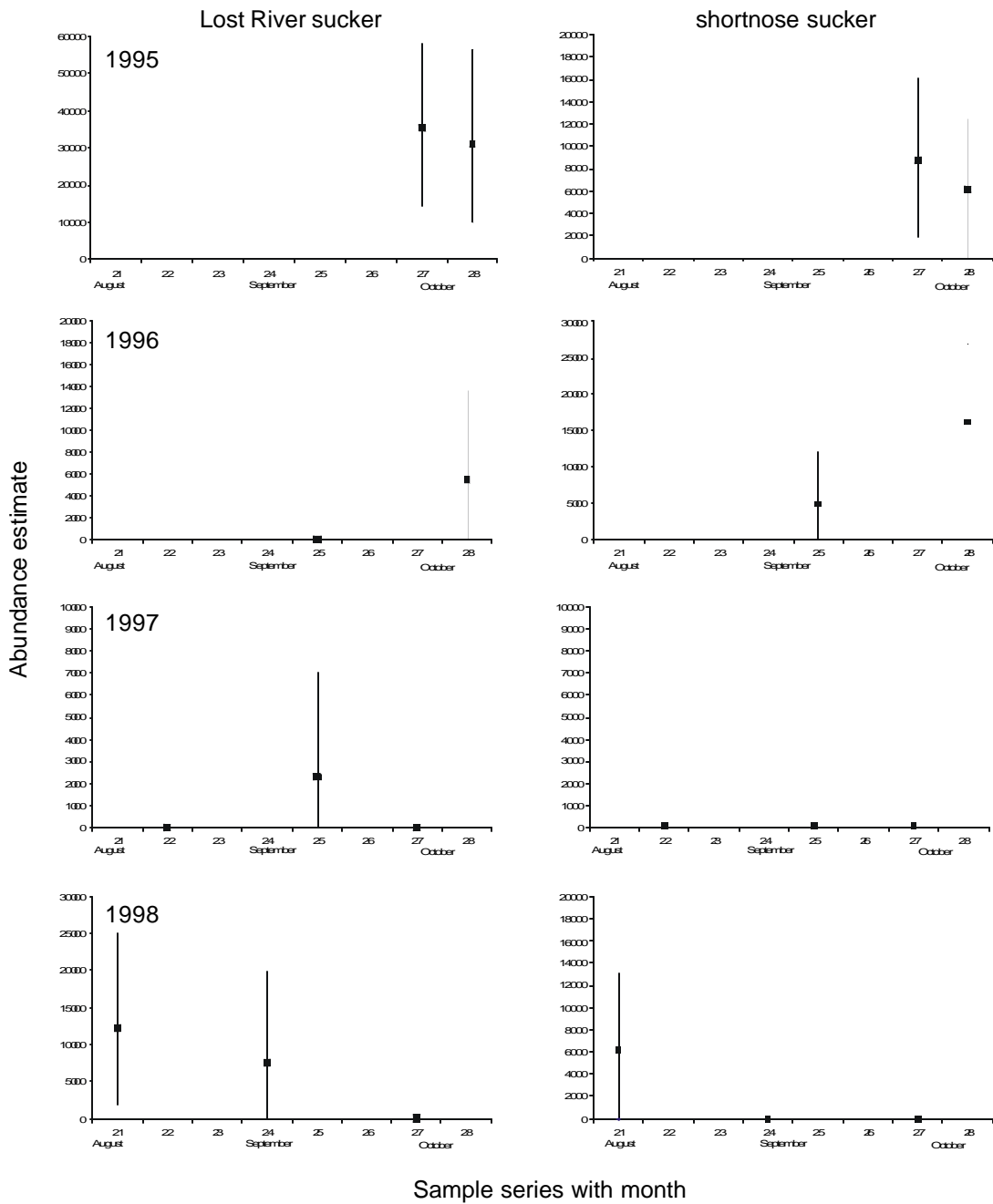


Figure 1.25. Offshore population estimates for each survey from otter trawl sampling in Upper Klamath Lake, 1995-1998.

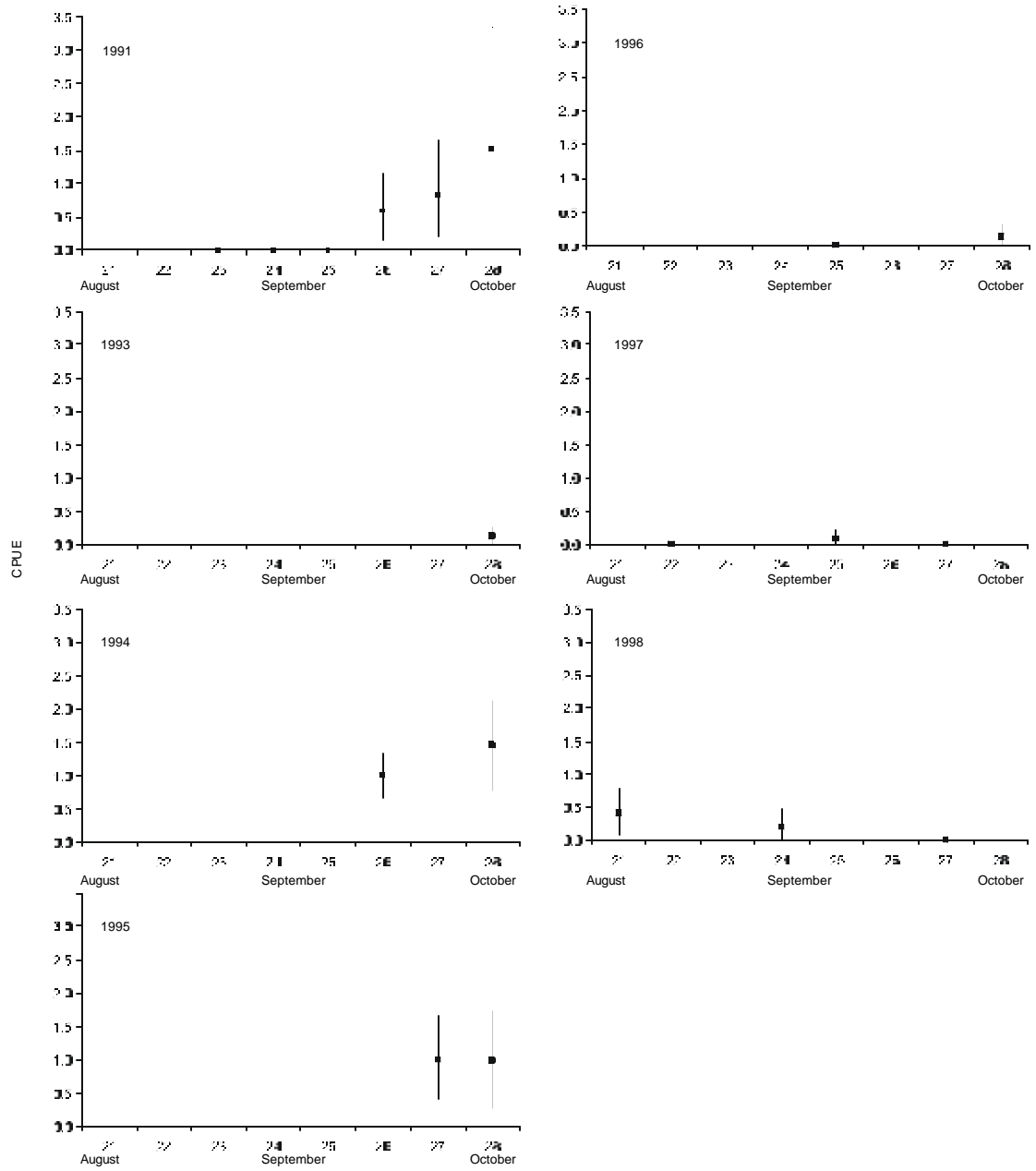


Figure 1.26. Otter trawl catch-per-unit-effort of age 0 LRS by sample series in Upper Klamath Lake, 1991-1998.

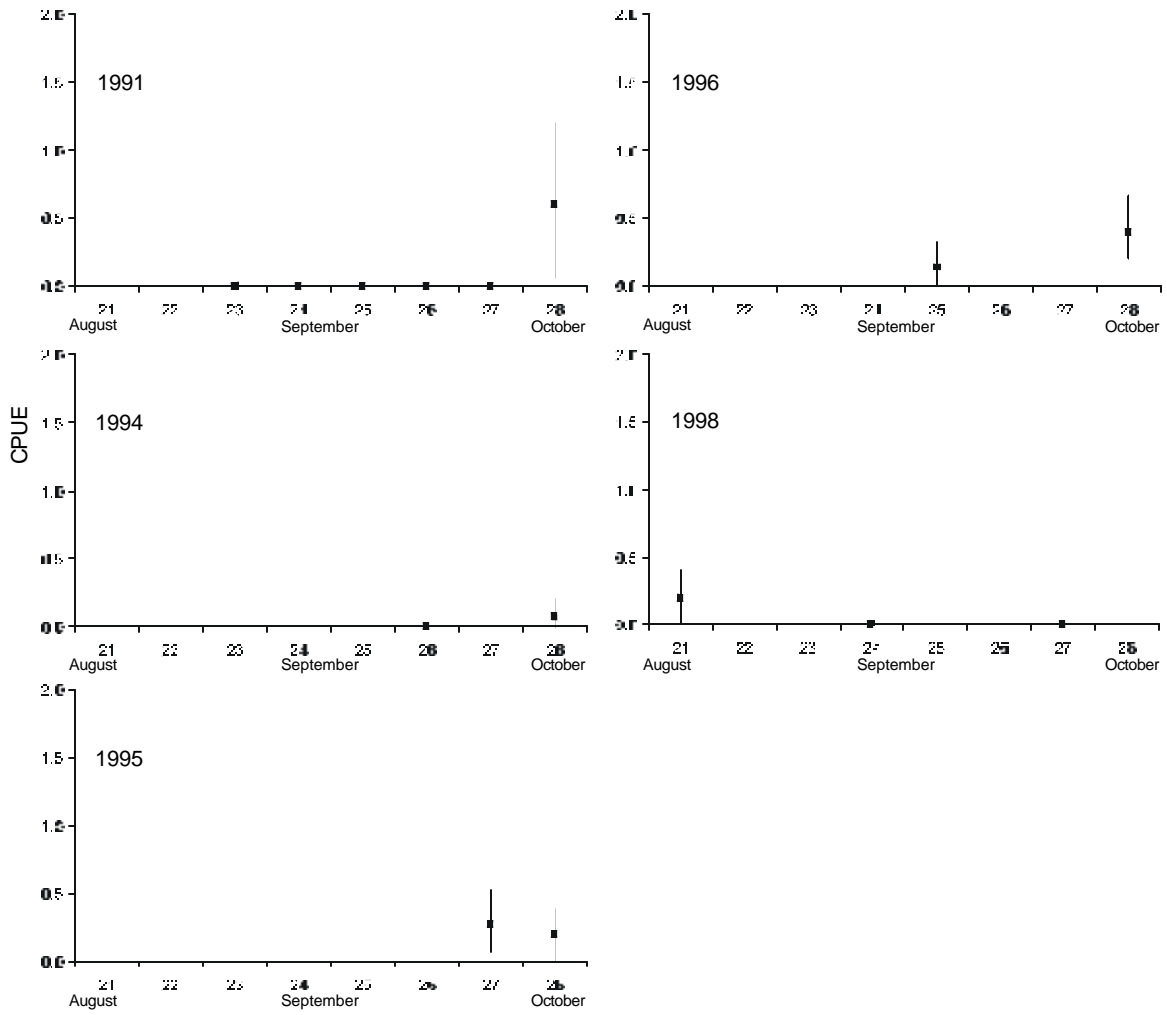


Figure 1.27. Otter trawl catch-per-unit-effort of age 0 SNS by sample series in Upper Klamath Lake, 1991-1998.

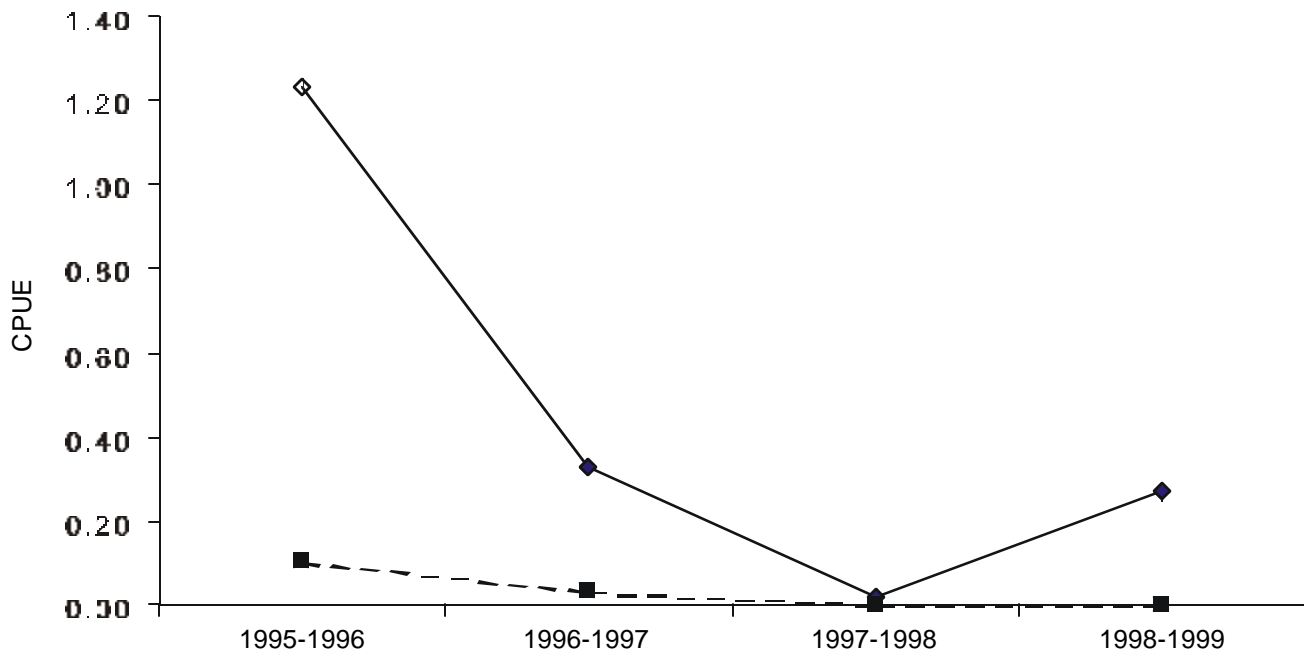


Figure 1.28. Catch-per-unit-effort of age 0 suckers in fall (solid line) and the subsequent spring (dashed line) from Upper Klamath Lake, 1995-1999. A unit of effort was a single tow.

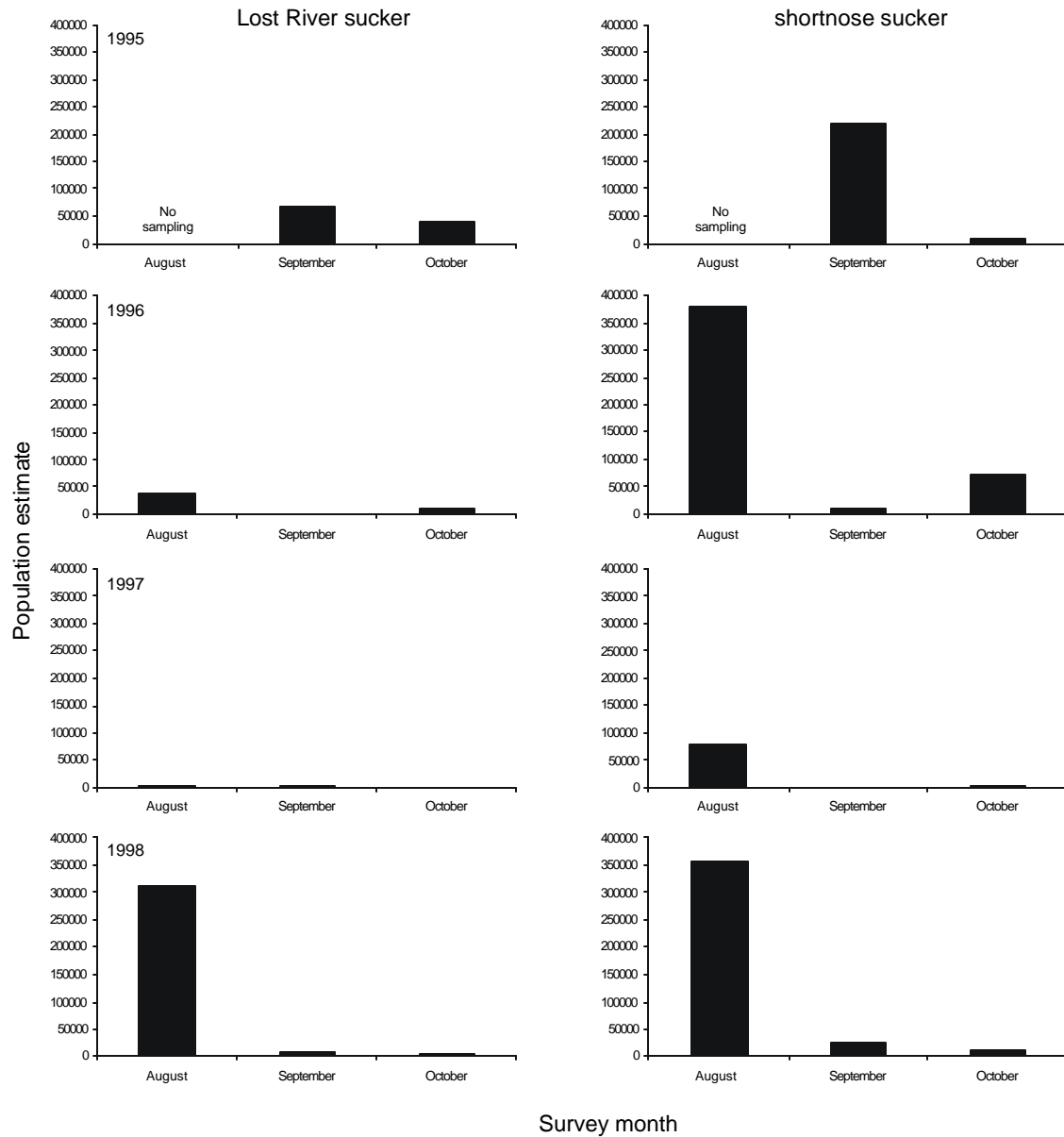


Figure 1.29. Population estimates for age 0 LRS and SNS by month, 1995-1998. Estimates calculated by summing shoreline and offshore estimates.

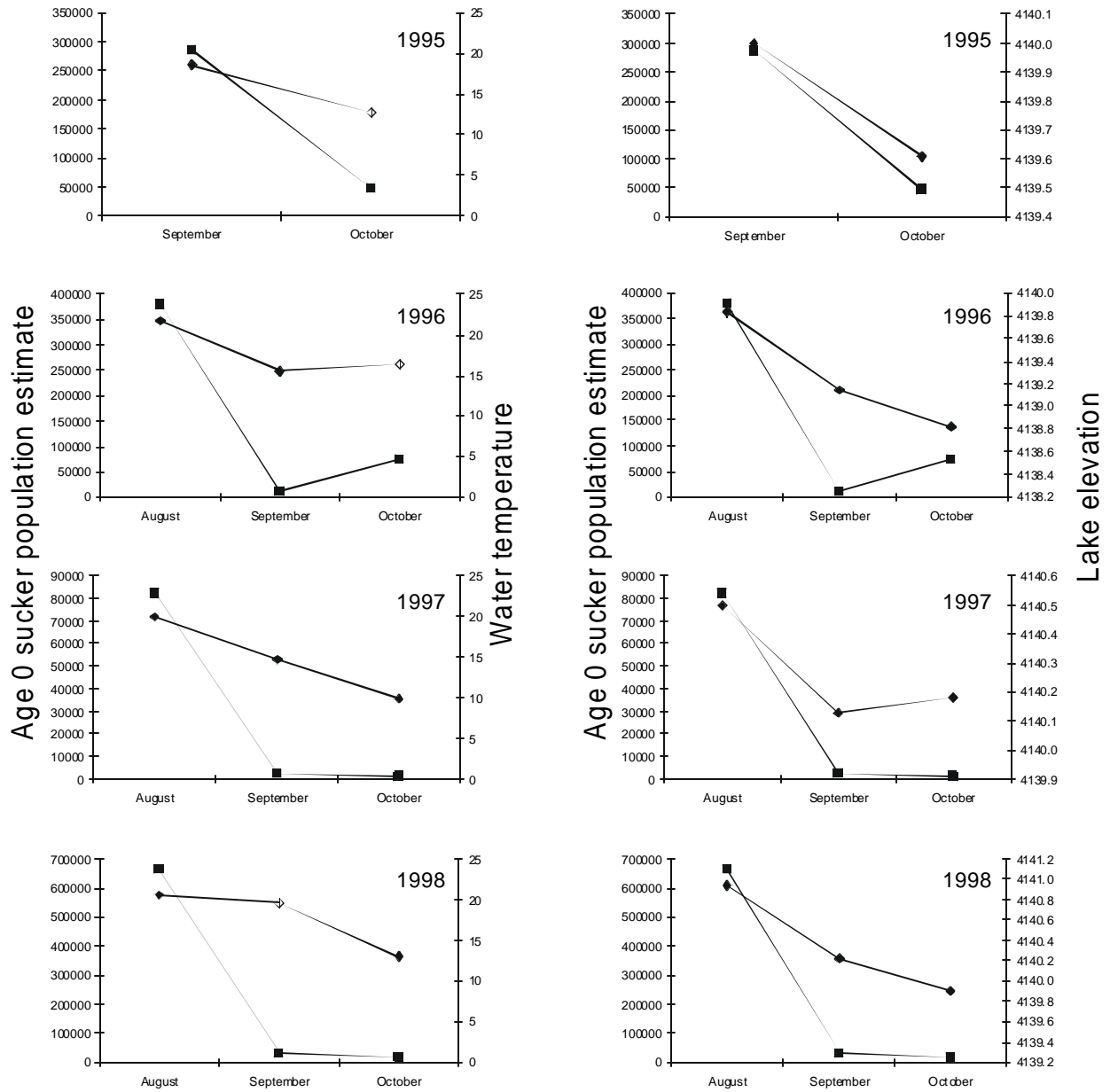


Figure 1.30. Relationship between age 0 sucker population estimates and water temperature and lake elevation, 1995-1998.

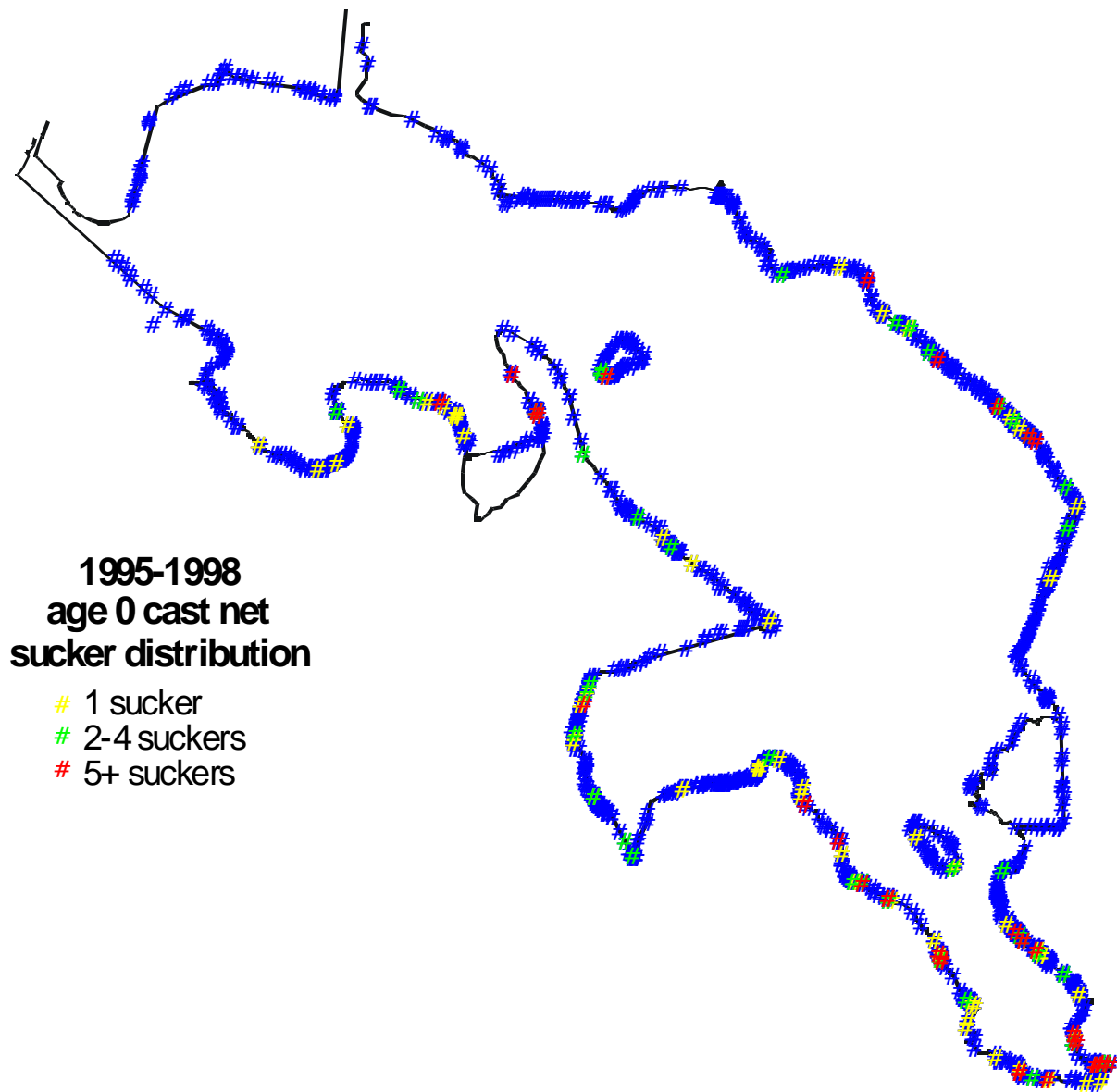


Figure 1.31. Distribution of age 0 suckers (both species) in Upper Klamath Lake from stratified random cast net surveys, 1995-1998. Blue dots are sample sites with zero suckers.

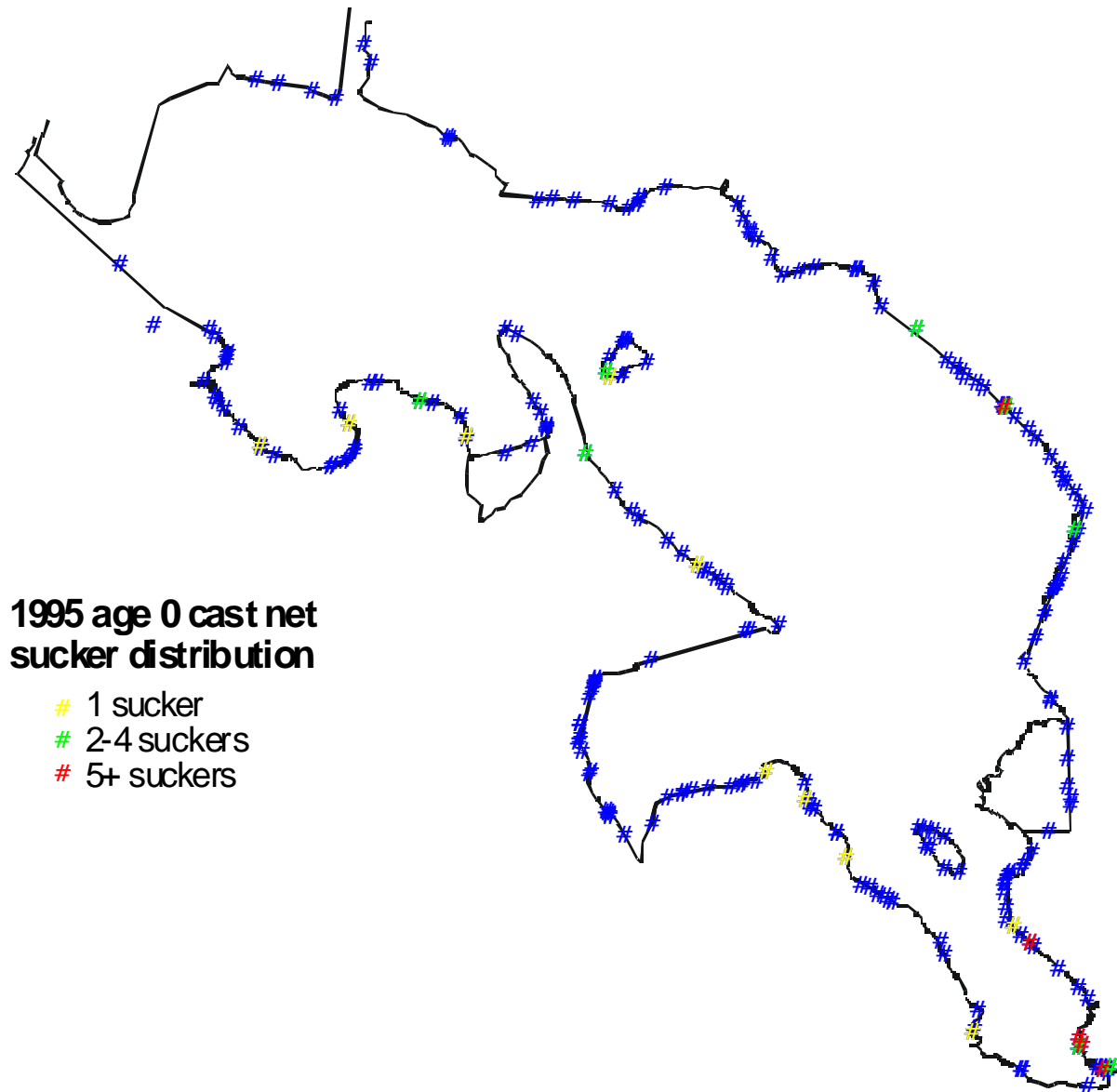


Figure 1.32. Distribution of age 0 suckers (both species) in Upper Klamath Lake from stratified random cast net surveys, 1995. Blue dots are sample sites with zero suckers.

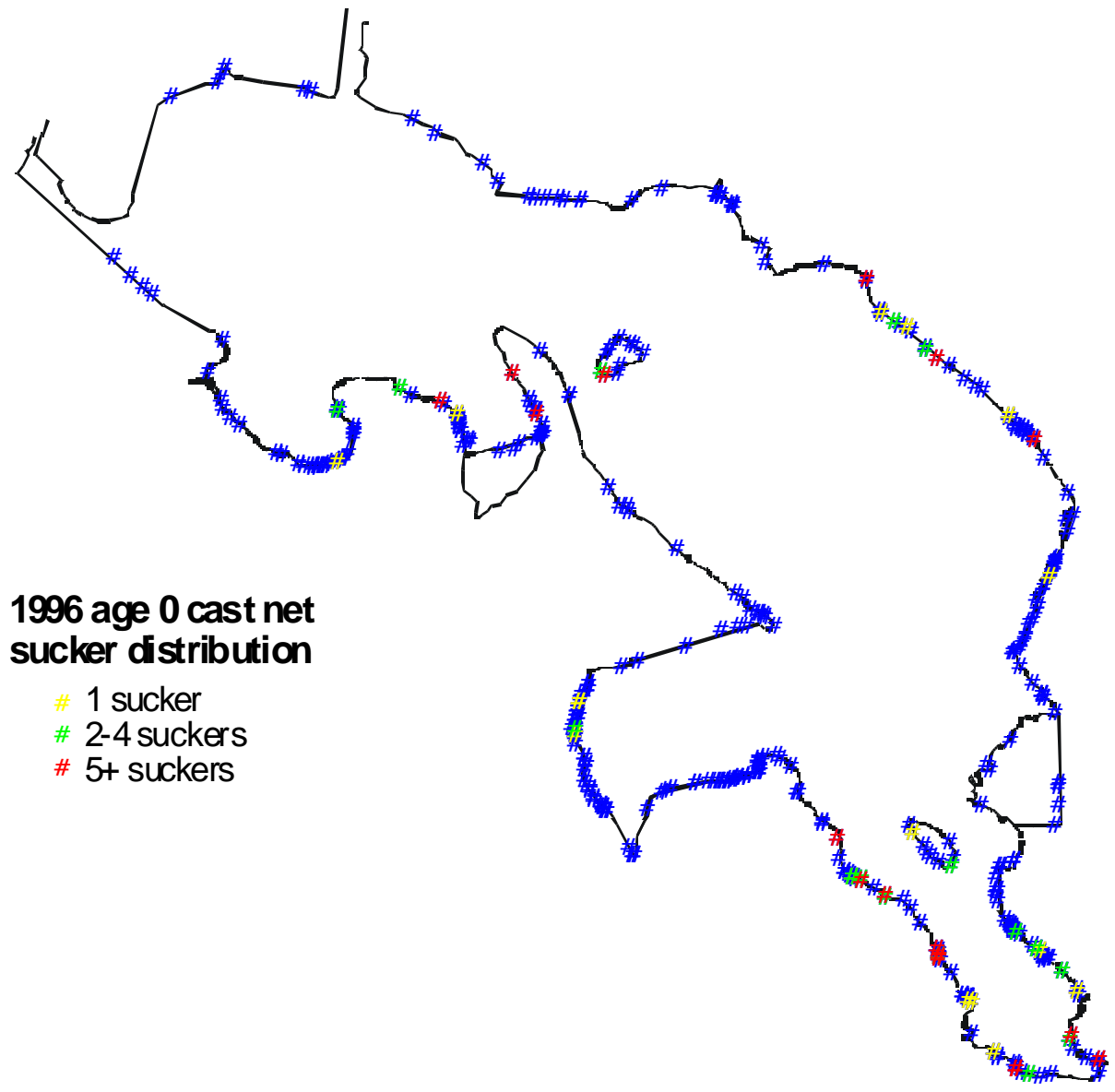


Figure 1.33. Distribution of age 0 suckers (both species) in Upper Klamath Lake from stratified random cast net surveys, 1996. Blue dots are sample sites with zero suckers.

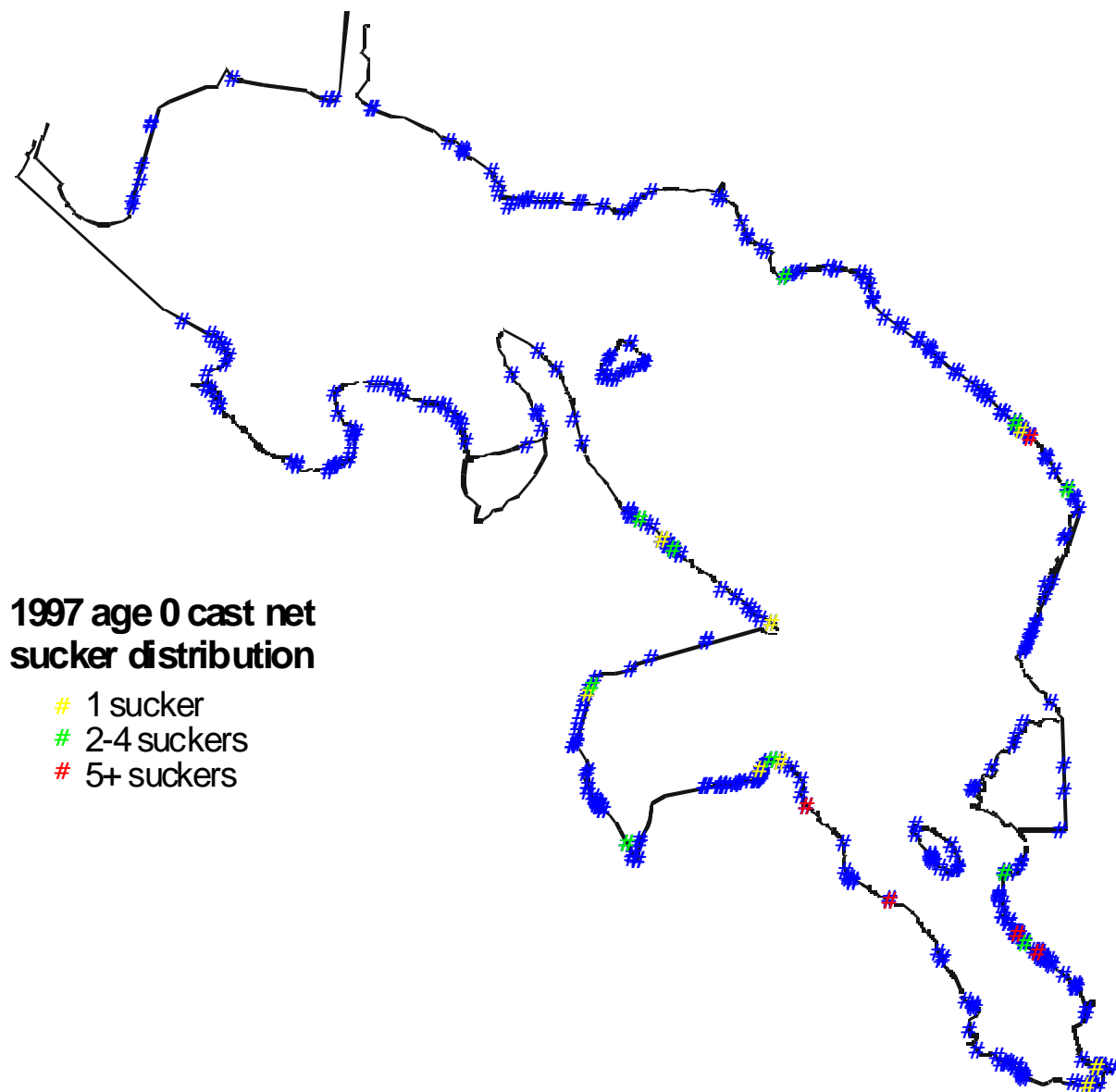


Figure 1.34. Distribution of age 0 suckers (both species) in Upper Klamath Lake from stratified random cast net surveys, 1997. Blue dots are sample sites with zero suckers.

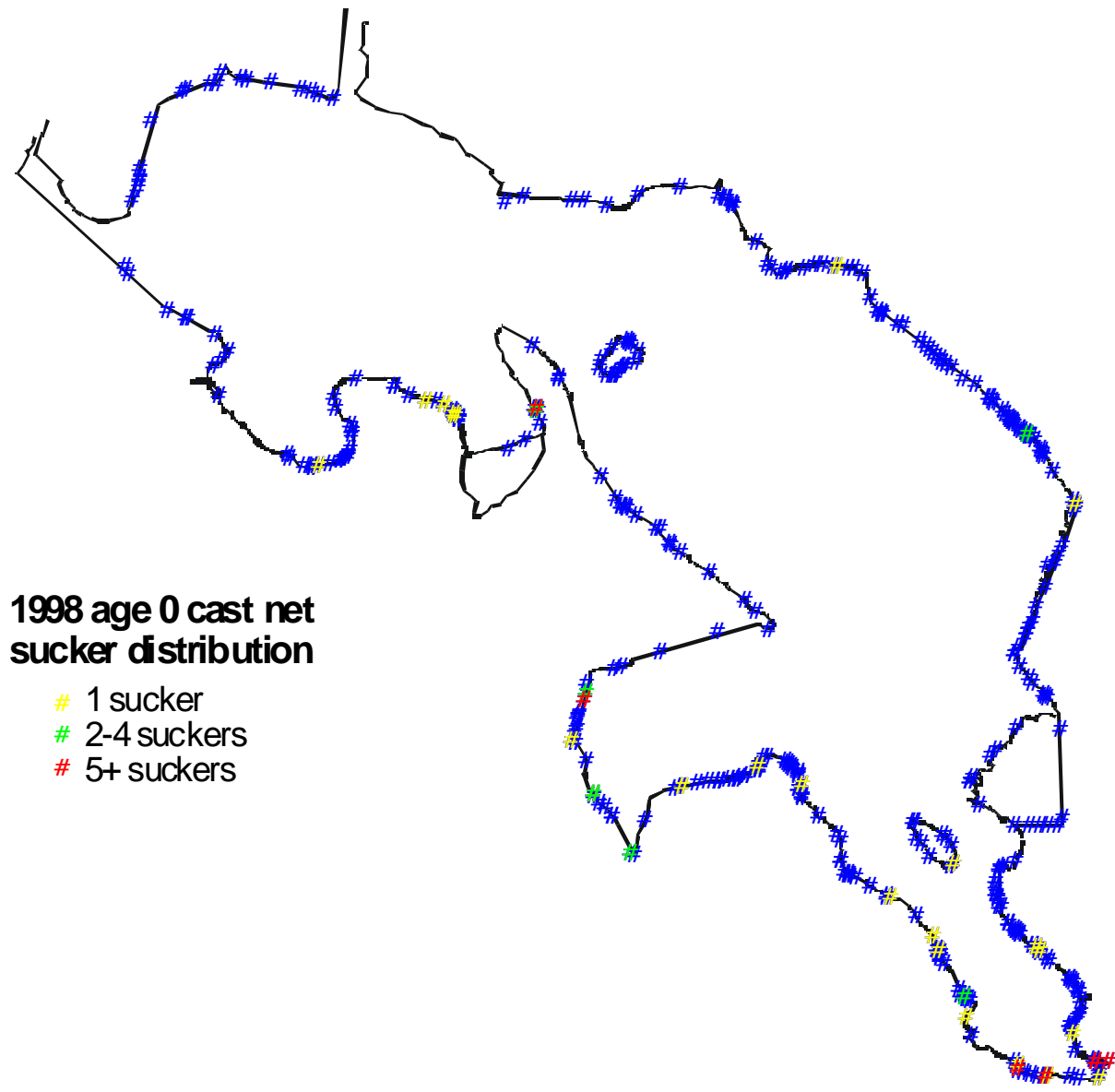


Figure 1.35. Distribution of age 0 suckers (both species) in Upper Klamath Lake from stratified random cast net surveys, 1998. Blue dots are sample sites with zero suckers.

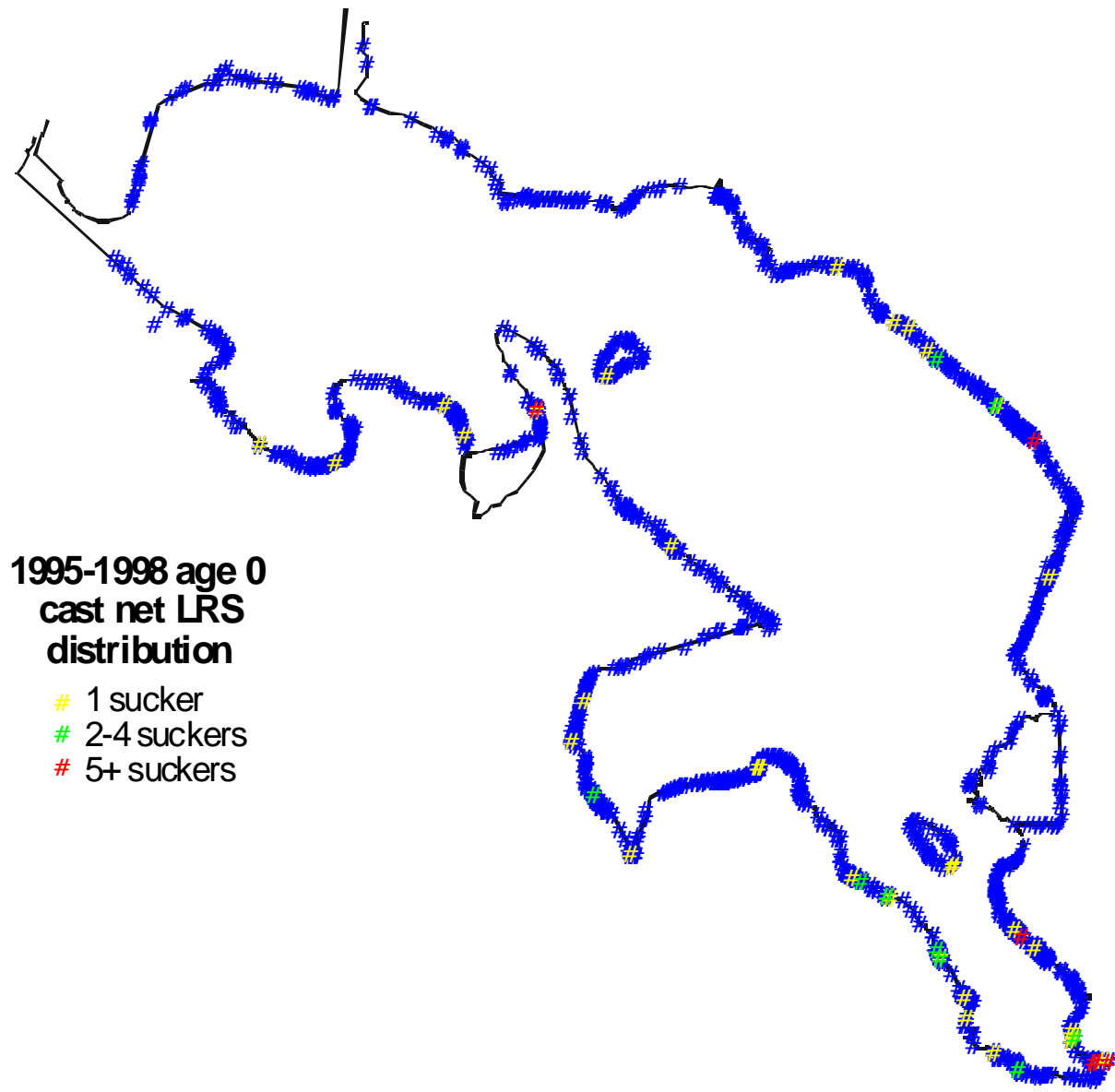


Figure 1.36. Distribution of age 0 LRS in Upper Klamath Lake from stratified random cast net surveys, 1995-1998. Blue dots are sample sites with zero suckers.

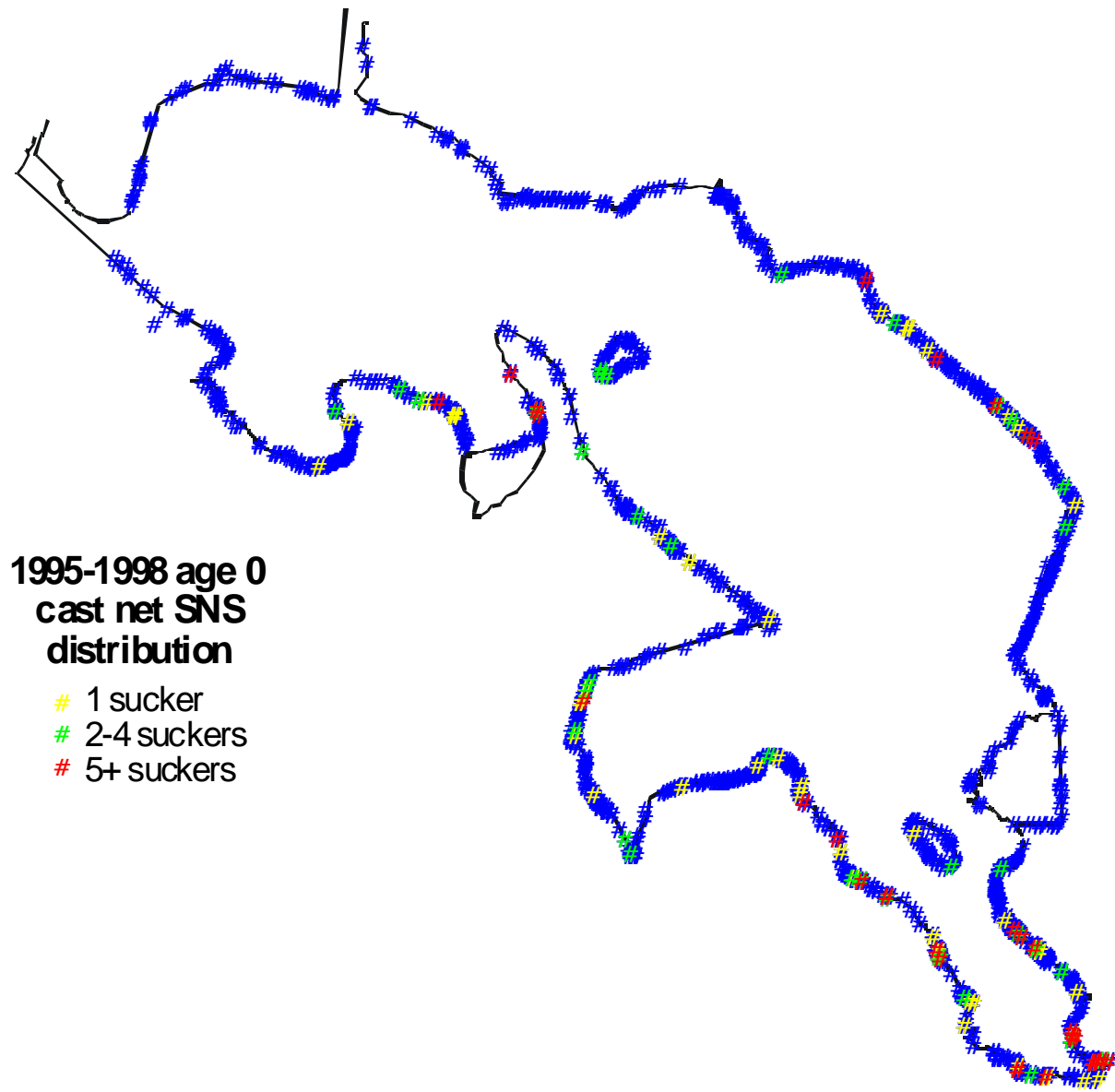


Figure 1.37. Distribution of age 0 SNS in Upper Klamath Lake from stratified random cast net surveys, 1995-1998. Blue dots are sample sites with zero suckers.

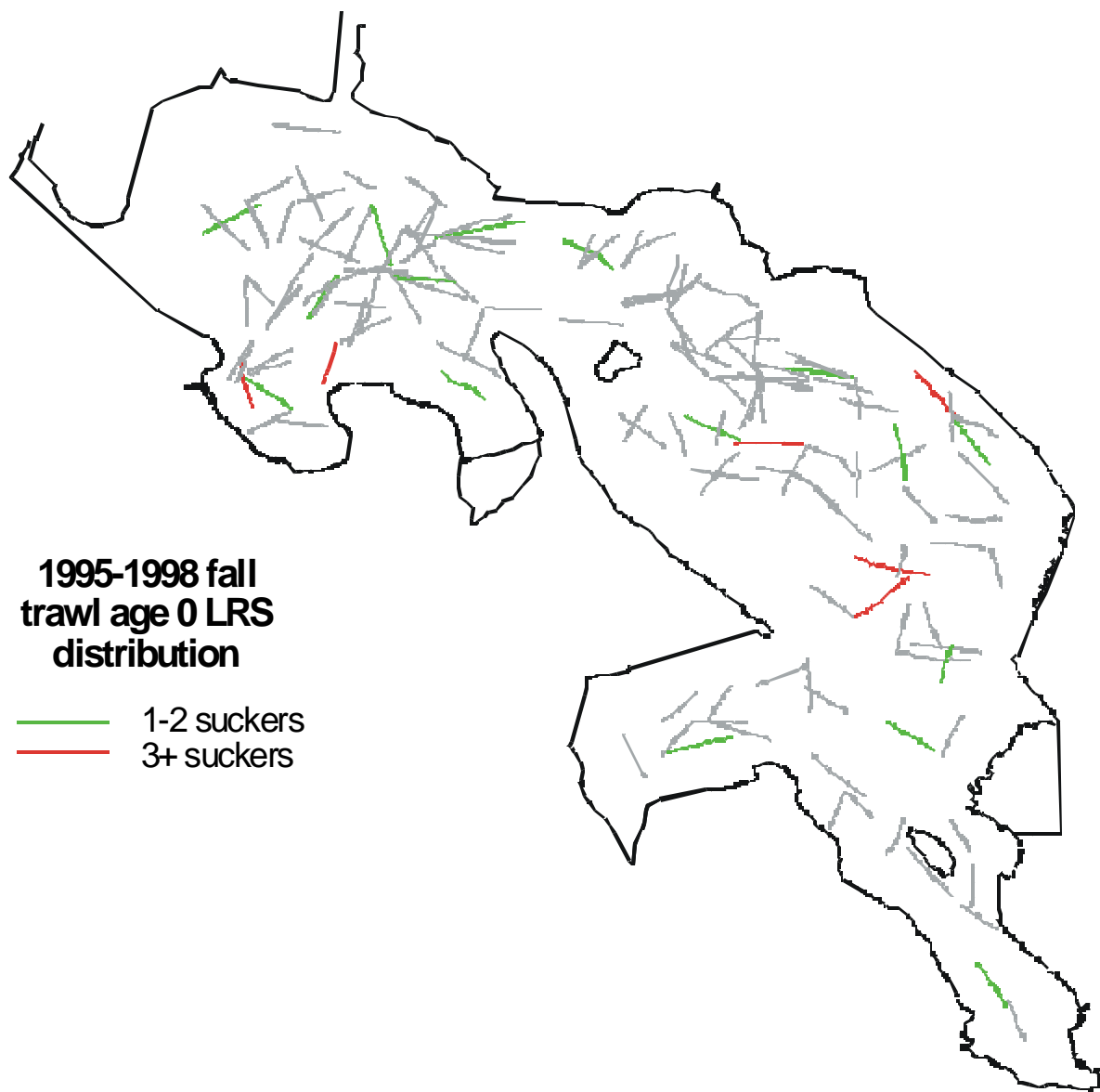


Figure 1.38. Distribution of age 0 LRS in Upper Klamath Lake from late summer/fall random otter trawl surveys 1995-1998. Gray lines are samples with zero suckers.

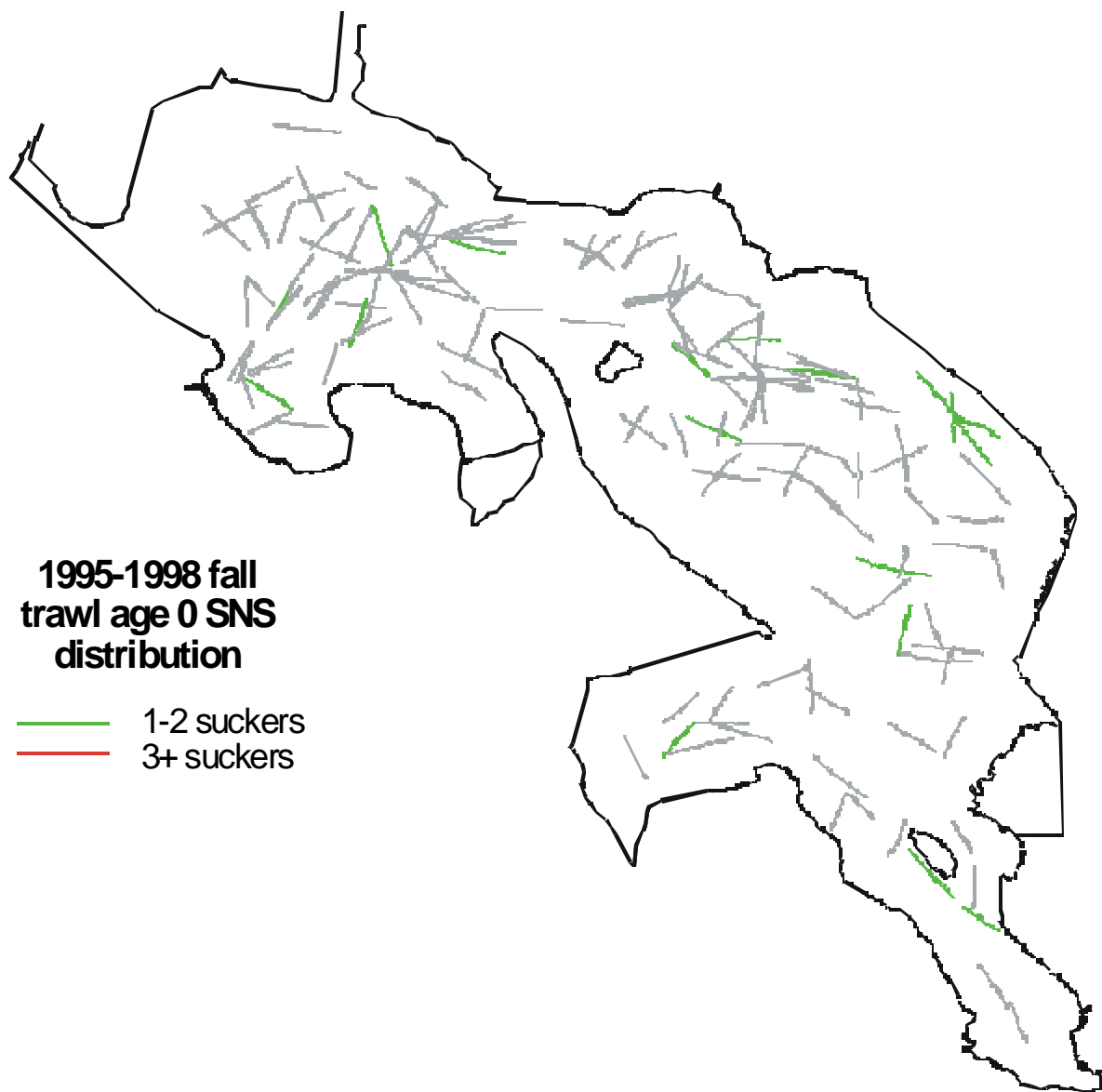


Figure 1.39. Distribution of age 0 SNS in Upper Klamath Lake from late summer/fall random otter trawl surveys 1995-1998. Gray lines are samples with zero suckers.

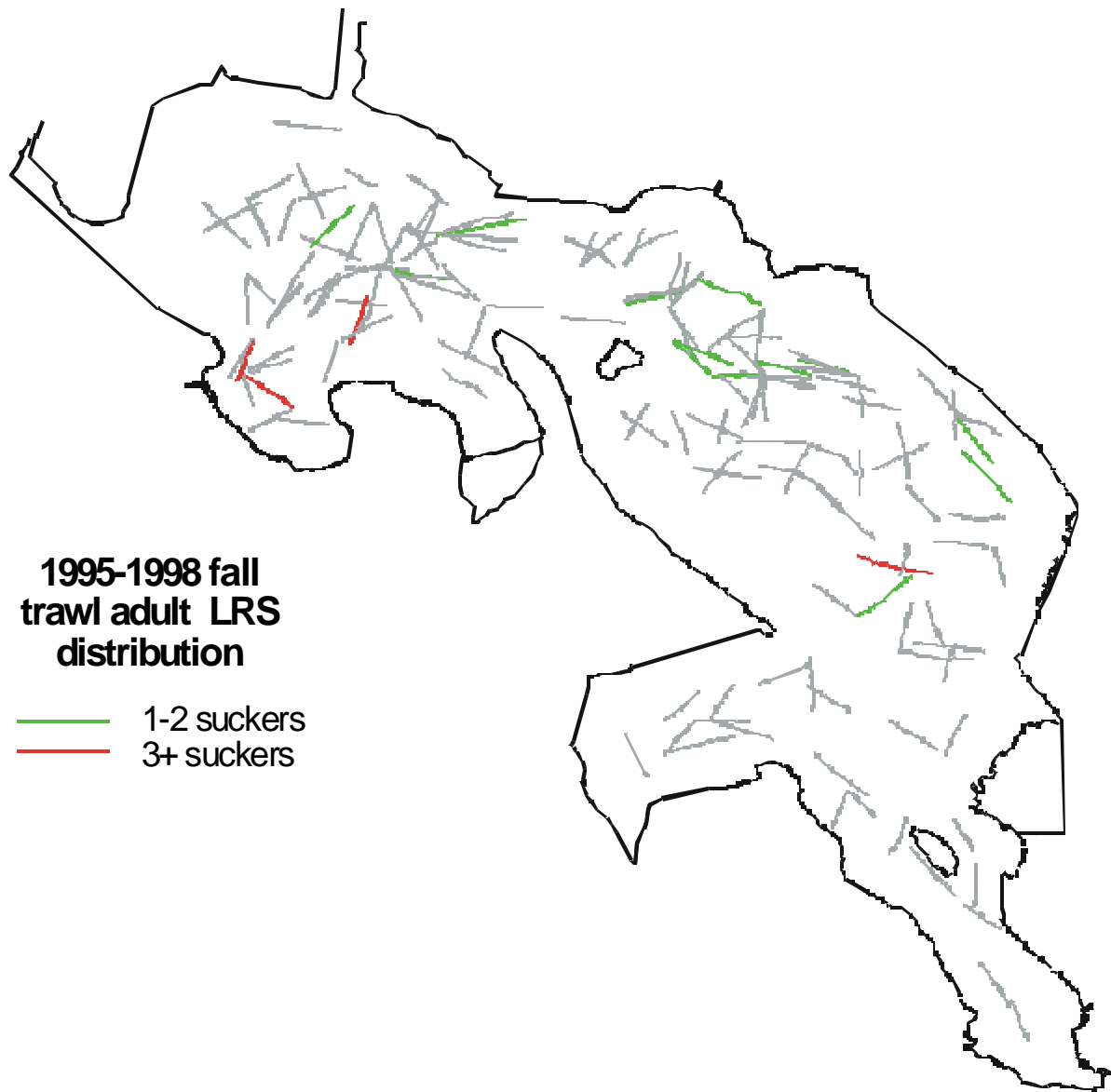


Figure 1.40. Distribution of age adult LRS in Upper Klamath Lake from late summer/fall random otter trawl surveys 1995-1998. Gray lines are samples with zero suckers.

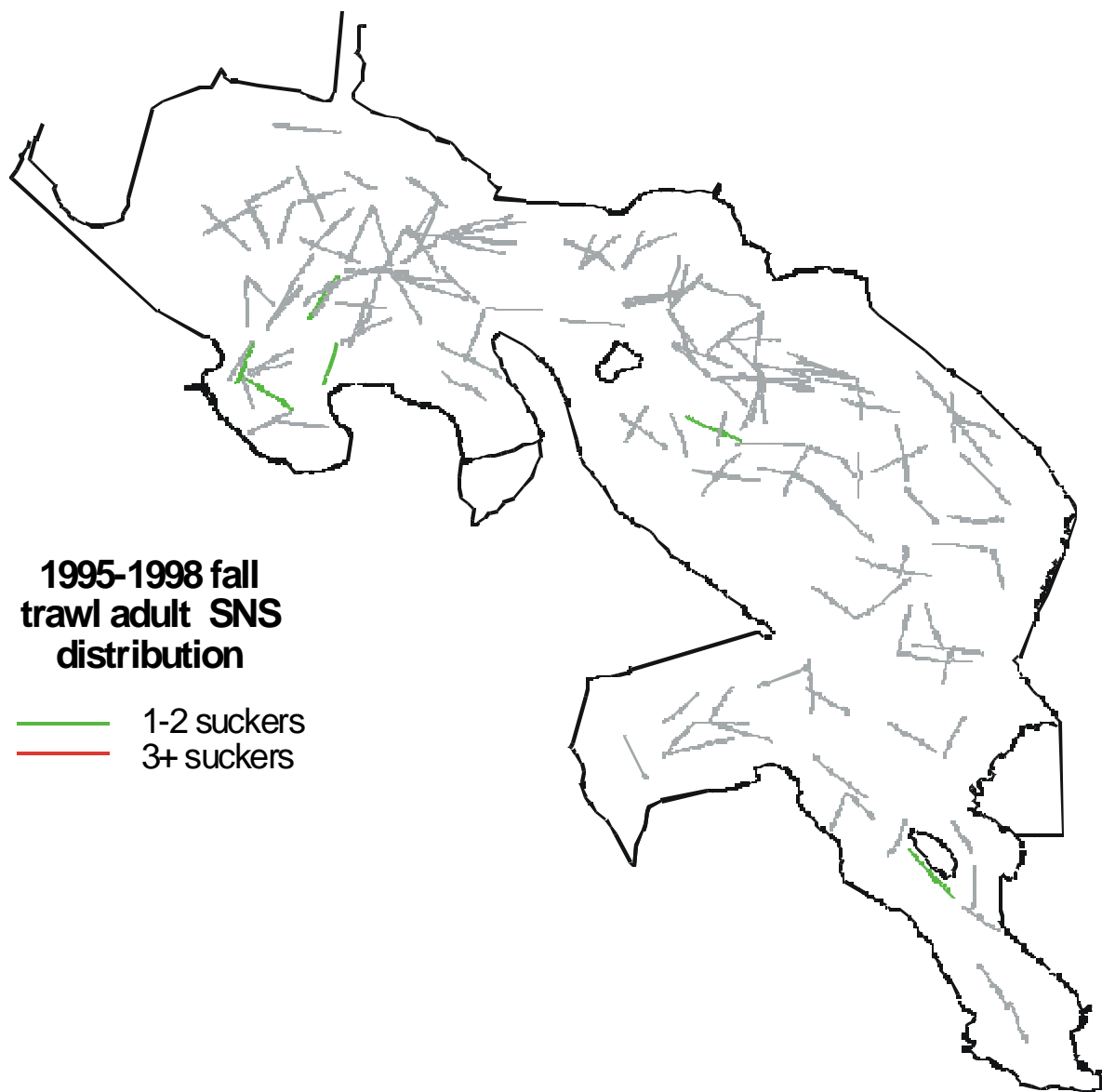


Figure 1.41. Distribution of adult SNS in Upper Klamath Lake from late summer/fall random otter trawl surveys 1995-1998. Gray lines are samples with zero suckers.

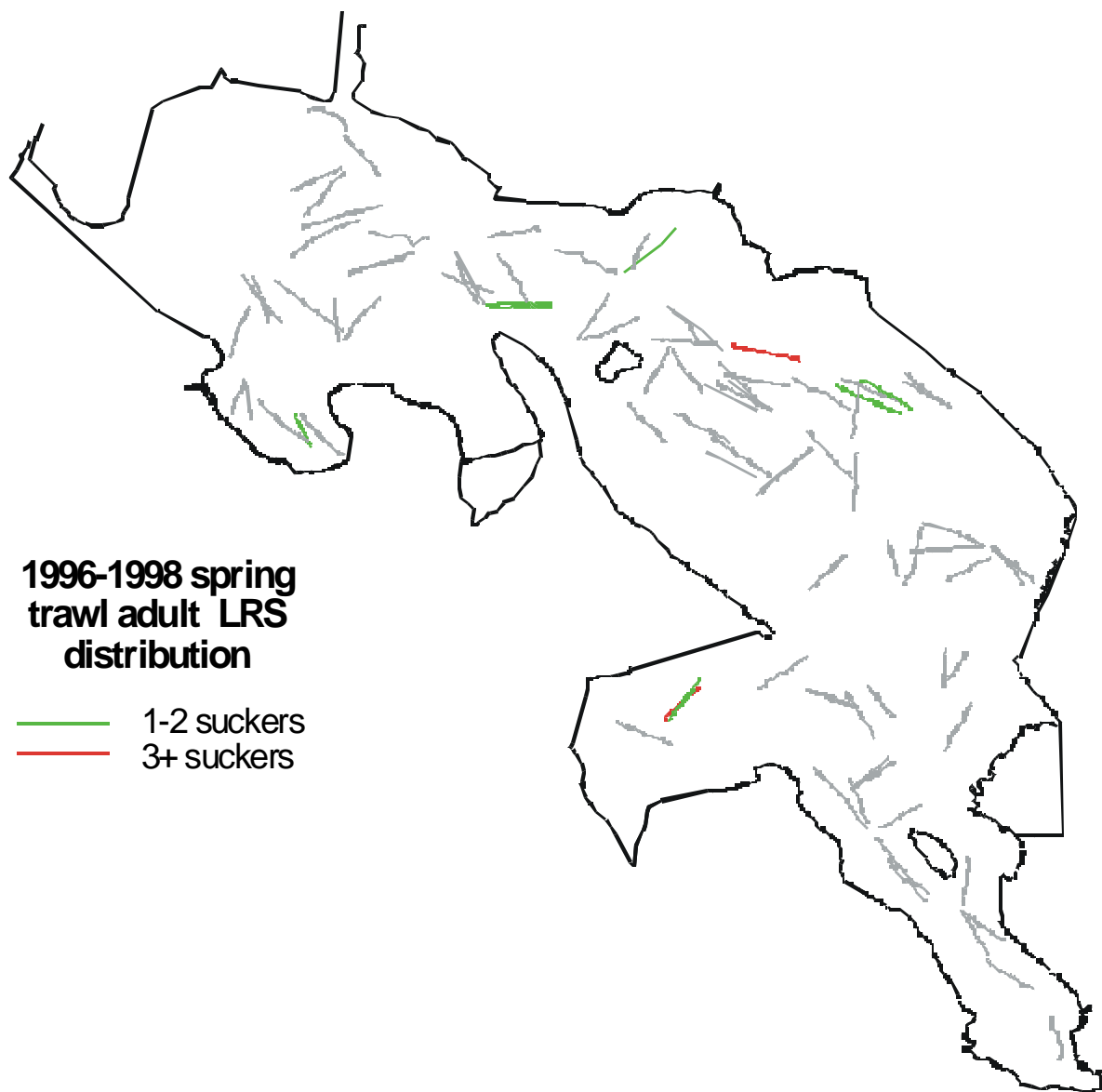


Figure 1.42. Distribution of adult LRS in Upper Klamath Lake from spring random otter trawl surveys 1996-1998. Gray lines are samples with zero suckers.

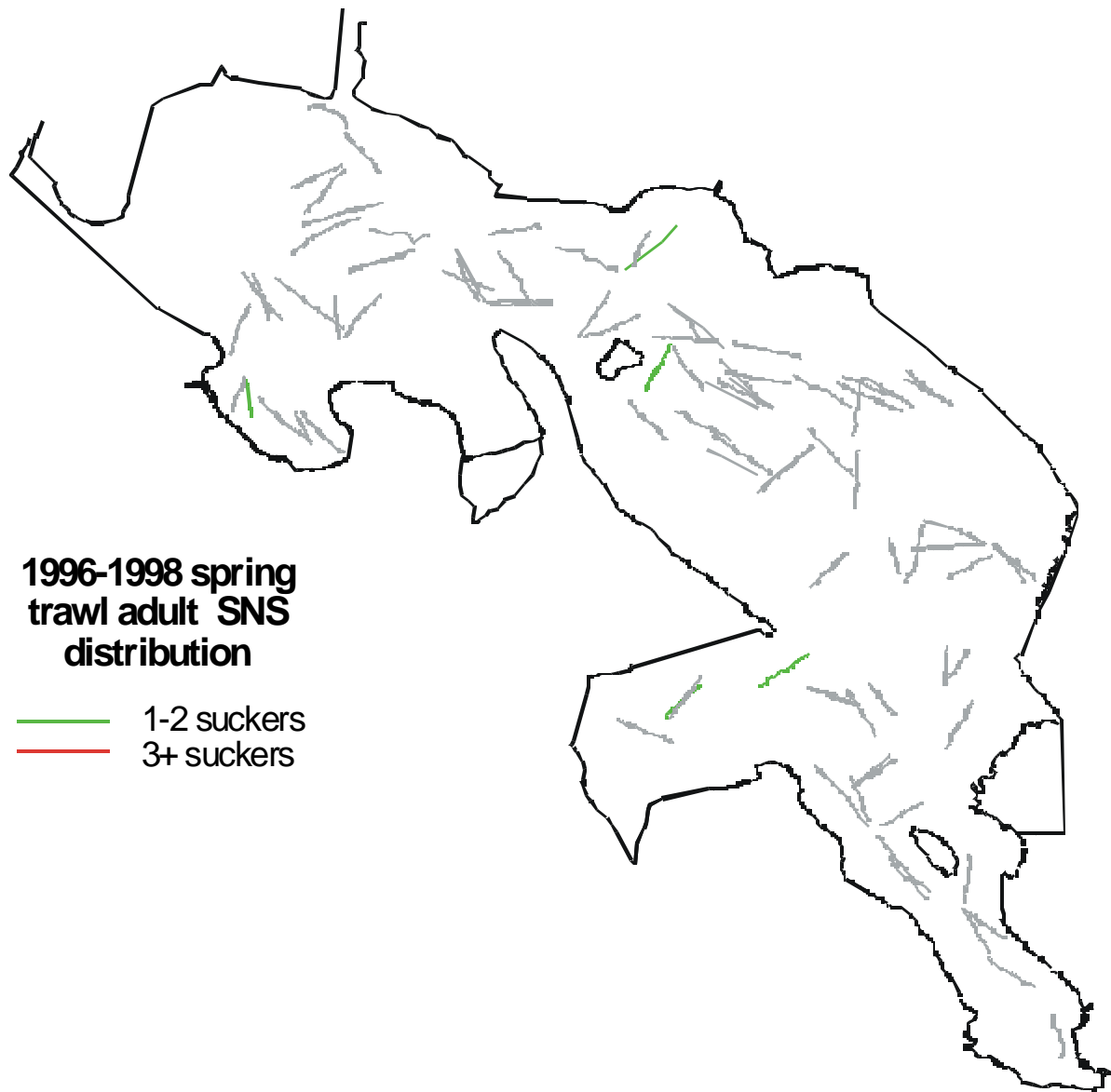


Figure 1.43. Distribution of adult SNS in Upper Klamath Lake from spring random otter trawl surveys 1996-1998. Gray lines are samples with zero suckers.

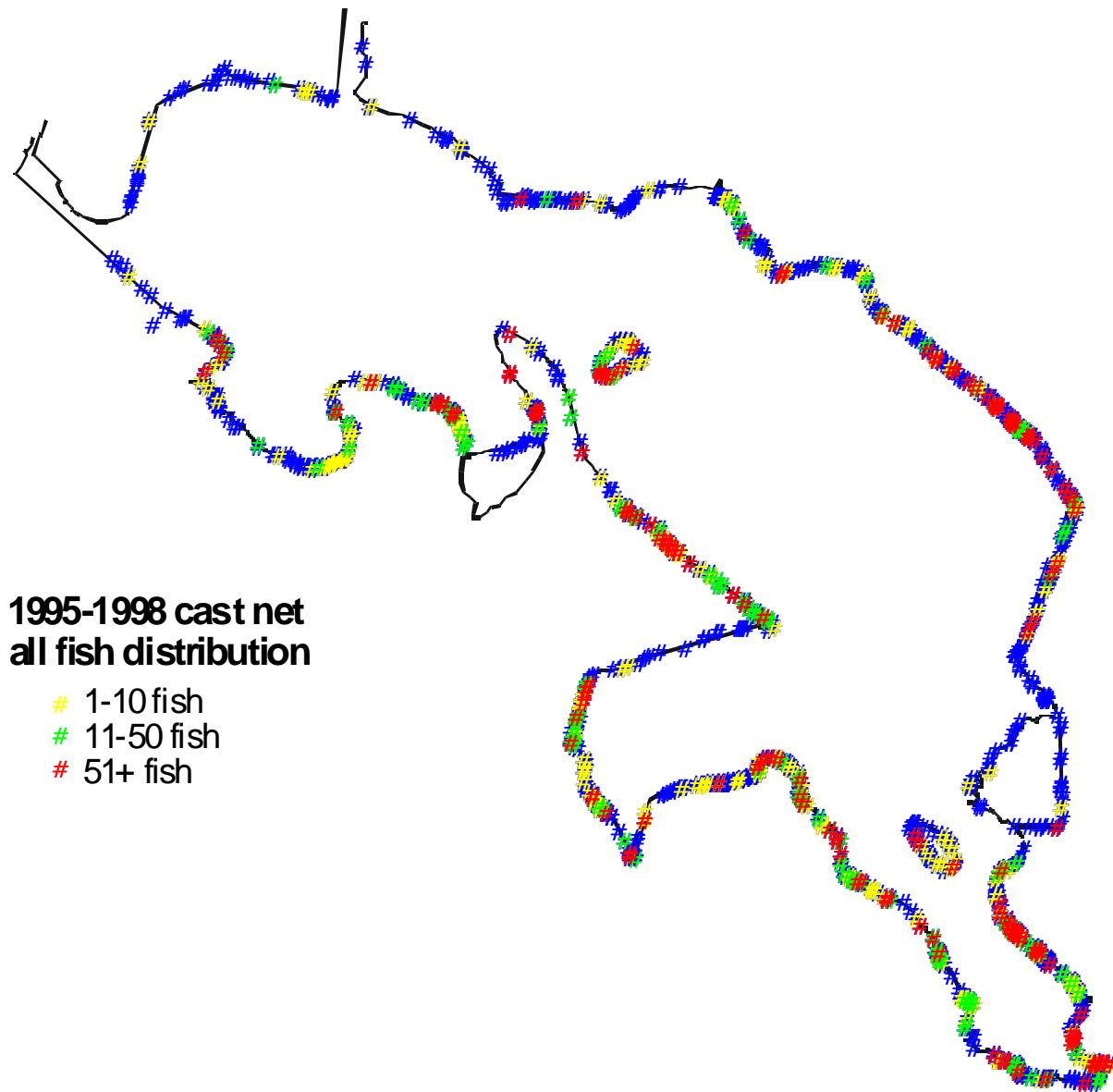


Figure 1.44. Distribution of all fish in Upper Klamath Lake from late summer/fall stratified random cast net surveys 1995-1998. Blue dots are samples with zero fish.

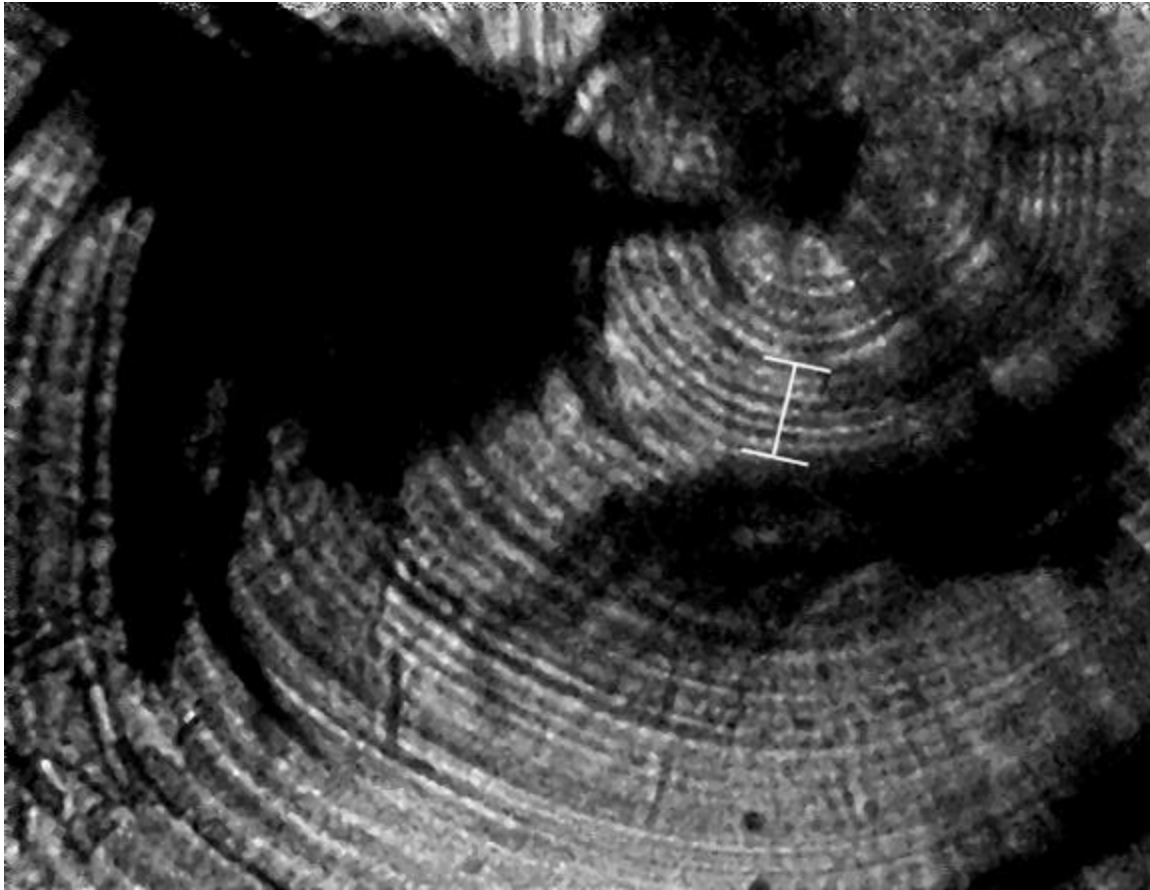


Figure 2.1. Core region of a shortnose sucker lapillus showing transition from relatively wide to narrow increments. Bar indicates range of narrow increments.

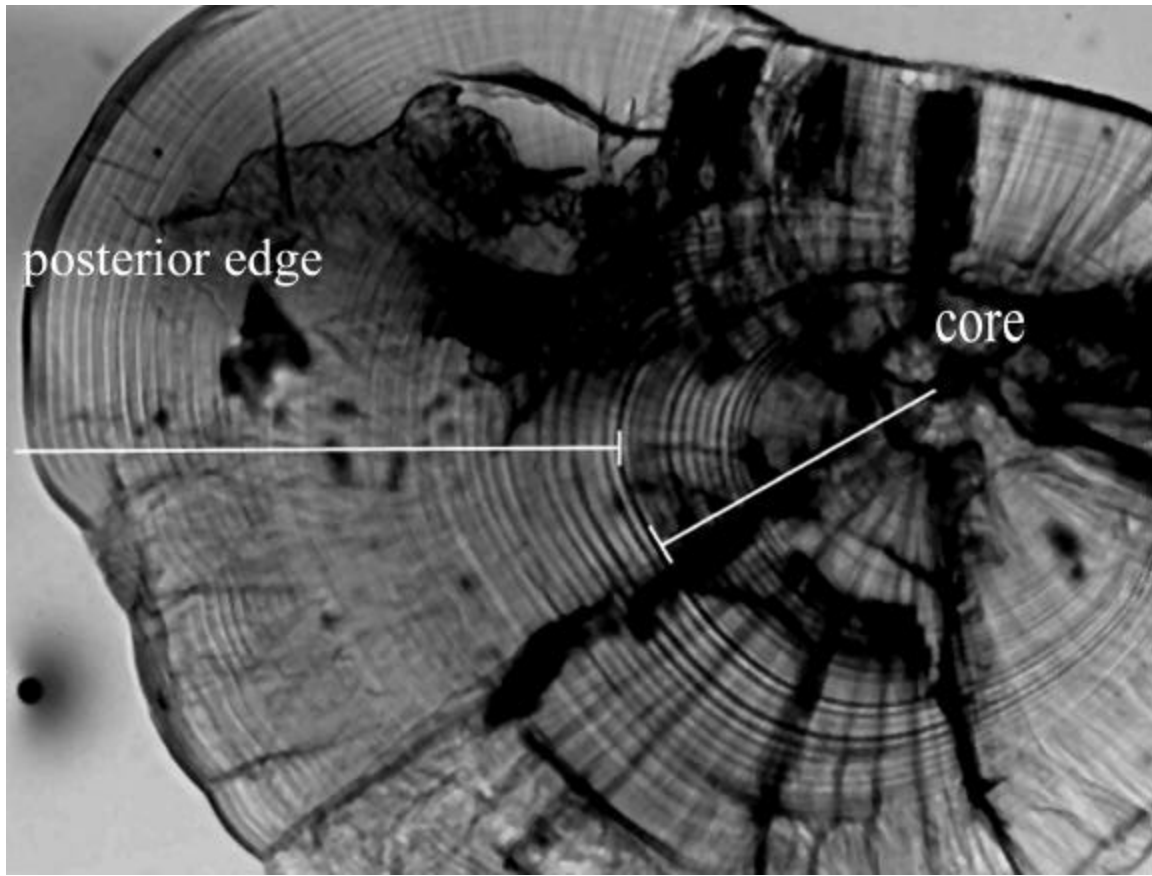


Figure 2.2. Shortnose sucker lapillus showing change in growth plane. Bars indicate two different growth planes.

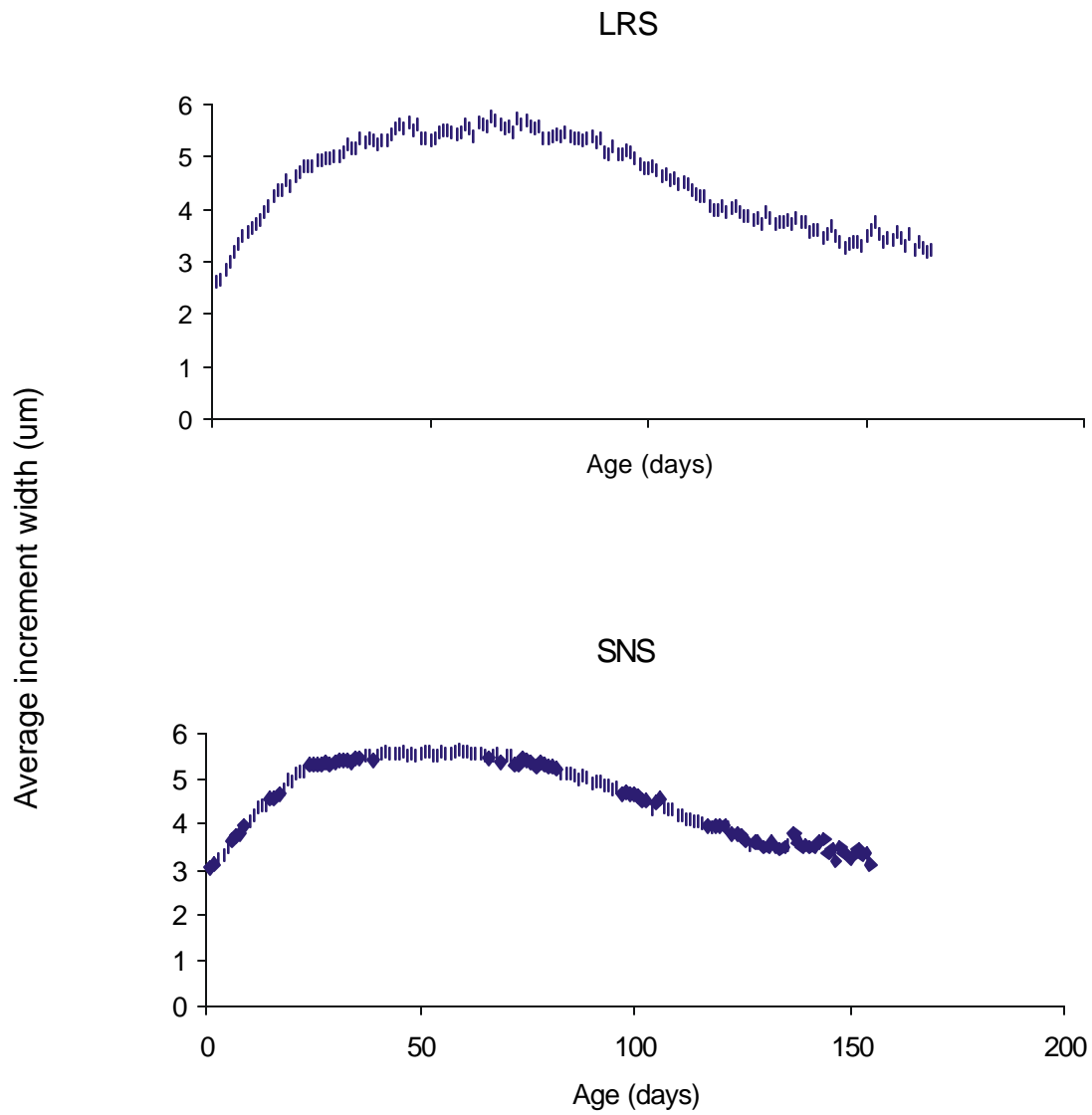


Figure 2.3. Mean increment width (um) for Lost River (LRS) and shortnose (SNS) suckers, all years combined (1991, 1993-1997).

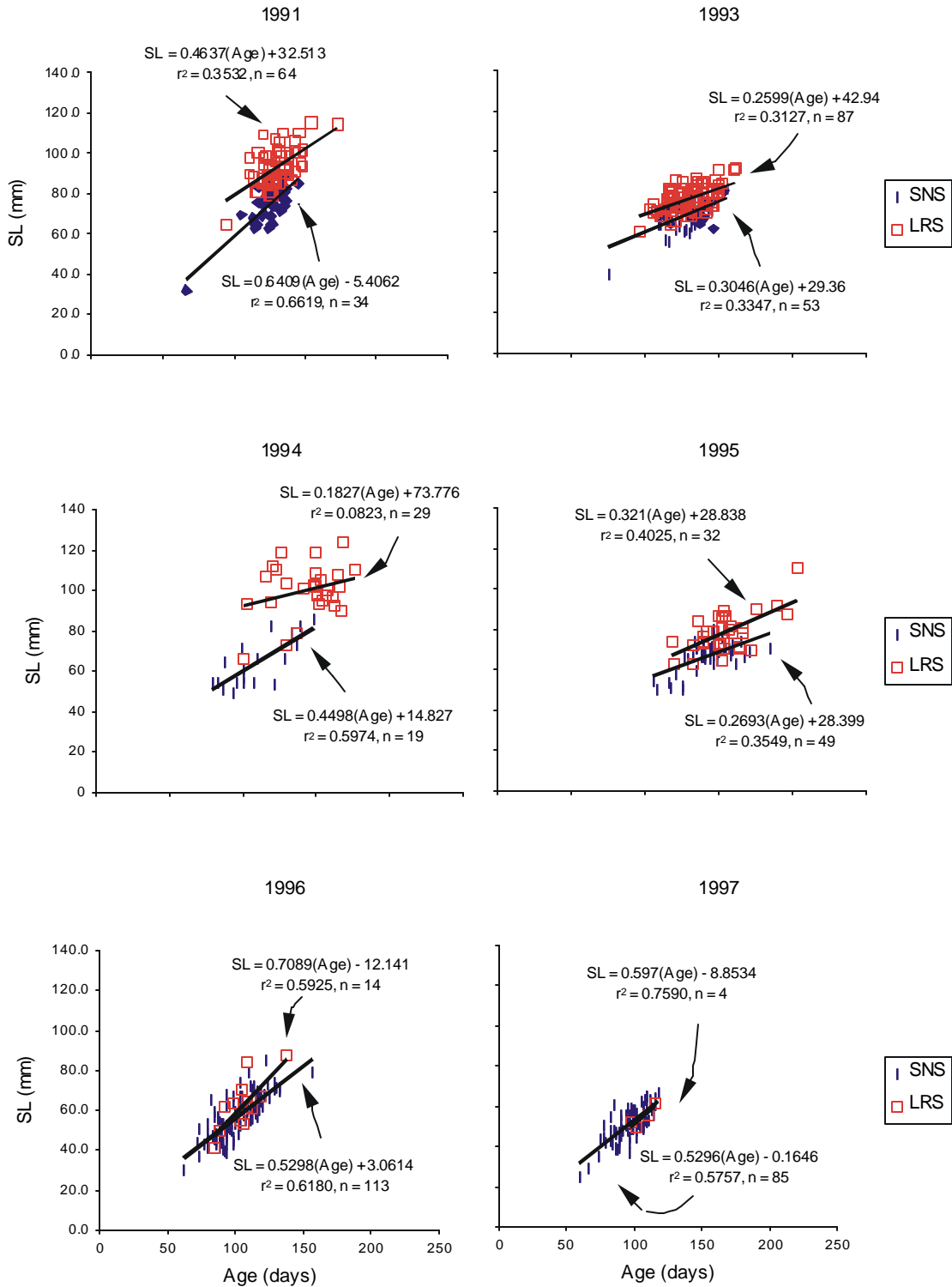


Figure 2.4. Regressions of standard length (mm) on age (days) for Lost River and shortnose suckers:1991, 1993-1997.

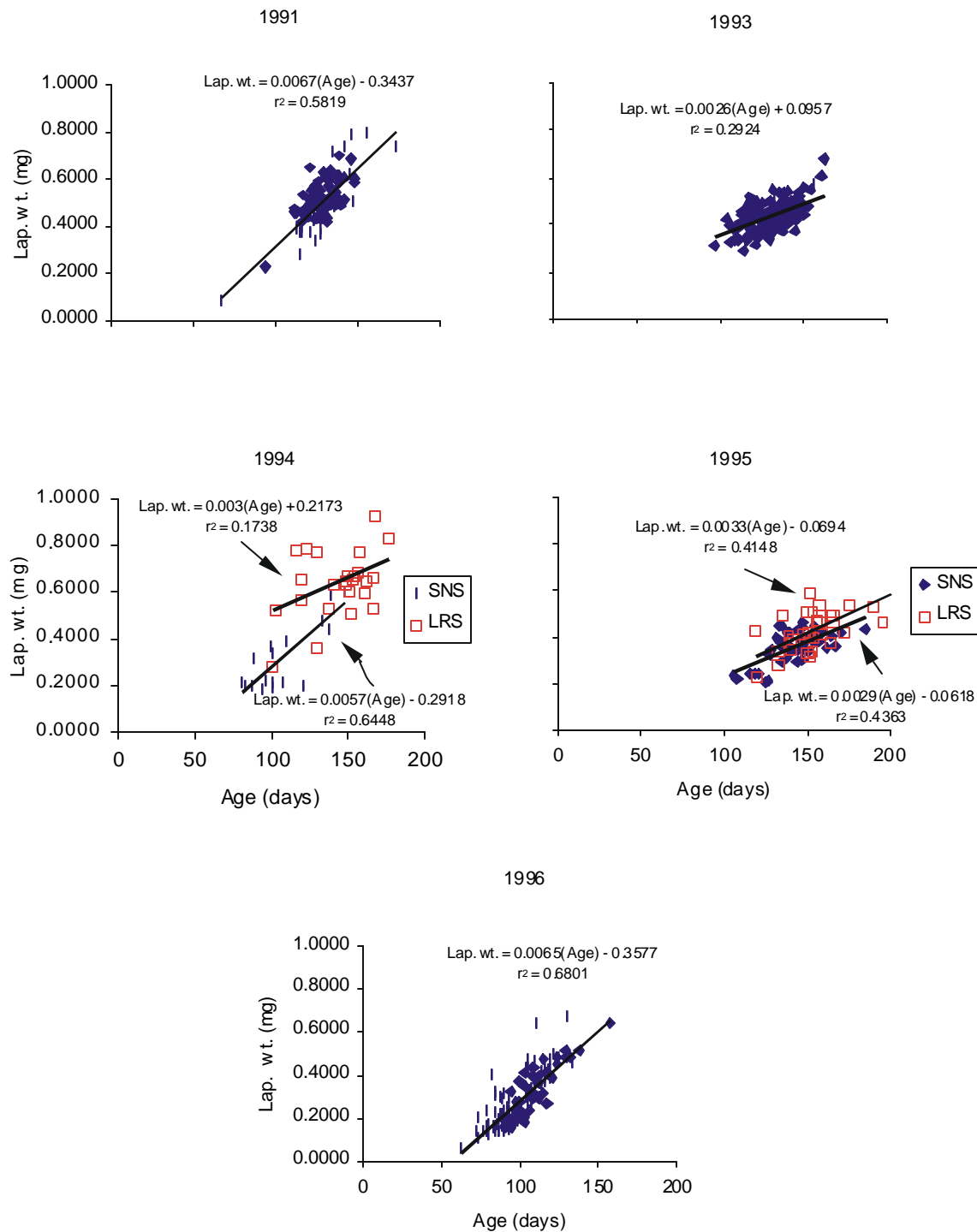


Figure 2.5. Regressions of lapillus weight (mg) on age (days) for Lost River and shortnose suckers: 1991, 1993-1996. Results of ANCOVA allowed pooling of data for 1991, 1993, and 1996.

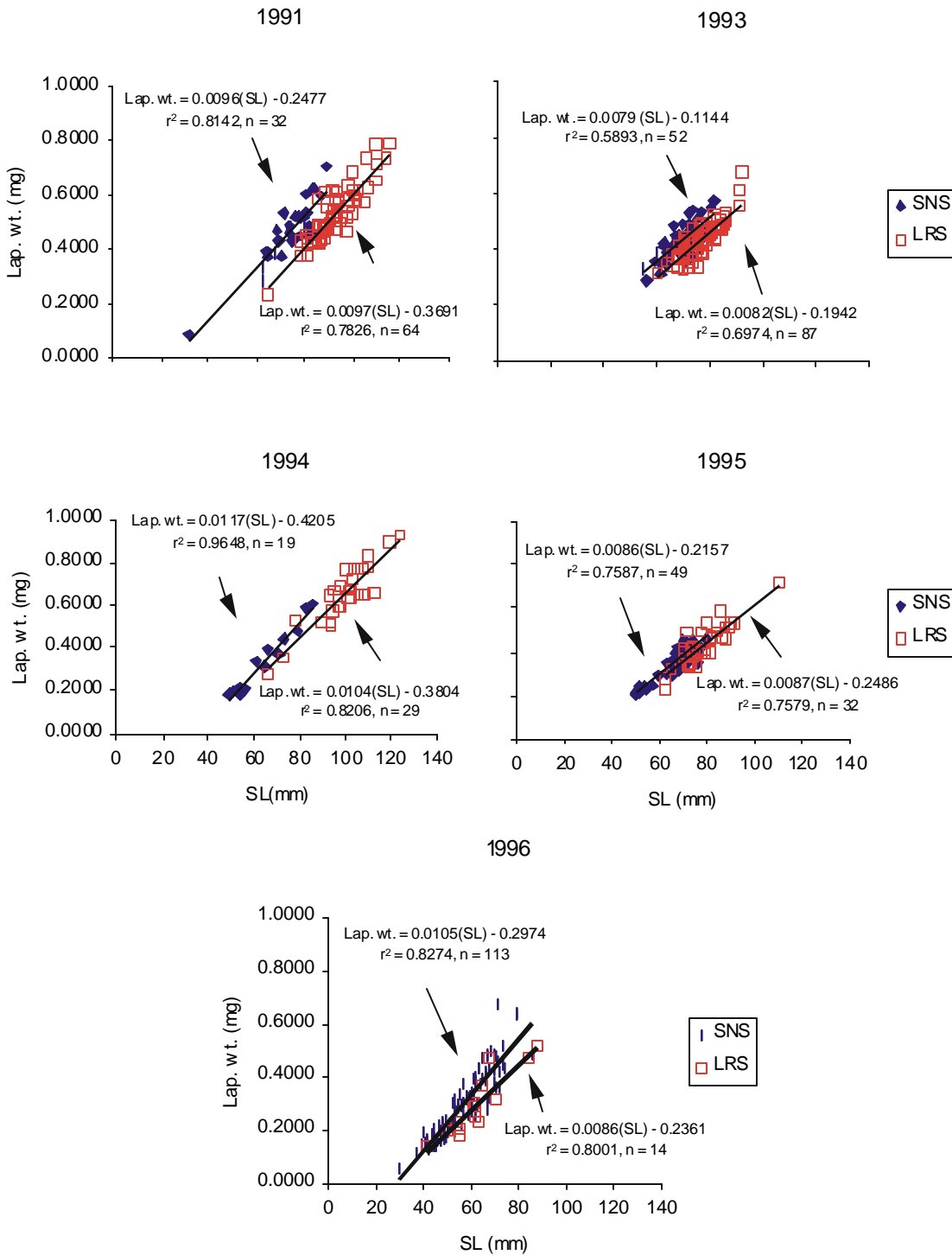


Figure 2.6. Regressions of lapillus weight (mg) on standard length (mm) for Lost River and shortnose suckers: 1991, 1993-1996.

Shortnose sucker

Lost River sucker

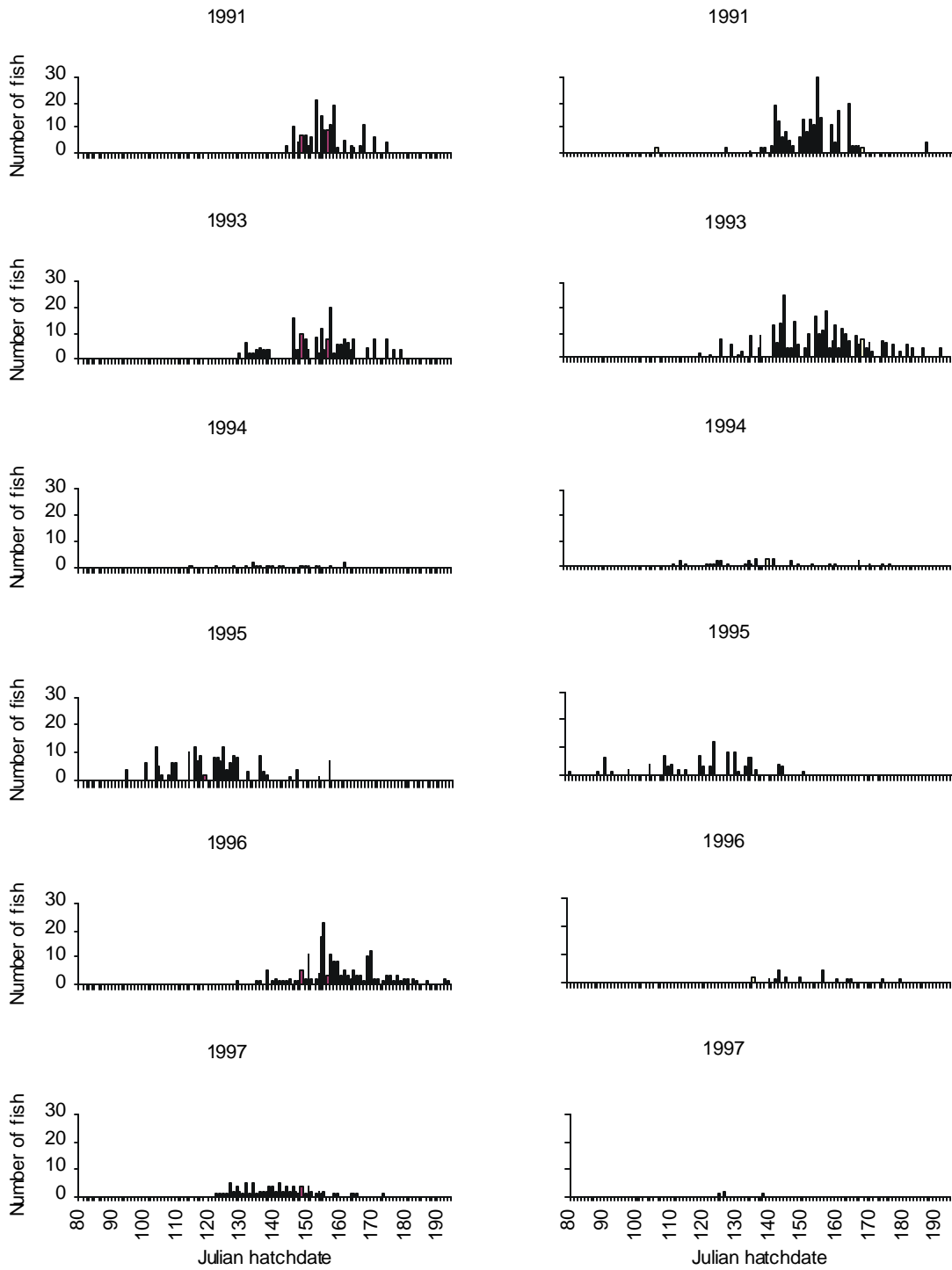


Figure 2.7. Julian hatchdate distributions for shortnose and Lost River suckers: 1991, 1993-1997.



Figure 2.8. Box-and-whisker plots of Julian hatchdates for shortnose and Lost River suckers: 1991,1993-1997. The central box covers the middle 50 percent of the data; the sides of the box are the lower and upper quartiles, and the vertical line drawn through the box is the median. The whiskers extend out to the lower and upper values of the data.

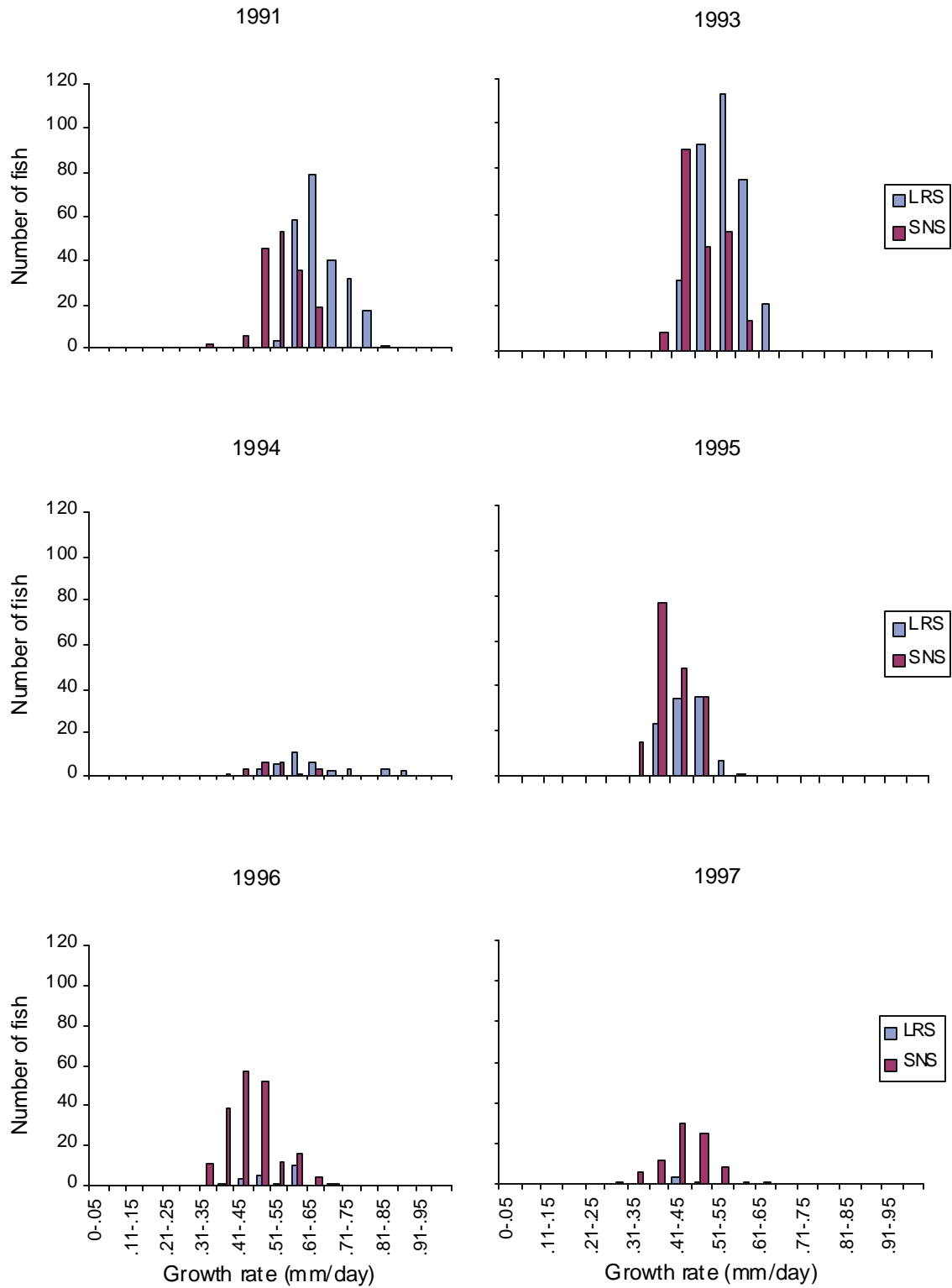


Figure 2.9. Growth rate distributions for Lost River and shortnose suckers: 1991, 1993-1997.

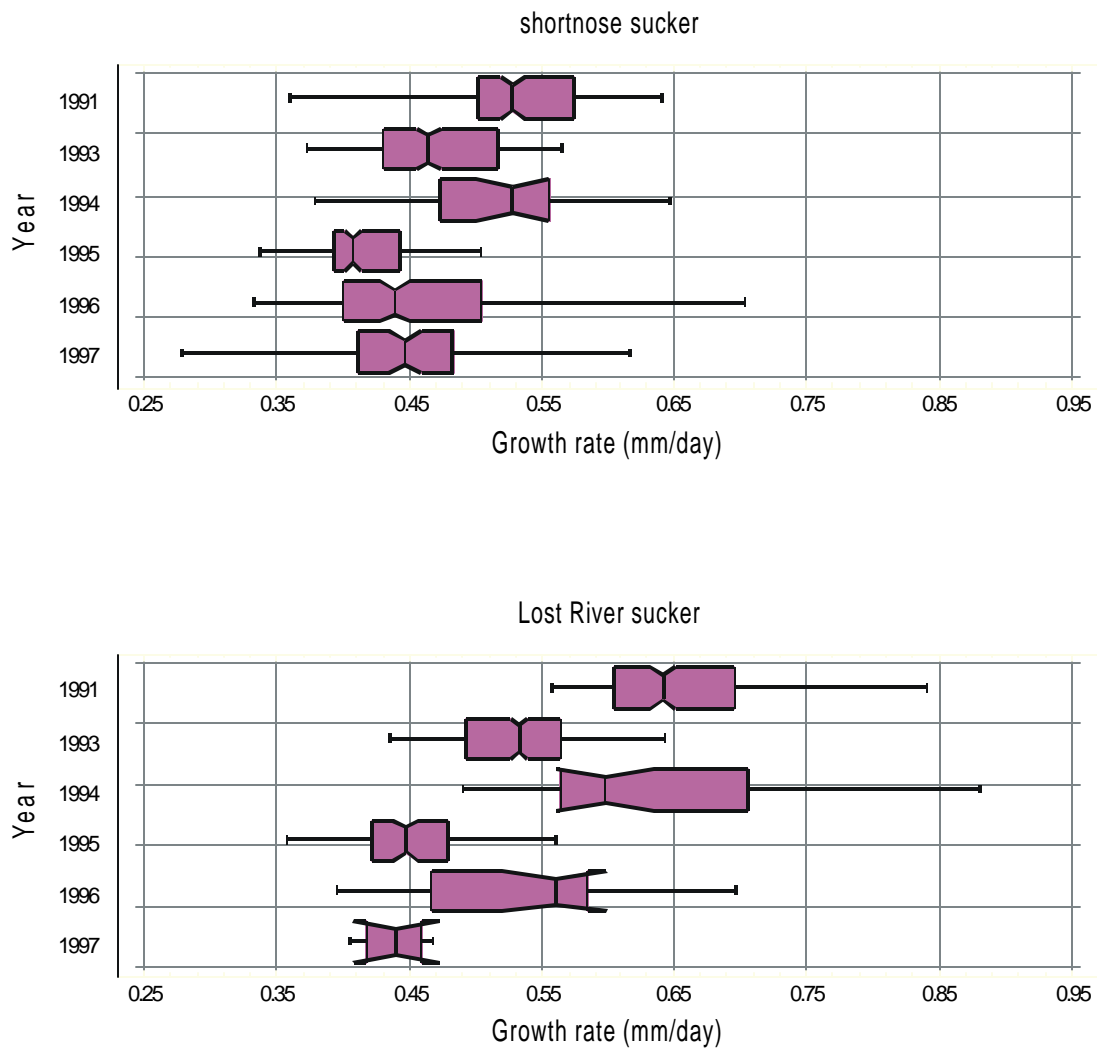


Figure 2.10. Box-and-whisker plots of growth rates for shortnose and Lost River suckers: 1991, 1993-1997. The central box covers the middle 50 percent of the data; the sides of the box are the lower and upper quartiles, and the vertical line drawn through the box is the median. The whiskers extend out to the lower and upper values of the data.

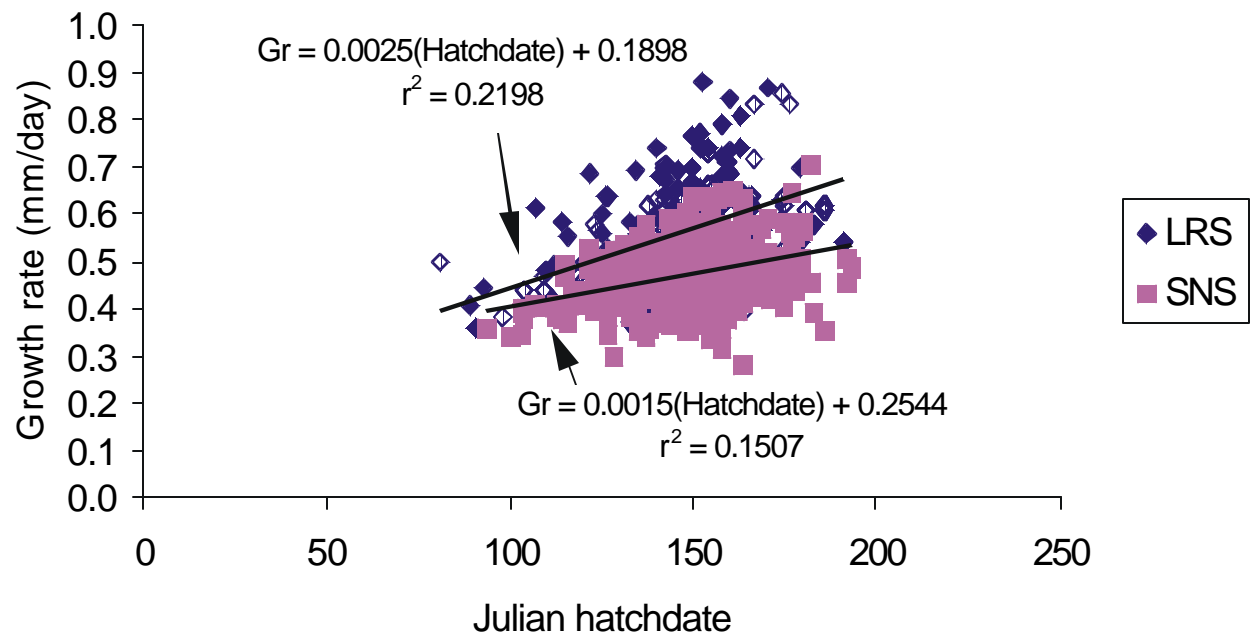


Figure 2.11. Regressions of growth rate (mm/day) on Julian hatchdate for Lost River and shortnose suckers, all years combined.

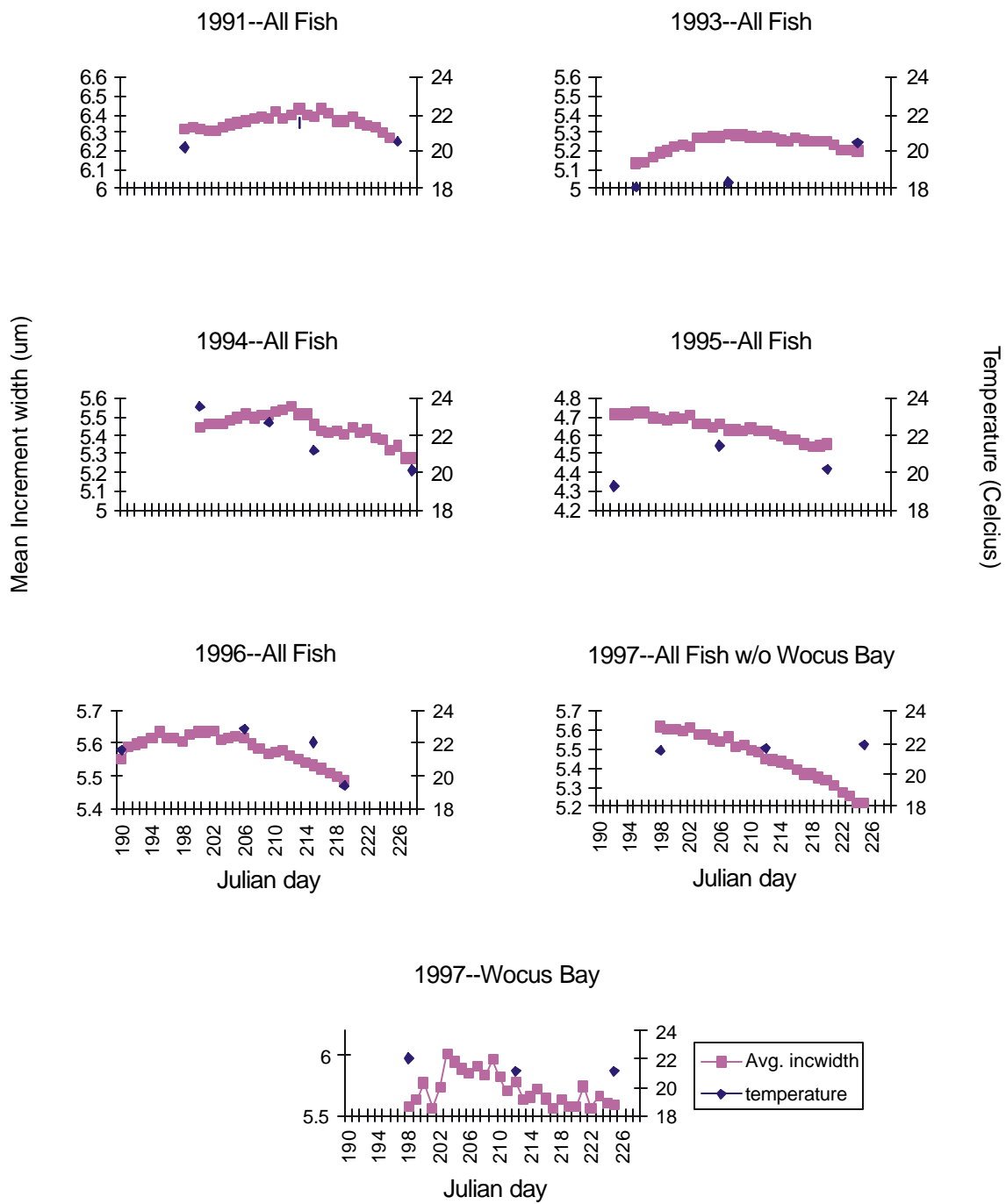


Figure 2.12. Mean increment width (µm) and temperature (degrees C.) vs. Julian day for Lost River and shortnose suckers combined: 1991, 1993-1997.

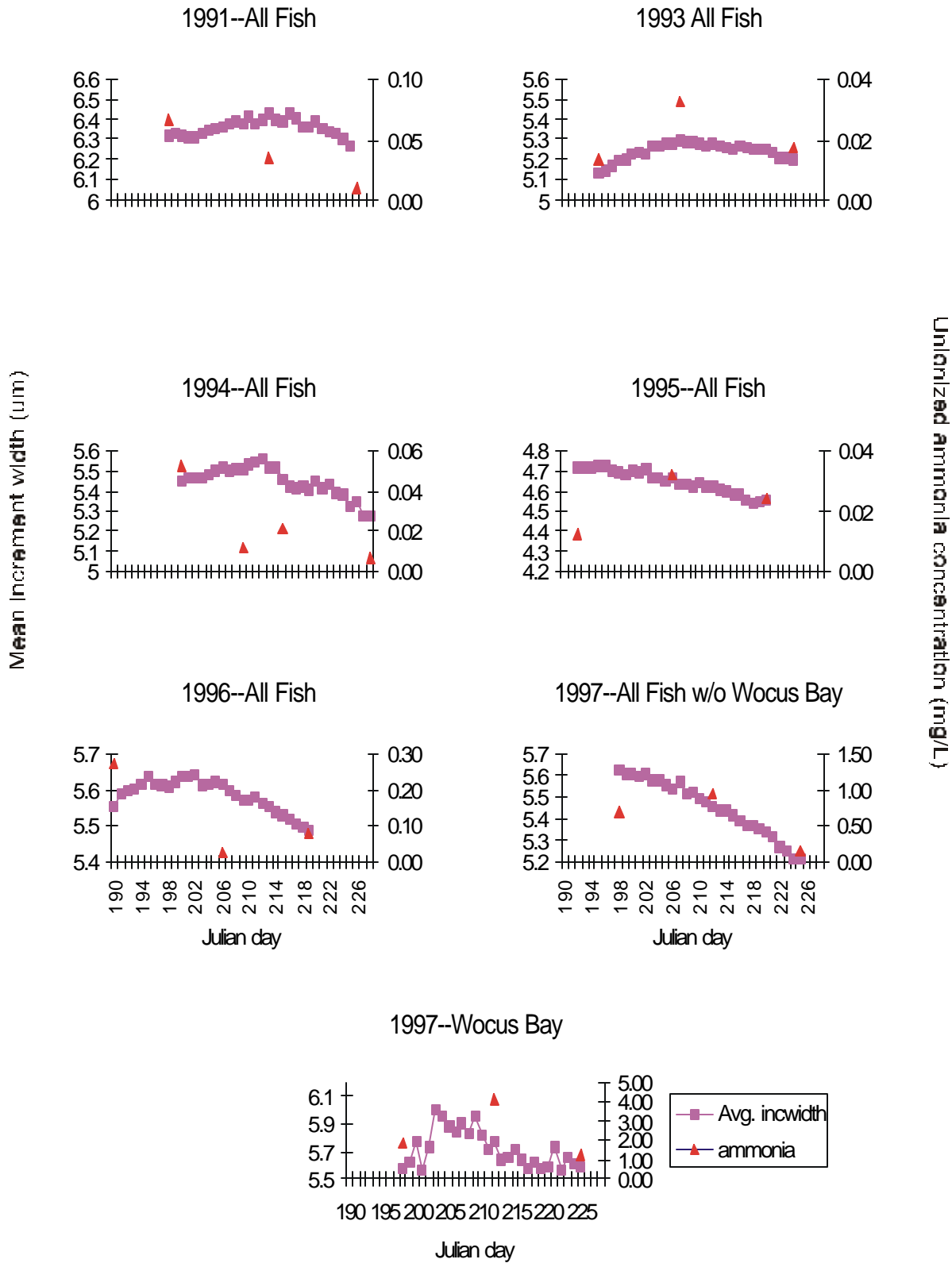


Figure 2.13. Mean increment width (um) and unionized ammonia concentration (mg/L) vs. Julian day for Lost River and shortnose suckers combined: 1991, 1993-1997.

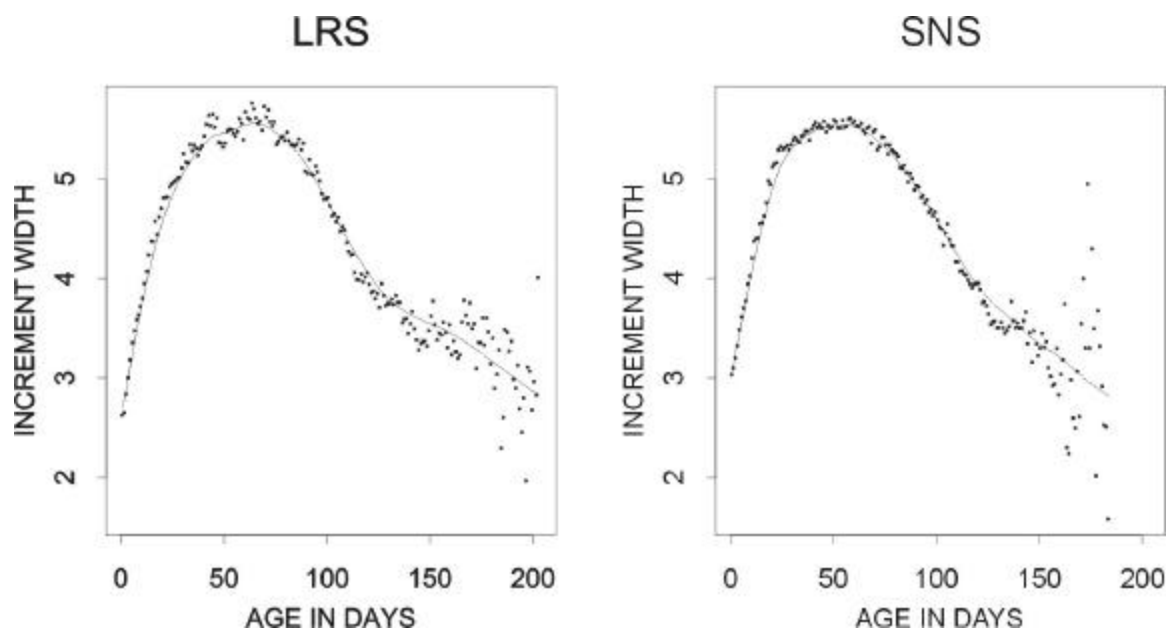


Figure 3.1. Average increment widths (μm), over multiple years, vs. age (days), for Lost River and shortnose suckers. Fitted curves were obtained from the S-PLUS function `supsmu`.

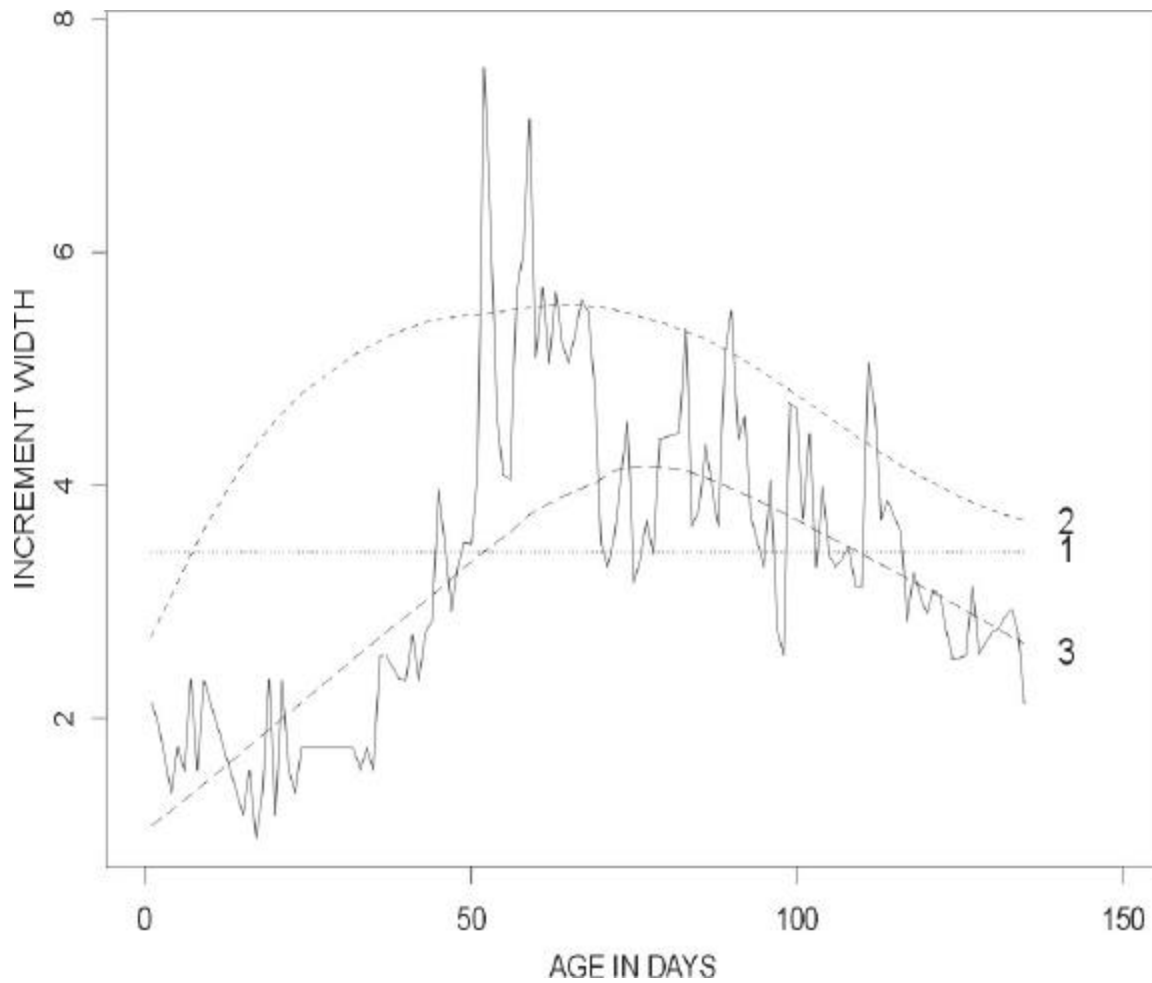


Figure 3.2. Average increment width (um) vs. age (days) for an individual Lost River sucker, with three baseline curves superimposed. The random effect for fish in Equation 2 allows baseline 2 to be shifted up or down for individual fish.

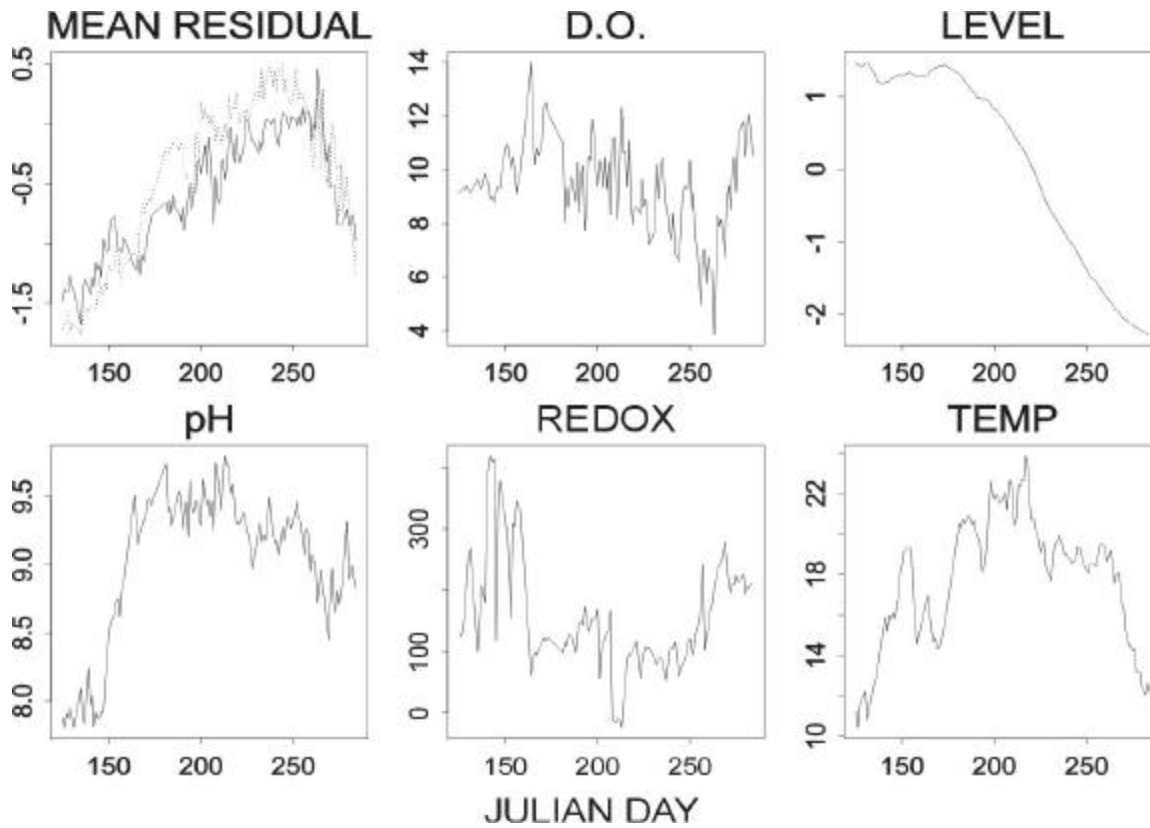


Figure 3.3. Average residuals (from baseline 2) and lakewide averages of the environmental variables vs. Julian day in 1995. In the upper left panel, the solid line represents Lost River suckers, and the dotted line represents shortnose suckers.