4-22-1993

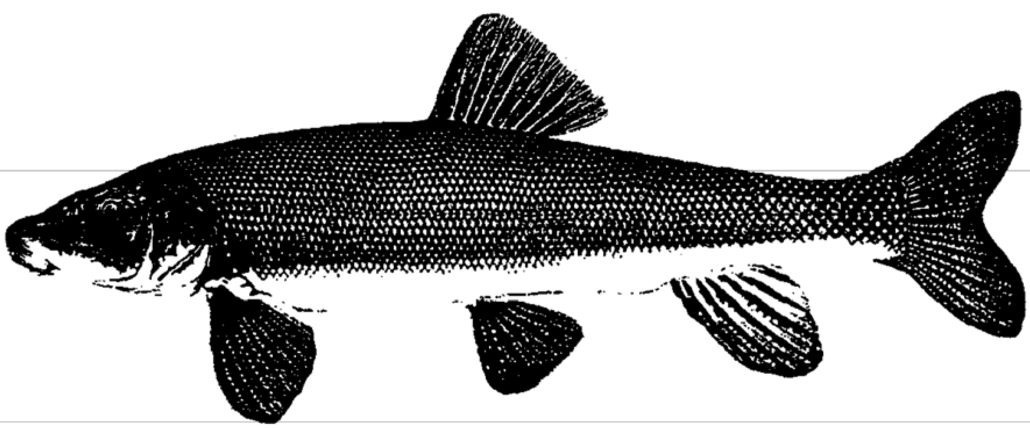
Ex. 281-US-414

Douglas F. Markle
Oregon State University, Department of Fisheries and Wildlife

David C. Simon
Oregon State University, Department of Fisheries and Wildlfe

PRELIMINARY STUDIES OF SYSTEMATICS AND JUVENILE ECOLOGY OF UPPER KLAMATH LAKE SUCKERS

Douglas F. Markle
David C. Simon



Deltistes luxatus

FINAL REPORT

PRELIMINARY STUDIES OF SYSTEMATICS AND JUVENILE ECOLOGY OF UPPER KLAMATH LAKE SUCKERS

Cooperators:
U. S. Bureau of Reclamation, Klamath Project
Oregon Department of Fish and Wildlife
U. S. Fish and Wildlife Service
The Klamath Tribe
U. S. Forest Service, Winema Forest
Pacific Power and Light

by

Douglas F. Markle and David C. Simon
104 Nash Hall
Department of Fisheries and Wildlife
Oregon State University
Corvallis, Oregon 97331-3803

22 April, 1993

ABSTRACT

Systematics

A number of univariate and multivariate approaches were taken to address the problem of identification of Upper Klamath Basin suckers. Total post-Weberian apparatus vertebral counts were a reliable method of identifying Lost River suckers. Of 950 suckers radiographed for vertebral counts, 94.3% of Lost River suckers had 45 or more vertebrae, whereas 98.8% of shortnose suckers and 100% of Klamath largescale suckers had 44 or fewer. Total vertebral counts for Klamath largescale and shortnose suckers were similar. Gillraker counts were also a useful diagnostic feature but are positively allometric with adult counts not set until at least 200 mm SL. Variation in gillraker counts with size is documented and it is argued that the variation is normal rather than enhanced due to hybridization.

Multivariate discriminant analysis of six continuous variables on a subset of 98 suckers less than 100 mm SL correctly classified 100% of Lost River suckers, 95% of Klamath largescale suckers, and 96% of shortnose suckers. Multivariate discriminant analysis of six discrete variables on a subset of 194 juvenile suckers correctly classified 100% of Lost River suckers, 90% of Klamath largescale suckers, and 96% of shortnose suckers. We found evidence of about 3% hybridization in the 1991 year class.

Many misclassified specimens were allopatric Klamath largescale suckers that were classified as shortnose suckers. We explore some evolutionary scenarios that might explain this

pattern and comment on fish evolution in lakes.

Ecology

An estimated 759,150 larval suckers were entrained into the A-Canal from mid-May to mid-July, 1991. Entrainment patterns appeared bi-modal for shortnose suckers and uni-modal for Lost River suckers. Sucker entrainment patterns were similar to 1990.

Sucker larvae were captured from "new" spawning areas in Wood River and Crooked Creek in 1991. Some have been identified as Lost River suckers. Otolith elemental concentrations of Lost River sucker larvae from different spawning sites (Wood River, Crooked Creek, Sucker Springs, and Williamson/Sprague rivers) were not significantly different, but multivariate discriminant analysis of four elements correctly classified 92% of lake-spawned larvae and 83% of river-spawned larvae.

Age 0 suckers were captured near shorelines during the summer with beach seines and cast nets, and in the fall with cast nets and trawls. Sucker species composition was different for each gear possibly reflecting size, behavioral, or distributional differences. Estimates of early growth indicate Lost River suckers had a 15 mm size advantage over shortnose suckers in 1991. Size frequencies of both species indicated two modal size groups in the 1991 year class. Trap net surveys suggested juvenile suckers concentrate near river mouth habitats in spring. The 1992 year classes of both sucker species appeared to fail whereas the 1991 year classes seemed good. Our ability to effectively sample suckers during the first year of life and assign correct identifications makes long-term assessment of variability of age 0 sucker abundance feasible.

TABLE OF CONTENTS

Discussion

List of Figures.

List of Tables

GENERAL INTRODUCTION

The Klamath Basin contains four recognized species of catostomids: Catostomus rimiculus Gilbert and Snyder, 1898 (Klamath smallscale sucker), Catostomus snyderi Gilbert, 1898 (Klamath largescale sucker, KLS), Chasmistes brevirostris Cope, 1879 (shortnose sucker, SNS), and Deltistes luxatus (Cope, 1879) (Lost River sucker, LRS) (Bond 1973, Andreasen 1975, Miller and Smith 1981). Two of the suckers, the shortnose sucker and the Lost River sucker, are federally listed endangered species.

Our long-term goal is to better understand juvenile sucker ecology with the hope of being able to evaluate year-class success of sucker populations. This goal is being pursued within an explicitly evolutionary context. We believe that understanding the historical context of sucker evolution will contribute to a better understanding of their adaptive constraints and present predicaments. Our objectives are to focus on 1) sucker systematics and 2) juvenile sucker ecology. The following report is divided into systematics and ecological sections. The systematics work involves the use of morphological, biochemical and ecological characters and, to date, has focused on alpha taxonomy (species identification, especially of juveniles) and morphological characters. The biochemical work is also in progress and will not be presented here. The ecological work has focused primarily on methods to monitor year-class success and better understand juvenile distribution and abundance in Upper Klamath Lake.

SYSTEMATICS

INTRODUCTION

Recent documents addressing ecosystem restoration and sucker recovery in the Klamath basin by the U.S. Bureau of Reclamation (USBR), the U.S. Fish and Wildlife Service (USFWS) and the Klamath Basin Waters Users Protective Association (KBWUPA) have lamented the difficulty of identifying these suckers and the complexity of historical changes in their scientific names. The former is partly due to inadequate taxonomic study. The latter seems to be due to ignorance about scientific nomenclature and the absence of an explicit phylogenetic basis for the higher level classification of sucker genera. By any standards, Klamath suckers have extremely simple nomenclatural histories. There are only two junior synonyms for Ch. brevirostris (stomias and copei), only one for D. luxatus (rex), and none for C. snyderi. Only C. snyderi has ever been confused with another recognized species (incorrectly referred to C. labiatus, one of the synonyms of C. occidentalis, by Girard, 1856). The latter was only marginally made worse by Andreasen's (1975) misspelling (lubiatus) and incorrect citation date (1857). Although the nomenclature is simple, the problems of genus-level classification and identification of individual specimens are not simple. Confusion about these three issues seems widespread.

The genus level classification is distinctly "classical", largely subjective, and has not been subjected to rigorous analysis. Deltistes, for example, is defined based on unique characters that serve to define the species but that may or may not define a genus. An explicit hypothesis of relationships is non-existent. Thus, the genus from which Deltistes was removed, Catostomus, risks being a "catch-all" of catostomids that are not "different enough" to be in another genus. As we explain below, concern about evolutionary relationships is more than a concern about names. The interpretation of any systematics data (morphological, biochemical, ecological) can be greatly altered if the Klamath suckers are interpreted as close relatives, such as sister species, rather than as three species from three genera that happen to coexist through historical coincidence.

The species level taxonomy is also inadequate. In drafts of the KBWUPA Ecosystem Restoration Plan and the USFWS Lost River and Shortnose Sucker Recovery Plan, authors note discrepancies in gillraker counts for shortnose suckers with Andreasen (1975) having reported 40 and Moyle (1976) having reported 34-49. The most comprehensive previous work reported 36-46 (Miller and Smith 1981). Part of the discrepancy can be traced to Andreasen (1975) who reported many numbers for the same structure in one species. For gillrakers in shortnose suckers, he reported 39-40 in his key (p. 75), 39-41 in his text (p. 53), and 33-48 in his figure 17. These and other purported discrepancies in the literature for diagnostic morphological characters of Lost River suckers and shortnose suckers are important to understand for they appear to have led some to conclude that: 1) morphological approaches to Klamath sucker taxonomy have failed; 2) hybridization and introgression are widespread in Klamath suckers; and 3) field studies are in jeopardy until better identification methods are available.

A fundamental taxonomic principle is to understand sources of variation in each character studied (Hennig 1966, Mayr 1969, Wiley 1981). Morphological variation within species of fishes can be caused by geographic and sexual differences and, more narrowly, by ontogenetic and individual variation. The presence of variability is to be expected, but variability has not been well analyzed in Klamath suckers. Differences between small samples collected decades apart were used by Miller and Smith (1981) as evidence of hybridization in Klamath suckers (also by Behnke (1992) for trouts). Although their conclusions may be correct, their method is flawed. The nature of historical samples (collection of typical, "best", or unusual specimens; of few specimens; of convenient sizes; at few sites; and at convenient times) makes rigorous comparison with recent collections difficult. Invariably, the character chosen to document the supposed hybridization is a character with a large absolute mean and with no variance reported. If these data are normal with variance independent of the mean, characters with high mean values will have larger ranges than they would if their means were smaller. As a first order conclusion from a poor data set, variation should be expected as a consequence of the nature of numbers not hybridization. In the following, we document patterns of individual and ontogenetic variation in some characters of Upper Klamath suckers and explore explanations of the patterns.

MATERIALS AND METHODS

We have collected various morphometric and meristic data on 1465 juvenile and adult suckers. We exclude larval suckers from the present analysis. Klamath basin suckers make up 1414 (97%) of the data set and three outgroup species (Catostomus macrocheilus (8), C. rimiculus (31), and C. occidentalis (10)) make up the remainder. Our emphasis has been on specimens from Upper Klamath Lake though we have limited material from the Lost River subbasin (especially Clear Lake) and make some tentative comments about these specimens. The material was either historical museum holdings, recent hatchery-reared museum holdings, or recently collected as part of this study on the authority of a scientific taking permit issued by the U.S. Fish and Wildlife Service (permit no. MARKDF). Most of the latter are also deposited as museum holdings. Abbreviations for museum acronyms follow Leviton et al. (1985).

There are several subsets of the Klamath sucker data set. The most complete data set contains all counts and measurements shown in Tables 1 and 2. All vertebral and vertical fin meristic data were taken from radiographs. Vertebral counts do not include the four Weberian apparatus centra. Unless noted otherwise, all methods follow standard procedures as outlined by Hubbs and Lagler (1964).

We used stepwise discriminant function analysis using a significance level to enter = 0.15 and significance level to stay = 0.15. A data set with primary diagnostic characters contained 379 Lost River, 444 shortnose and 166 Klamath largescale suckers from the Upper Klamath Lake subbasin and 11 suckers from Clear Lake. All upper tributary suckers were presumed to be Klamath largescale suckers. From our 1991 field sampling in Upper Klamath Lake, we identified all specimens greater than 85 mm using the primary diagnostic data set. For specimens less than 85 mm, Lost River suckers were identified based upon vertebral counts. Of the remaining specimens less than 85 mm, selected subsets of different size groups have been identified to species. Only three Klamath largescale suckers were identified in these subsets (Table 3). The remaining specimens, 402 juveniles, (Table 3, column UNK) have been radiographed and await further analysis. Our cursory examination of these individuals, particularly of lip morphology, suggests this group is composed almost wholly of shortnose suckers. Thus, for the distributional and growth studies in this report, we are assuming all of these individuals are shortnose suckers. All specimens from our 1992 field sampling have been identified to species. As the overall data set expands, especially as Klamath largescale suckers from different areas are added, we will expand the multivariate analyses and more critically examine subtle differences in shape (using sheared principal components analysis) and expand the analysis to smaller life history stages.

Data analyses were facilitated with statistical software packages Statgraphics version 5.0 (STSC, Inc., 1991), SAS (SAS Inst., 1988), and Tablecurve (Jandel Scientific, 1991). Data were initially examined as bivariate data sets with size in order to uncover allometric patterns. Tablecurve was used to generate 1351 equations to estimate gillraker allometry and the equation(s) with the highest F value used to model the relationship. Residual values of gillraker counts from one of these equations were used in subsequent discriminant function analyses. Discriminant function analyses were conducted using the SAS statistical package (SAS Institute Inc., 1988) with pooled covariance matrices and proportional classification probabilities.

RESULTS

Morphometric data

The 22 morphometric characters measured are listed with abbreviations in Table 1. The complete set of measurements was taken on at least 30 specimens of each of the three Upper Klamath Lake species (Table 4). The means and ranges of most morphometric features are very similar among the three species (Table 4) and younger individuals, especially, are very similar (Fig. 1).

Single characters that have moderate utility in distinguishing a species or pairs of species often have complex allometry. The caudal peduncle depth as a percent of standard length tends to be narrower in Lost River suckers (Fig. 1) and shows positive allometry (Fig. 2). In the other two species, it is thicker, more variable and the allometry is more isometric (Fig. 2). The dorsal-fin origin tends to be further posteriad in Klamath largescale suckers. The placement can be seen in the LOD/LDOC ratio where a value of 100 would indicate placement midway between the snout and the caudal-fin base. In a comparison of shortnose and Klamath largescale suckers, the LOD/LDOC tends to be negatively allometric to about 50-60 mm SL and isometric at larger sizes (Fig. 3).

Meristic data

The 23 meristic characters counted are listed with abbreviations in Table 2. The complete set of counts was taken on at least 24 specimens of each of the three Upper Klamath Lake species (Table 5). Counts were also taken of selected characters from some Clear Lake suckers (Table 5). There was overlap in most meristic characters between species (Table 5) but there were mean differences in upper and lower procurrent caudal-fin rays, gillrakers on the first arch, vertebrae to anal-fin origin, vertebrae to dorsal-fin origin, precaudal vertebrae, caudal vertebrae, and total vertebrae.

The total post-Weberian apparatus vertebral count was an almost perfect diagnostic character for Lost River suckers (Table 5). In our largest data set, 94.3% of 368 Lost River suckers had 45 or more vertebrae, whereas 98.8% of 431 shortnose suckers and

100% of 151 Klamath largescale suckers had 44 or fewer vertebrae. Including the Weberian centra, the demarcation is 49 or more vertebrae for Lost River suckers and 48 or less for shortnose and Klamath largescale suckers.

The number of gillrakers on the first arch was positively allometric with standard length (Fig. 4) and generally followed the relationship: $Y=a+b/X$, where Y is gillraker count, X is SL and a and b are constants. For Lost River suckers the relationship was approximately asymptotic with adult counts set at about 250 mm SL (Fig. 5A). The equation for Lost River suckers in Fig. 5A ($Y=29.1 - 271.0/X$) had the highest F value (142.9) of the 1351 equations fitted to these data. For combined Klamath largescale and shortnose sucker data the relationship was also approximately asymptotic with adult counts set at about 240 mm SL (Fig. 5B). The equation for Fig. 5B ($Y=39.4 - 472.7/X$) had the highest F value (850.2) of the 1351 equations fitted to these data. At sizes less than 100 mm SL, the gill raker-size relationship was more linear for combined Klamath largescale and shortnose suckers (Fig. 6). The equation for Fig. 6 ($Y=20.6 + 0.167X$) had the highest F value (470.99) of the 1351 equations fitted to these data.

When shortnose sucker and Klamath largescale data were treated separately, the shortnose sucker data suggested that the relationship for that species was non-asymptotic whereas the relationship for Klamath largescale suckers continued to be asymptotic (Figs. 8A and B). The equation for shortnose suckers in Fig. 8A ($Y=62.3-123.4/\ln X$) had the second highest F value (947.2) of the 1351 equations fitted to these data. We rejected an equation with a slightly higher F value (949.6) which had the square root of X in the denominator, for ease of subsequent calculations. Both equations were non-asymptotic. The equation for Klamath largescale suckers in Fig. 8B ($Y=34.7-357.9/X$) had the highest F value (657.6) of the 1351 equations fitted to these data. The adult count of gillrakers in Klamath largescale suckers is set at about 200 mm SL.

Because mean gillraker counts suggested differences between species (Table 5) and because the counts are size-dependent (Figs. 4-7), we calculated a gillraker count residual for each specimen. Gillraker count residuals were calculated from the equations generated from combined Klamath largescale and shortnose data (Figs. 5B and 6). For specimens less than 100 mm SL, we used $Y=20.6+0.167X$ and for specimens greater than 100 mm SL, we used $Y=39.4-472.7/X$. Gillraker residual summary statistics are in Table 5. Shortnose suckers tended to have the most positive residuals (highest gillraker counts at size), Lost River suckers tended to have the most negative residuals (lowest gillraker counts), and Klamath largescale and Clear Lake suckers tended to be intermediate (Table 5). For Klamath largescale and shortnose suckers less than 100 mm SL, the interaction of dorsal-fin position and the number of gillrakers was a moderately useful diagnostic bivariate character set (Fig. 8).

Multivariate analyses of anatomical data

We performed multivariate analyses on continuous and discrete data separately. Although based on discrete gillraker counts, the gillraker residual value is continuous and is treated with morphometric data.

Because of problems with allometry noted above we restricted the first morphometric data set to specimens less than 100 mm SL. A stepwise discriminant function analysis of continuous data selected six variables: gillraker residuals (GRRESID), dorsal fin to caudal distance (LDOC), depth at the pectoral (DP1), snout length (LAE), head length (HL) and caudal peduncle depth (DCAUDPED). Initial discriminant analysis of these variables showed consistent misclassification of hatchery reared specimens. A subset of our data with no missing values or hatchery-reared fish contained 60 Klamath largescale, 12 Lost River suckers and 26 shortnose suckers less than 100 mm SL. The functions are as follows:

$$DF1 = 2.69 + 2.49(GRRESID) - 0.31(LDOC) + 0.08(DP1) - 2.03(LAE) + 0.52(HL) + 2.28(DCAUDPED);$$
$$DF2 = -0.82 + 0.31(GRRESID) + 0.55(LDOC) - 0.62(DP1) - 0.13(LAE) - 0.85(HL) + 1.06(DCAUDPED).$$

These functions (Fig. 9) correctly classified 100% of Lost River suckers, 95% of Klamath largescale suckers and 96% of shortnose suckers. The classification of most specimens strongly supports the identification with posterior probabilities greater than 90%. In two of the four cases of misclassification, the probabilities of membership in the reclassified species were only 60 - 64%.

When gillraker count residuals were excluded, classification success remained above 90% suggesting that some shape differences exist among taxa. The most obvious differences were caudal peduncle depth and dorsal fin position. In a larger subset over the size range available, a discriminant function analysis of SL, LOD, LDOC and DCAUDPED correctly classified 80% of 233 shortnose suckers, 85% of 67 Klamath largescale suckers and 80% of 59 Lost River suckers (Fig. 10). Although there are size-related shape changes not accounted for in the analysis shown in Fig. 10, it serves as a useful approximation of two aspects of shape of Upper Klamath suckers. First, all three suckers have the same general appearance, especially as juveniles and young adults. Second, Lost River and shortnose suckers have a tendency for some individuals to differ from the generalized appearance whereas Klamath largescale suckers have less tendency to differ from the generalized appearance (Fig. 10).

A stepwise discriminant function analysis of discrete data selected seven variables: gillrakers, total vertebrae, precaudal vertebrae, upper procurrent caudal rays, vertebrae to dorsal fin origin, vertebrae to anal fin origin, and caudal vertebrae. In our multigroup discriminant function analysis we used six of these variables and excluded total vertebrae as it is predicted by two of the other variables. A subset of our data with no missing values contained 68 Klamath largescale, 57 Lost River suckers and 69 shortnose suckers. The functions are as follows:

DF1 = -42.87 -0.17(GR) +0.50(PRECAUDVER) -0.28(UPCAUD)
+0.31(VDO) +0.38(VAO) +1.16(CAUDVER)

DF2 = -14.53 +0.29(GR) -0.12(PRECAUDVER) -0.12(UPCAUD) - 0.71(VDO) +0.17(VAO) +0.74(CAUDVER)

These functions (Fig. 11) correctly classified 100% of Lost River suckers, 90% of Klamath largescale suckers and 96% of shortnose suckers. Reanalysis of these data with ln-transformations produced essentially identical results with two fewer misclassified shortnose suckers and three more misclassified Klamath largescale suckers. A third analysis of these data with three species identifications assigned randomly gave correct classifications of 23-58%, further suggesting that our results are not artifacts of data.

As in the discriminant analysis of continuous variables, the classification of most specimens strongly supports our identifications with posterior probabilities greater than 90%. Six of seven misclassified Klamath largescale suckers were from allopatric populations in Pole Creek in the upper Sprague River basin (4 specimens) and above Klamath Marsh from the Williamson River (2 specimens). There were three specimens from Upper Klamath Lake with an approximately equal probability of being either Klamath largescale or shortnose sucker (probabilities between 46-53%) and one specimen with an approximately equal probability of being either Lost River (41%) or shortnose sucker (58%).

A Gerber Reservoir sucker (OS 11015) was classified as a shortnose sucker. Two Clear Lake suckers were classified as shortnose suckers with probabilities greater than 90%, two were classified as shortnose suckers at 77-80%, and two were classified as Klamath largescale suckers at 64-66%.

DISCUSSION

Species and hybridization

Our analyses to date agree with previous studies suggesting that there are three species of suckers in the Upper Klamath Lake drainage. These species are superficially similar but variable with the greatest external differences in lip and mouth morphology of adults (Miller and Smith 1981, Buettner and Scoppettone 1991).

No previous study has included a serious evaluation of ontogenetic changes in diagnostic characters. We have focused, initially, on the ontogeny of gillraker counts (Figs. 4-7) because this meristic has been central to many claims of introgression. Andreasen (1975), for example, claimed that adult gillraker counts were established at sizes as small as 46 mm SL in shortnose suckers (p. 54) and 65 mm SL for Lost River suckers (p. 49). Unfortunately, he did not document the largest size at which adult counts were achieved nor did he quantify the variation to be expected at a given size. We suspect that subsequent reports of "hybrids" have been based, in part, on a misreading of these sizes as absolutes rather than as the leading "tail" of the distribution of gillraker counts. At a minimum, the adult gillraker count in Upper Klamath Lake suckers is not reached until 200+ mm SL and the shortnose sucker may continually add gillrakers throughout its life (Figs. 5A, 7A and 7B).

We do not have evidence to support the contention of massive hybridization among Upper Klamath Lake suckers. In our discriminant analysis of meristic characters, six of seven Klamath largescale suckers that were misclassified as shortnose suckers were from allopatric upstream sites where shortnose suckers are absent. The presence of allopatric Klamath largescale suckers with meristic features resembling shortnose suckers can not be explained as a consequence of hybridization. At this stage in our analysis, the best candidates for hybridization are four specimens from the discriminant analysis of meristic characters. We found three specimens with about equal probabilities of being Klamath largescale or shortnose suckers and one specimen with about equal probability of being shortnose or Lost River sucker. All four specimens had caused us difficulty prior to the discriminant analysis. Intermediacy in characters is often assumed for hybrid fishes but it must be demonstrated on a case by case basis (Neff and Smith 1979). For example, brook trout x bull trout hybrids have consistently higher not intermediate characters (Leary et al. 1983). Recognizing this limitation, these four specimens suggest a first order estimate of hybridization in our 1991-1992 Upper Klamath Lake samples of 2.2% KLS X SNS hybrids and 0.8% LRS x SNS hybrids.

Our cursory examination of suckers from Gerber Reservoir and Clear Lake does not present a clear picture. These fish may be no different than our allopatric Klamath largescale suckers that were also classified as shortnose suckers. However, Buettner and Scoppettone (1991) suggest that Clear Lake suckers are shortnose suckers that have diverged from Upper Klamath Lake shortnose suckers because of isolation and different selection pressures. Considering the features we document in allopatric Klamath largescale suckers as well as the presence of stream resident "shortnose suckers" in the Willow Creek tributary of Clear Lake, one should not discount the possibility that these fish are Klamath largescale suckers.

Lacustrine fish evolution

Freshwater lakes are the sites of a many taxonomic problems in ichthyology. The problems center around (1) lacustrine and lotic forms of a single clade, or (2) around two or more lacustrine forms of a single clade. Often, the morphological differences between the various forms are linked to resource use (eg. Schluter and McPhail 1992) and appear to be "controlled by selection for a few genes not observed in assays of allozymes and mtDNA" (Smith 1992). In a variety of lakes the morphological differences are feeding-related (Fryer and Iles 1972) and frequently involve gillraker morphology such as in Great Lakes coregonids (Smith and Todd 1984), British Columbia sticklebacks (McPhail 1984), New Zealand smelt (Ward et al. 1989), and Klamath suckers. A common pattern is for a lacustrine form to have more gillrakers than a lotic form (Ward et al. 1989). More generally, there is the presence of two major habitats in lakes (benthic and limnetic) with only one available to the presumed ancestor.

For example, only the planktonic habitat seems exploited by marine three-spine sticklebacks, yet in lakes both benthic and limnetic (planktonic) habitats are exploited (Schluter and McPhail 1992). Schluter and McPhail (1992) proposed the following scenario to explain evolution in three-spine sticklebacks. (1) An anadromous ancestor was planktonic with a high gillraker count. (2) The initial invasion and subsequent isolation of a lake resulted in a form with an intermediate gillraker morphology able to exploit both benthic and planktonic (limnetic) habitats. (3) Subsequent reinvasion of the lake by the anadromous planktivorous ancestor resulted in a morphological shift of the first invader to a benthic (low gillraker) morphology while the new invader retained the planktivorous (high gillraker) morphology. Their model emphasizes that the first invader changed the course of future evolution in a lake. They note that the process can occur quickly, in less than 13,000 yr, and that hybridization between the resulting species is low (less than 1%).

This model may have relevance to evolution of lacustrine suckers in western North America and, at a minimum, might constructively focus taxonomic and phylogenetic research. Obviously, the model makes little sense if catostomid classification is correct and Upper Klamath Lake has three genera of suckers. However, it should be noted that there is no rigorous phylogenetic data supporting classification of Lost

River suckers in a genus separate from Catostomus and there are no characters independent of feeding morphology to define Chasmistes. As the Schluter and McPhail model suggests and as Smith (1992) noted, "differentiation in lacustrine species flocks is dominated by ecologically adaptive characters--these are usually apomorphic for intralacustrine clades, and often convergent in other species at similar depths." In other words, the results of fish evolution in lakes may be highly predictable and convergent for some clades. Benthic three-spine sticklebacks in different lakes are not each others closest relatives, but rather represent the predictable results of three-spine stickleback evolution after double invasions of lakes. Although it seems unlikely because of their Miocene age, the lacustrine suckers in western North America (Chasmistes) might not be each others closest relatives and could also represent the predictable convergent results of lacustrine fish evolution. However, the rejection of a monophyletic Chasmistes would require an a priori demonstration of homoplasy (convergence) in a suite of feeding-related characters that otherwise would overwhelm phylogenetic reconstruction. This would not be an easy task and further underscores the need for better understanding of phylogenetic relationships of western suckers.

Of the patterns we see in the three Upper Klamath Lake suckers, one seems to require explanation and might provide some needed insight: the presence of allopatric specimens of Klamath largescale suckers with meristic features that fit our multivariate description of shortnose suckers. A congruent pattern of variation was also found in an LDH-B2 allele in eye tissue by Harris (1991). Both Moyle and Berg (1991) and Harris (1991) found an allele of LDH-B2 that was slightly less mobile (scored as allele 95 relative to the common allele's mobility of 100) in shortnose suckers and Lost River suckers. Klamath largescale suckers were fixed for the widespread 100 allele except in allopatric upper Williamson (Klamath Marsh) fish where 43% were heterozygous and 14% were homozygous for the 95 allele (Table 2 in Harris 1991). In other words, sympatric shortnose and Klamath largescale suckers in Upper Klamath Lake were distinct showing a fixed difference whereas some allopatric Klamath largescale suckers exhibited the shortnose pattern (14%) or an intermediate pattern (43%). Clear Lake fish mostly (97%) exhibited the shortnose pattern (Moyle and Berg 1991).

These patterns might be explained as: (1) evidence that shortnose suckers and Klamath largescale suckers are a single species with the capacity of some individuals to become lacustrine (shortnose form) while others stay stream resident (Klamath largescale form); (2) evidence that two former species have become completely introgressed; or (3) evidence that there are two species that show character displacement when in sympatry but tend to share the similar features when allopatric. As a first approximation, our discriminant analysis suggests that we are sampling two species (Klamath largescale and shortnose suckers) with few intermediates. However, all three explanations must be further explored in the context of lake evolution.

Ecophenotypic plasticity (first explanation) is potentially part of the variability seen in all three species. It may be most discernable in Klamath largescale suckers which have been collected, as adults, in three different habitats (small streams, large stream or river channels, and lakes). Our small sample of Clear Lake - Lost River drainage suckers (not including Lost River suckers) suggests that they could be Klamath largescale suckers that are, at least partly, lacustrine (but see Buettner and Scoppettone (1991) for an equally probable alternative explanation). If the Klamath largescale sucker is analogous to the Warner sucker, which also has both lacustrine and stream resident populations, then at least part of the variability and confusion over these fish can be explained. Klamath largescale suckers are more often misclassified in our discriminant analyses than either shortnose or Lost River suckers, a result that is also consistent with the presence of two ecophenotypes in that species.

In terms of eutrophic lake evolution, ecophenotypic plasticity may be more difficult to tract than in a more static environment. If a shortnose form (species) evolves in lakes, what happens when the lake evolves into a marsh? Upper Klamath Lake, Clear Lake and Klamath Marsh are a continuum in eutrophic lake evolution. Clear Lake and Klamath Marsh suckers could represent the atavistic reversal of a shortnose form to a Klamath largescale form. Alternatively, lake evolution might result in the extinction of the shortnose species and competitive release of the Klamath largescale species to fill the void. Central to resolution of these alternatives is the nature of Klamath basin sucker species. Our tentative view, in agreement with Buettner and Scoppettone (1990), is that there are three sucker species in the Upper Klamath Lake subbasin, one of which, Klamath largescale sucker, has two ecophenotypes.

Based on our analyses to date, hybridization (second explanation) between two, or all three, species seems less likely a major cause of variation. However, we would not discount the possibility that hybridization has been, and continues to be, a source of variation. Botanists have many examples of syngameons, groups of hybridizing species. Some, such as balsam poplar and cottonwoods, have been ecologically and evolutionary distinct for 12 million yr and have been hybridizing throughout (Templeton 1989). Zoologists are also discovering syngameons (Templeton 1989) and these inter-species relationships may be critically important for the evolutionary success of their constituent species. If Upper Klamath Lake suckers are part of a syngameon, perhaps also including, at least historically, one or more of Klamath smallscale, Warner, and Sacramento suckers, the potential pitfalls for phylogenetic analyses and management increase.

For example, cladistic analyses of phylogeny assume that taxa (such as species and genera) are distinct over time and that they may persist, go extinct, or subdivide (speciate). The conceptual result is a tree. Because taxa, or branches, stay distinct over time, they do not grow back together or form reticulate patterns. That is, the conceptual result is not a network. The tree is discovered by finding unique characters that define each branch or node on the tree. Some characters that appear to be unique may, in fact, represent convergent adaptations that are sprinkled around the tree at many nodes. These are discovered as inconsistencies with other characters. Above, we have suggested that some of the unique characters that define branches of the sucker evolutionary tree (the Chasmistes node) might be convergent and that the suite of convergent characters could easily swamp real evolutionary relationships. We also do not discount the notion that hybridization, perhaps a syngameon, has contributed to phenotypic and perhaps genetic plasticity of Upper Klamath Lake suckers. These potential pitfalls to better understanding the interrelationships of these species can be discovered and their impacts on reconstructing phylogeny can be understood by using a variety of datasets, reflecting both phenotypes and genotypes. Ideal phenotypic data sets should include anatomical, enzymatic and ecological information. Ideal genotypic data sets should include mitochondrial (maternal) and nuclear (biparental) information.

The systematics of Upper Klamath Lake suckers and their relatives must finally consider the application of knowledge of relationships. To the extent that species or other evolutionary units are allopatric (geographically restricted), subsequent taxonomic decisions are simple. Where sympatry over all or part of the life cycle exists, subsequent taxonomic decisions should be easy, cost-effective and non-lethal when appropriate. Collection methods are lethal for early life history stages and less so for older individuals. Field conditions frequently make formalin or ethanol preservation preferable to freezing. Consequently, morphology, amplified DNA products, and muscle-based allozyme characters are the desired diagnostic characters for future work.

ECOLOGY

Our ecological studies are conveniently grouped into three subheadings based on the sampling area and objectives. These are (1) A-Canal sampling for estimating the number of larvae entrained into the Klamath Project Irrigation system, (2) natal origin sampling for documentation of spawning areas and for material for otolith microchemistry studies, and (3) juvenile field sampling for evaluating long-term sampling techniques, habitat utilization, growth rates, and year class success. The following treats each subheading separately.

A-CANAL SAMPLING

INTRODUCTION

The A-Canal diverts water at Klamath Falls, Oregon from Upper Klamath Lake into the U.S. Bureau of Reclamation's Klamath Project. Our sampling at the A-Canal was intended to determine the identity, abundance and spatial and temporal distribution of fish diverted at the A-Canal.

MATERIALS AND METHODS

We used a drift net made of 24.84 m^2 1mm Nitex mesh netting with a mouth opening of 0.45 m^2 (internal dimensions: length of 1.0 m and height of 0.45 m). A calibrated TSK flowmeter was suspended in the mouth opening. The net was suspended in the water from the boom across the lagoon in front of the headworks of the A-Canal. The long axis of the net was horizontal and the opening was perpendicular to the water flow. The daily discharge through the A-Canal headworks was provided by the Klamath Irrigation District.

Collections made in 1990 were reported by Harris and Markle (1991 MS) and are compared with 1991 samples herein.

Eighteen sample series (numbered 1 and 3-19) were collected between April 8 and August 12, 1991 (Table 6). Except for series 1 and 19, each series consisted of 18 samples from three time periods; 6 from the time period 2400-0800 hours, 6 from 0800-1600 hours, and 6 from 1600-2400 hours. Series 1 consisted of 9 samples from 0800-1600, and series 19 consisted of 6 samples from 1600-2400. Thus, a total of 303 samples were collected from the Headworks of the A-Canal in 1991. All samples were collected from 6 stations designed to represent the entire vertical and horizontal profile of the canal, and were chosen randomly.

The total volume of material collected in each net, primarily the filamentous blue-green alga, Aphanizomenon, was measured to the nearest liter. Samples were sorted in the field using a garden hose sprayer to force Aphanizomenon through a 1 mm Nitex screen. Fishes were removed, fixed in 5% formalin or 95% ethanol and returned to the laboratory where they were identified, counted and measured.

The total number of fish in each sample was log-transformed (ln (x+1)) and converted to fish per cubic meter of water based on volume estimates from the flowmeter. The antilog, minus 1, was taken to arrive at a normalized number of fish per cubic meter for each sample. The mean normalized number of fish per cubic meter was then estimated for each series. Data supplied by KID was used to calculate the mean daily discharge of water through the headworks by series. We estimated the number of fish per day entering the A-Canal for each series using the formula:

$$\text{Fish/day} = (\text{fish/m}^3)\ (\text{discharge as m}^3\text{/second})\ (\text{seconds/day}).$$

This procedure was also used to estimate numbers of suckers per day during each series. To make comparisons comparable between 1990 and 1991, we use the 1990 results based on the unstratified sampling assumption using KID flow rates (Harris and Markle 1991 MS).

RESULTS

A total of 318 fish were caught. The numbers caught and relative percentages of each species were: unidentified lampreys, Petromyzonidae, 1, 0.31%; unidentified chubs, Gila sp., 101, 31.76%; blue chubs, Gila coerula, 65, 20.44%; tui chubs, Gila bicolor, 34, 10.69%; fathead minnows, Pimephales promelas, 40, 12.58%; suckers, Catostomidae, 51, 16.04%; Klamath Lake sculpin, Cottus princeps., 3, 0.94%; unidentifiable, 23, 7.23%.

We estimated that 5,319,944 larval or early juvenile fish were entrained into the A-Canal between mid-April and mid-August (Table 7). The number of fish per day reached a high of 271,696 during series 14. This peak corresponded with peak entrainment rates found in 1990 (Fig. 12). After peaking, fish entrainment rates declined similarly in both years. A second peak in series 7 during 1990 was caused by a single catch of 652 fish in one sample, inflating this estimate.

We estimated 759,150 larval and early juvenile suckers were entrained into the A-Canal between May 13 and July 15, 1991 (Table 8). The number of suckers per day reached a high of 43,887 during series 9. A second peak developed during series 14. Based on myomere counts, we have identified the first peak as Lost River suckers and the second peak as shortnose suckers. However, about 50% of the collections during series 10 (the trailing edge of the first peak) appear to be shortnose. Thus, while there appears to be a single mode of Lost River sucker entrainment, shortnose sucker entrainment patterns may be bi-modal. We consider these identifications tentative at this time. Sucker entrainment rates in 1991 exhibited patterns that were similar to 1990, but were slightly lower (Fig. 13). Similar patterns of sucker entrainment in both years suggest that a large pulse of suckers may have been missed in the 1990 sampling. Through series 10, the number of suckers per day is the same as, or only slightly less than, the number of fish per day, indicating that nearly all larval fish that were entrained prior to mid- to late-June were suckers. Estimated entrainment rates for suckers were similar for night, day, and evening sampling periods (Fig. 14, Tables 9-11), but tended to be highest during daylight hours.

DISCUSSION

During the time period when both 1990 and 1991 sampling were coincident, the mean estimates of numbers of fish per day and numbers of suckers per day are very similar (Figs. 13 and 14). It is therefore reasonable to assume that the 1990 sampling missed the first pulse of suckers being entrained into the A-Canal. Our best estimate of the number of young suckers entrained into the A-Canal therefore comes from the 1991 sampling. Interannual differences in timing of spawning might change the period of vulnerability. Interannual differences in egg and larval production might change the pool of vulnerable larvae and result in higher or lower numbers of entrained larvae.

If preliminary sucker larvae identifications are correct, our data show a single mode of Lost River sucker and two modes of shortnose sucker entrainment in 1991. Larval emigration studies in the Williamson River in 1987 and 1988 (Buettner and Scoppettone 1990) have suggested a single pulse of Lost River sucker emigration and two pulses of shortnose sucker emigration; the first shortnose pulse being concurrent with the Lost River pulse. These emigration patterns could be reflected in A-Canal sucker entrainment patterns. The small number of suckers in series 6 (also Lost River suckers) could be larvae from Sucker Springs reproduction. We do have a small number of specimens preserved in 95% ethanol, and preliminary otolith microchemical analyses show promise of distinguishing river-spawned from lake-spawned suckers (see below).

NATAL ORIGIN SAMPLING

INTRODUCTION

Although spawning is known to occur at Sucker Springs and below Chiloquin Dam on the Sprague River, historical spawning sites were more numerous (Andreasen 1975). It is reasonable to assume that populations that used historical sites have gone extinct. However, there has been little or no monitoring of potential sites and the known sites are convenient to humans, suggesting that sites with low levels of spawning activity or sites that are inaccessible by depth or location might be undetected.

The clear possibility of population or "stock" differences between Lost River suckers from Sucker Springs and the Williamson/Sprague system, and the possibility of many other "stocks" historically, suggests that it would be prudent to have materials available to begin to address questions of natal origin. We chose to monitor known and potential spawning areas by collecting larval stages. Larval stages can be collected in areas where adults can not be seen or captured, can be sacrificed in relatively large numbers without impact on the population, and because of their numerical abundance, may be more easily detected in areas where adult abundance is low. Because a student thesis was also being prepared to examine otolith microstructure, we also wanted to evaluate if otolith microchemistry would contribute to detection of stock differences. The latter assumes that otolith microchemistry might reflect natal water characteristics such as pH or elemental concentrations. Several authors (Mulligan et al. 1987; Kalish 1989,1990; Radtke 1989) have used otolith microchemistry to characterize groups of fishes. In the most relevant study, Kalish (1990) found that he could distinguish anadromous from resident salmonids by analyzing the core of the otolith.

MATERIALS AND METHODS

Field sampling

We conducted qualitative sampling of known or suspected sucker spawning areas from 19 April to 18 July 1991. Similar sampling from 3 June to 10 July 1992 was reported by Logan and Markle (1993 MS) and is compared with 1991 results. Sampling dates were irregular and sampling methods differed according to the site. Three sampling devices were used: small aquarium dip nets to collect visually sighted individual larva (1991), a 700-micron mesh plankton net with a 0.5-m diameter circular mouth (1991), and three 100-micron mesh plankton nets with 0.25 m circular mouths fixed within a single re-bar frame (1992). The plankton nets were either staked in the current of streams or towed behind a small boat. About half of the collected larvae were preserved in 5% formalin and half in 95% ethanol.

For each of the following sites we list sampling dates in 1991 and sampling methods.

Sucker Springs: 19 April, 3 May, 14 May, 24 June, 18 July -- dip net, daylight sampling.

Williamson River: at county park one mile west of Chiloquin, 23 May and 30 May -- staked plankton nets, night (0200-0700) sampling.

Williamson River: at highway 97 crossing, 6 June and 13 June --staked plankton nets, night (0200-0700) sampling.

Wood River: at Weed Road crossing, 1 June, 19 June, 3 July, 10 July and 12 July -- staked plankton nets, night (0200-0700) sampling.

Crooked Creek: at highway 62 crossing, 24 May, 7 June, 14 June, 20 June, 4 July and 11 July -- staked plankton nets, night (0200-0700) sampling.

Recreation Creek: 5 June and 12 June -- towed plankton net, daylight sampling.

Odessa Creek: 5 June -- towed plankton net, daylight sampling.

Harriman Springs: 12 June -- dip net, daylight sampling.

Lost River: at Anderson-Rose dam, 11 June -- dip net, daylight sampling.

We had not planned to sample in the Lost River, but did so at the request of the U.S. Bureau of Reclamation after sucker spawning activity had been observed at the Anderson-Rose dam (Robert Davis, U.S.B.R., pers. comm.). The 1992 sampling sites were restricted to the Agency Lake subbasin at Crooked Creek, Fort Creek, and Wood River (Logan and Markle 1992 MS).

Otolith microchemistry

Only Lost River suckers were used in the otolith microchemistry analysis. Larval Lost River suckers were identified by myomere counts. Ethanol-preserved specimens were placed into a glass petri dish, covered with phenol to clear the somatic tissues, and myomeres counted under a dissecting microscope at 40X. Only specimens with 50 or more total myomeres were used in this study. We obtained otoliths from the 1991 year class as follows: eight specimens from the Agency Lake subbasin (two from Crooked Creek, 10.05-10.85 mm NL (notocord length) and six from Wood River, 11.25-12.75 mm NL) and 20 specimens from the Upper Klamath Lake subbasin (13 from Sucker Springs, 12.95-13.15 mm NL and seven from the Williamson River, 10.25-11.95 mm NL).

The right astericus otolith was surgically removed, washed in a 10% sodium hypochlorite (NaOCl), and rinsed with distilled water. The otoliths were mounted to a 5 mm x 23 mm microscope cover glass using crystal bond mounting media and the cover glass attached to a 25 mm x 75 mm glass microscope slide using cyanoacrylate. After drying overnight, the mounted otoliths were ground using 600 grit paper and polished with 0.05 μm alumina. After polishing, otoliths were placed on a single 28 mm X 47 mm petrographic slide, washed with detergent and rinsed with filtered water. Prior to microprobe analysis, the polished otoliths were carbon coated.

A wavelength dispersive spectrometer (Cameca SX-50 microprobe) was operated at an accelerating voltage of 15 kV, beam current of 20 nA, beam diameter of 15 μm and counting time of 20 seconds. Three sites on each otolith were compared: the core, midway between the core and the edge, and the edge. Elements were measured as normalized weight percent concentrations after adjustments to known concentrations in standards using the Cameca PAP algorithm, which includes atomic number, fluorescence, and absorption corrections. The elements analyzed (Table 11) are found in Upper Klamath Lake and its tributaries in measurable amounts (Miller and Tash 1967).

Analyses where performed to differentiate among spawning sites, between subbasins, and between the core and edge of the otoliths. Data were analyzed using analysis of variance and Duncan's multiple range test to identify differences among individual test components.

RESULTS

Field sampling

No sucker larvae were collected in Recreation Creek, Harriman Springs or Odessa Creek in 1991. In the Agency Lake subbasin, sucker larvae were collected from Crooked Creek on 7 and 14 June 1991, and from Wood River on 19 June, 3, 10 and 12 July 1991. Preliminary myomere count identifications have indicated some of the larvae from Wood River to be Lost River suckers, and some may be shortnose or possibly Klamath largescale suckers. All of the larvae from Crooked Creek appear to be Lost River suckers. We consider our identifications to be tentative. In the Upper Klamath lake subbasin, sucker larvae were collected on every sampling date in Sucker Springs and Williamson River. In the Lost River subbasin, three sucker larvae were collected on the single sampling date at Anderson-Rose Dam; all were tentatively identified as shortnose suckers based on myomere counts. No sucker larvae were collected in 1992 sampling in Agency Lake tributaries (Logan and Markle 1993 MS).

Otolith microchemistry

Mean element concentrations were generally similar between localities and confidence intervals overlapped. Means of three elements (Zn, Cu and Mg) were, however, slightly dissimilar. There were no significant differences among the mean normalized weight percent concentrations of any tested element at the core or edge among the four spawning sites. Within individual otoliths, there was no significant difference between the mean normalized weight percent concentrations of elements between the core and the edge of the otoliths for any of the four spawning sites.

Figure 15 illustrates the Sr:Ca ratio which shows a tendency for specimens from Sucker Springs (site 2) to have a lower ratio than the other four sites.

Discriminant function analyses that compared either individual or all otolith sampling sites (core, middle, edge) for each of the localities and for each of the two subbasins usually could achieve 65-75% correct classifications. Because the Sr/Ca ratio suggested a lake-river dichotomy (Fig. 15), we also used this classification factor. An analysis of core and midway otolith samples for Cu, Sr, Zn and Mg correctly classified 83% of the river-spawned and 92% of the lake-spawned Lost River suckers. It should be noted that these correct classifications are from each of two samples for each fish rather than an average. The function (F) calculated was:

$$F= -2.96-(14.90*Cu)+(60.89*Sr)-(6.85*Zn)+(7.68*Mg)$$

Specimens with function values greater than -0.1093 were river-spawned fish.

DISCUSSION

Field sampling

The duration of time that sucker larvae were available in the tributaries of the Agency Lake subbasin, 7 June to 12 July

1991, indicates spawning activity may have been occurring over a period of several weeks. Our capture of sucker larvae from Crooked Creek is evidence of reproduction in this stream, either in the stream channel or at Tecumseh Springs. Sucker larvae captured from Wood River may have been spawned in Wood River, Fort Creek, Sun Creek, or Annie Creek. The 1992 sampling might indicate that use of these sites is annually intermittent or that our 1992 sampling missed the spawning. Anecdotal observations by us and others suggest that the 1992 spawning was as much as a month earlier than in other recent years.

Otolith microchemistry

The preliminary results of the otolith microchemistry are suggestive that this tool can be used to distinguish lake-spawned from river-spawned Lost River suckers using either a bivariate measure (Fig. 15) or a multivariate measure of elemental composition. Elemental concentrations in fish otoliths can vary based on species differences, or differences in thermal environment, stage of development, maternal characteristics, stress or a combination (Kalish 1989, Toole and Neilsen 1991). At present we can not address the source of differences. For example, all of the Lost River suckers from Sucker Springs were larger than those from the river sites used in this analysis. Presumably, the use of core and middle otolith sampling sites corrects for this ontogenetic difference, but more sampling is necessary. Similarly, changes in Sr:Ca ratios have been attributed to different thermal histories where non-optimal temperatures (usually lower) contribute to physiological mistakes (more Sr deposited). The pattern illustrated by Figure 15 shows that fish from thermally stable, and warmer, Sucker Springs have lower Sr:Ca ratios as would be expected from the thermal hypothesis. Thus, the patterns might reflect thermal characteristics of spawning habits independent of habitat locality or type.

Because the power of this analysis was low due to small sample size, a larger sample size is needed to verify the utility of this tool. The sample size could be increased by making radial transects on each of the otoliths and the variance could be reduced by increasing microprobe counting times at each site (Toole and Neilsen 1991). The potential of otolith microchemistry coupled with otolith microstructural analysis is that of a tool that can identify birthdates, spawning habitat type or locality, and growth rate in an analysis of the causes of differential mortality.

JUVENILE FIELD SAMPLING

INTRODUCTION

The endangered species listing of Lost River suckers and shortnose suckers was based, in part, on the perception that recruitment had failed for many years. When we began these studies there was both documented and anecdotal evidence of the following: (1) adult suckers still spawned at Sucker Springs and in the lower Sprague/Williamson rivers; (2) larval suckers were produced and drifted downstream to the lake; and (3) juvenile suckers could be captured with beach seines in summer.

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 focused our efforts on the first year of life in Upper Klamath Lake suckers. Our goal has been to develop a procedure to evaluate recruitment success and failure. Initial objectives have been: (1) to find methods that effectively sample early life history stages; (2) to develop an annual index or estimate of recruitment; and (3) to collect materials for analyses of growth and development.

Little is known about the distribution and abundance of juvenile suckers once larvae have entered the lake. Although age 0 suckers have been collected in summer (Buettner and Scoppettone 1990), catch rates rapidly declined and suckers were presumed to have moved offshore. Our primary goal in the 1991 field sampling, in addition to collecting specimens for taxonomy, was to evaluate the use of several different gears to effectively monitor age 0 population status throughout the first summer of life. Our goal for 1992 was to use methods developed in 1991 to investigate the post-wintering distribution and abundance of the 1991 year class of suckers and to assess the 1992 year class of suckers.

MATERIALS AND METHODS

1991 sampling

Juvenile sampling was conducted using weekly sample series that continued from the 1991 A-Canal series numbers (Table 6). Field activities (seining, cast netting, and trawling) began on 18 July, 1991 (series 15) and concluded on 17 October, 1991 (series 28).

Ten sites in Upper Klamath Lake and 5 sites in Agency Lake (Figure 16) were seined between 18 July and 4 October. A 6.1-m seine with 4.8-mm bar mesh and a 2 x 2 x 2-m bag and a 30.5-m seine with 13-mm bar mesh and a 2 x 2 x 2-m bag were used. Because of difficulty seining offshore, the 30.5-m seine was used only one day in Agency Lake (3 hauls). Most seining was conducted as a standardized sampling program where a single unit of effort was defined as a standard swing arc (1/4 circle) with the 6.1-m seine. Each arc of the 6.1-m seine sampled approximately 7.3 m^2. Non-standard seining (hauls of long distance parallel or perpendicular to shore) was conducted on occasion but the results not quantified by area sampled.

Fifteen sites in Upper Klamath Lake and 2 sites in Agency Lake (Figure 17) were sampled with a 5-m diameter 9.5-mm bar mesh cast net (small cast net). Initially, most cast netting effort was directed along the eastern shore of Upper Klamath Lake where seining was conducted. Later we expanded our cast netting to other areas. Cast netting was performed by drifting along the shoreline in a Boston Whaler and casting the net towards shore. In Upper Klamath Lake, sampling within 3 m of the shoreline was standard for all sites except site U12, which was only sampled once and was offshore. Sites U15, U2, U4, and U5 were also sampled 30-100 m offshore in water less than 1.5 m deep to compare onshore-offshore patterns. Each cast of the cast net sampled approximately 5.4 square meters. Although preliminary cast netting was conducted on 18 July and 1 August, regular cast net sampling began on 12 September and ended 17 October. Some sites were sampled once or twice weekly, others only once or twice the entire field season.

Five sites in Upper Klamath Lake (Figure 18) were trawled using a 3-m semi-balloon trawl with 13-mm bar mesh. Trawling began on 13 September and ended 17 October. One to several trawls were made at each site weekly, and trawl duration ranged from 10 to 30 min. All trawling sites except U14 were open-water sites away from the influence of the shoreline. Trawls at site U14 were generally about 30 feet offshore.

1992 sampling

Spring

Over-wintering mortality can often be a substantial contribution to total mortality during the first year of life. A whole-lake stratified sampling program for spring 1992 was designed to examine post-wintering abundance and distribution of the 1991 year class of suckers. Upper Klamath and Agency lakes were divided into 5 strata (Figure 19). Within each strata, four transect lines were drawn. On each of these transect lines, 2 to 4 sites were chosen for sampling. Sampling was conducted with a 6.1-m diameter cast net with 13-mm bar mesh (large cast net). Five cast net samples were taken at each site. Each cast sampled approximately 8.4 square meters. Cast net sampling began on 23 March and ended on 30 March.

Twelve tows with the same trawl used in 1991 were made in Upper Klamath Lake (Figure 20). Each tow lasted for 12 minutes for a total of 144 minutes of sampling. Trawling began on 1 April and ended on 3 April.

Gill net and trammel net sampling was conducted on 8 April and 9 April. Gill nets were used near Odessa Creek, Modoc Point boat launch, and at Eagle Ridge (Figure 20) for a total of 7.5 hours. Trammel nets were used in Goose Bay and the Straights for a total of 21.5 hours. The experimental gill net was 3.7 x 67 m with eleven 6.1-m panels of the following bar mesh sizes; two 19 mm, two 32 mm, two 45 mm, two 57 mm, two 67 mm, and one 89 mm. The one 89-mm bar mesh size panel was located in the center of the net and was flanked on each side by the smaller mesh sizes in descending order. The trammel net was 3.7 x 68.6 m with a 19-mm bar mesh interior panel and two 305-mm bar mesh exterior panels.

Trap netting was conducted in Upper Klamath Lake and in river mouth habitats from 21 April to 11 May, and in Agency Lake from 2 June to 4 June. Three sites were sampled in Upper Klamath Lake, four sites in Agency Lake, one site in the Straights, and five sites at river mouth habitats including Crystal Creek, Thomason Creek, Recreation Creek, and two in the Williamson River (Figure 20). Trap nets set in river mouth habitats were situated with the cod end upstream and the open face of the trap facing downstream and were located in mid-stream less than 100 meters upstream from the mouth, except for one site in the Williamson River was 2 miles upstream from the mouth. The trap nets had a single 2.4 x 23 m lead, two 2.4 x 10.7 m wings, a 1.2 x 1.2 m square frame with two 10-cm throats, and were constructed with 6.5-mm bar mesh.

Fall

To assess the 1992 year class of suckers, we resampled our 1991 cast net sites in Upper Klamath Lake (Figure 21). We conducted two surveys and sampled each site once during each survey. The first survey began on 29 September and ended on 7 October. Because shallow water and receding shoreline in 1992 made conventional boat access difficult, sites were accessed by air boat and cast netting was conducted from the shoreline. As in 1991, all sites were sampled close to the shoreline except U12, which was exclusively offshore. Sites U15, U2, SS, U4, and U5 were also sampled 50 meters offshore to compare onshore-offshore abundance. Ten casts were made at each site (including 10 at the onshore and 10 the offshore locations at U15, U2, SS, U4, and U5) for a total of 200 casts. Our primary gear was the small cast net, however, the large cast net constituted 50% of the effort at both onshore and offshore locations at sites U15, U2, SS, U4, and U5 for comparison of efficiency and selectivity between the two nets. The second survey only involved the small cast net and began on 26 October and ended on 27 October. Sites U12, U5, and U6 were sampled 50 meters offshore; all other sites were sampled only along the shoreline. Ten casts were made at each site except U6 where 5 casts were made. Site U1 was dropped from the second survey because shallow water and mucky substrate made access impossible. Thus, a total of 135 casts were made in the second survey.

Fall trap netting in 1992 was conducted in Upper Klamath Lake from 7 October to 8 October and from 22 October to 23 October. During each period, two trap net sets were made; one near Modoc Point boat launch and one near Sucker Springs (Figure 21). All sets were 50-70 m offshore. Trap netting was conducted in the Williamson River (Figure 21) from 20 October to 23 October. Two trap net sets were made near the mouth and two sets made one mile upstream from the mouth. The trap nets were the same used during spring sampling.

RESULTS

1991 sampling

Seine

From our standardized seining survey, 399 age 0 suckers from 143 seine hauls were captured; 11 have been identified as Lost River suckers (Table 12), 366 identified as shortnose suckers (Table 13), and 22 unidentified. Of the 22 unidentified suckers, 15 were immediately frozen on dry ice (5 from U2, 5 from U4, 5 from U5), 5 were lost when a strong wind gust tipped over a bucket into the lake (U8), and 2 larger individuals (79 and 86 mm FL) were released alive (U10) under a 75 mm FL size restriction of federal collection permit MARKDF (this permit was later revised to allow us to retain larger specimens). Age 0 suckers were not abundant in Agency Lake; only one shortnose was captured. In contrast, juvenile suckers were captured at every seining site in Upper Klamath Lake except U3.

Densities of both Lost River suckers (Table 12; Figure 22) and shortnose suckers (Table 13; Figure 23) calculated from seine catches were highest in an area extending from the mouth of Williamson River (U6) south along the eastern shore of Upper Klamath Lake. Shortnose sucker densities would be higher than we indicate if, as we presume, most of the 22 unidentified suckers are shortnose suckers. Catches of suckers along the western shore were considerably lower (Tables 12,13; Figures 22,23). In 18 non-standard seine hauls age 0 suckers were captured from the following locations: 6 Lost River suckers (1 at site U4, 5 at site U10), 40 shortnose suckers (1 at site A1, 1 at site U4, 38 at site U10), and 2 unidentified and released (both 79 mm FL) from site U10.

Based on our beach seine data, regression analysis of standard length and weight on time indicates that age 0 Lost River suckers grew at a rate of 3.68 mm and 0.26 g per week between series 15 and 19 (Figure 24), and that age 0 shortnose suckers grew at a rate of 3.88 mm and 0.47 g per week between series 15 and 25 (Figure 25). The length-frequency distribution of age 0 shortnose suckers may have been bi-modal (Figure 26). A single large catch of 177 age 0 shortnose suckers on 6 August may be obscuring the mode of larger-sized shortnose in series 18. Insufficient numbers of age 0 Lost River suckers were captured to present meaningful length-frequency data.

All of our seining sites were selected and fully sampled by series 18. We spent series 15 to 17 locating sites and conducting preliminary seining. Catch rates of age 0 suckers in Upper Klamath Lake were initially high (Figure 27). The single catch of 177 suckers in one seine haul on 6 August at the mouth of Williamson River produced a peak for series 18; however, excluding this catch, catches at the mouth of Williamson River were similar to other sites along the eastern shoreline. Catch rates rapidly declined, and many sites were eliminated as suckers were no longer captured at most sites or as receding water levels made seining impossible due to deep muck. In September our sampling efforts began to shift to cast netting and trawling.

Cast net

A total of 470 juvenile suckers were captured in 646 cast net samples from Upper Klamath Lake; 468 were age 0 and 2 were age 1 or older (163 mm FL SNS, 255 mm FL SNS--both captured at U2 offshore site). Of the age 0 suckers, 222 have been identified as Lost River suckers (Table 14), 241 identified as shortnose suckers (Table 15), 3 identified as Klamath largescale suckers (Table 3), and 2 not identified. Of the 2 unidentified suckers, one (105 mm FL, site U5) was released as per federal collection permit MARKDF; the other escaped from capture (site U5). Age 0 suckers were abundant in many areas where catches with the seine had declined or become absent. Distribution of age 0 Lost River and shortnose suckers did not appear to be appreciably different, although shortnose suckers were more abundant in samples from sites U4 and U5, whereas Lost River suckers were more abundant at sites U15, U19, and U21 (Tables 14,15; Figures 28,29). Catch rates in Upper Klamath Lake tended to increase over time (Figure 30) as we became able to identify and sample additional areas that seemed likely to have high sucker concentrations. Each site in Agency Lake was sampled only once and no suckers were caught.

Based on our cast net data, regression analysis of standard length and weight on time indicates that age 0 Lost River suckers grew at a rate of 3.91 mm and 1.11 g per week between series 17 and 28 (Figure 31), and that age 0 shortnose suckers grew at a rate of 3.81 mm and 0.76 g per week between series 17 and 28 (Figure 32). Length-frequency distributions for both Lost River

(Figure 33) and shortnose (Figure 34) suckers suggest two modes may have been present.

Trawl

A total of 57 suckers were captured in 53 trawls in Upper Klamath Lake. Suckers were captured in 18 of 38 trawls from 2 October to 17 October, but no suckers were captured in 15 trawls from 13 September to 1 October, suggesting there may be some offshore movement. Fifty two of the suckers were age 0 and 5 were age 1 or older. Forty three of the age 0 suckers have been identified as Lost River suckers (Table 16) and 9 identified as shortnose suckers (Table 17). Of the age 1 and older fish, 2 have been identified as Lost River suckers (193 mm SL, 173 mm SL-both site U20), 1 identified as a shortnose sucker (309 mm SL-site U20), and 2 tentatively identified as possible SNS x LRS hybrids (179 mm SL-site U13, 198 mm SL-site U20). Age 0 suckers were captured at all sites except site U13.

Based on our trawl data, regression analysis of standard length and weight on time indicates that age 0 Lost River suckers grew at a rate of 5.51 mm and 2.42 g per week between series 26 and 28 (Figure 35). All ten shortnose suckers were captured during series 28 and growth could not be estimated. Length-frequency distributions of Lost River and shortnose suckers again suggest a bi-modal distribution in age 0 lengths (Figure 36).

When standard length was regressed on time for all three gears combined, growth rates from series 15 (mid-July) to series research will help us to identify birthdates, growth rates, and other early-life characteristics of surviving suckers.

1992 sampling

Spring

Cast net, trawl, gill net, trammel net

Forty eight of the 50 designated cast net sampling sites were sampled; 2 sites in area C were not sampled. Although suckers were common and easily captured with cast nets throughout 1991, no suckers were captured in 240 casts of effort in the entire spring survey. Further, no suckers were captured in 12 trawls totaling 144 minutes of effort, and no suckers were captured in 7.5 hours of gill netting or 21.5 hours of trammel netting. In late April, we began to direct our sampling towards possible over-winter sucker refugial areas--river mouth habitats.

Trap net

A total of 63 suckers were captured from 9 samples representing 258.5 hours of effort from the lower Williamson River, including 37 Lost River suckers, 25 shortnose suckers, and 1 Klamath largescale sucker (Table 18). An additional 3 Lost River and 6 shortnose suckers were caught in 2 samples from Thomason Creek, and 1 Lost River and 3 shortnose suckers in a single 99 hour sample from Crystal Creek. No suckers were captured in a single 18.5 hour sample from Recreation Creek. In lake habitats, 1 Lost River sucker was captured in a single 22

28 (mid-October) are essentially equal; 4.84 mm per week for Lost River suckers and 4.86 mm per week for shortnose suckers (Figure 37). The difference in the Y-intercept of the Lost River suckers regression line (-37.61) and the shortnose suckers regression line (-53.05) is 15.44 mm. The Y-intercept difference indicates that age 0 Lost River suckers have an approximate 15 mm size advantage (about 3 weeks of growth) over age 0 shortnose suckers by mid-July and maintain this size advantage throughout the year. The size advantage may have multiple causes: 1) larval or early juvenile growth of surviving Lost River suckers is substantially greater before mid-July than for shortnose suckers, 2) larval or early juvenile growth of surviving shortnose suckers is substantially less before mid-July than for Lost River suckers, 3) larval Lost River sucker emigration is about three weeks earlier than shortnose suckers and all other factors are equal, or 4) substantial species- or size-selective differential mortality is occurring. Larval emigration studies by Buettner and Scoppettone (1990) suggest two distinct modes of larval shortnose sucker emigration about three weeks apart in both 1987 and 1988, with the first mode concurrent with peak Lost River sucker emigration. If these patterns of emigration are annually consistent, our data would suggest that the first mode of emigrating shortnose suckers in 1991 may have been subjected to higher differential mortality. We are currently in the initial stages of age and growth of larval and juvenile suckers by analyzing otolith daily growth rings and microchemistry. This

hour sample in the Straights, 3 Lost River suckers in 5 samples totaling 274 hours from Upper Klamath Lake, and no suckers from 8 samples totaling 188 hours from Agency Lake. Mean catch rates for all river mouth habitats was 0.18 suckers per hour (Table 18), compared to less than 0.01 suckers per hour in lake habitats.

Age 1 (1991 year class) Lost River and shortnose suckers constituted 87.5% of the spring trap net catch (43 Lost River suckers, 27 shortnose suckers); however, two or possibly three year classes of Lost River suckers and three or possibly four year classes of shortnose suckers were also present (Figure 38). Sub-adult suckers (greater than age 1 but not yet mature) represented 10% of the catch (6 shortnose suckers, 2 Lost River suckers), and one adult breeding male shortnose was captured. Although our trap net sampling near the mouth of the Williamson River corresponded with the annual adult spawning migration (Bienz and Ziller 1987; Buettner and Scoppettone 1990), the lack of adult suckers in our trap net samples should not be a concern because we used traps with small throat diameters specifically designed to catch smaller fish. The total number of suckers captured was small when compared to the total number of fish caught (<1%, D. Markle and D. Simon, unpublished data), but their sedentary nature makes them less susceptible to passive gears than more mobile species such as blue chubs Gila coerulea or tui chubs Gila bicolor. Again, there appears to be a bi-modal distribution of lengths in the 1991 year class of Lost River suckers, but only one mode is apparent in the age 1 shortnose (Figure 38).

Mean standard length of age 1 Lost River and shortnose suckers from spring trap net samples was 105.5 mm and 97.9 mm, respectively. Mean standard length of age 0 Lost River and shortnose suckers from cast net and trawl samples collected during series 28 in 1991 was 90.2 mm and 79.3 mm, respectively (Figure 39). If we obtained representative samples of the same sucker populations, mean growth between mid-October 1991 and April/May 1992 was 15.3 mm for Lost River suckers and 18.6 mm for shortnose suckers (Figure). Using 197 days as the time interval from the mid-point of the 1991 series 28 sampling to the mid-point of the 1992 April/May sampling, Lost River suckers grew at a rate of 0.54 mm per week and shortnose suckers 0.66 mm per week.

Fall

Cast net

No age 0 suckers were captured in the first fall survey in 1992. One shortnose sucker (234 mm FL) was captured at site U2. Because no suckers were captured, we could not compare gear efficiency and selectivity between the large and small cast net. No suckers of any age were captured during the second cast net survey.

Trap net

One age 1 shortnose sucker (150 mm FL) was captured from one of 4 samples totalling 81 hours of effort in Upper Klamath Lake. This sucker was captured 50 m offshore of Sucker Springs. No suckers were captured from 4 samples totalling 92.5 hours of effort in the lower Williamson River.

DISCUSSION

Sampling methods and habitats

Although Buettner and Scoppettone (1990) were able to capture age 0 suckers with beach seines in summer, there have previously been no methods developed to monitor relative abundance and distribution of juvenile Klamath suckers. Our beach seine data indicate that, by the time we fully implemented our seining survey (early August, 1991), some age 0 suckers were vulnerable and easily captured along the shoreline. We suspect suckers would have been easily captured with seines earlier in the summer as well. As observed by Buettner and Scoppettone (1990), catch rates rapidly declined and suckers essentially disappeared from our seine samples by late summer suggesting either a shift in habitat use or substantial mortality. However, cast net sampling indicated age 0 suckers were still abundant and were continuing to use shoreline nursery habitat at least until mid-October. Thus, rather than shifts in habitat use or massive mortality of suckers, declines in catch rates with seines appears to be due to gear avoidance. Seining tends to be a very disruptive method of sampling, particularly over muck bottom or loose sediments. We suspect that as age 0 suckers increase in size, their ability to avoid the seine increases. In contrast, cast netting is a much less disruptive method of sampling. Cast net catch rates did not decline but rather tended to increase throughout the summer. Cast net catches from offshore locations were lower, suggesting shoreline habitats are important nursery areas. Catches of age 0 suckers in the trawl were low, but we suspect that the efficiency of this gear is low and is under-representing the actual number of suckers in open-water areas. Suckers did not appear in trawl samples until early October, suggesting that there may indeed be some offshore movement of age 0 suckers.

There were marked differences in species composition of age 0 suckers in our 1991 beach seine, cast net, and trawl samples. Lost River suckers constituted 4% (17 of 407) of the sucker catch from beach seines (standard and non-standard), 48% (222 of 466) from cast net samples, and 83% (43 of 52) from trawl samples. Gear-related differences in sucker species composition may reflect differences in size and species distribution. Our growth data indicated age 0 Lost River suckers were larger throughout the summer. The rapid decline in beach seine catch rates suggests that small size increases can greatly increase seine avoidance. Because they are larger, most age 0 Lost River suckers may have avoided our beach seine sampling. Cast net sampling demonstrated that Lost River suckers were abundant and in association with shortnose suckers along the shoreline. The large proportion of age 0 Lost River suckers in trawl samples may indicate that 1) age 0 Lost River suckers have greater offshore tendencies than age 0 shortnose suckers, 2) age 0 shortnose sucker are less effectively sampled with trawls, or 3) offshore movement is a function of size and because age 0 Lost River suckers are larger, they are moving offshore earlier. Shortnose suckers did not appear in trawl samples until 2 weeks after Lost River suckers, perhaps supporting the idea that there is a size-depth relationship independent of species. In contrast, there is some support for differential behavior. Even though our cast net samples suggest equality of the 1991 year classes, age 1 shortnose suckers constituted the vast majority of the suckers in canal salvage operations by the U.S. Bureau of Reclamation in 1992 (D. Simon, pers. obs.). Vulnerability to canal entrainment could be a reflection of behavioral or distributional differences between Lost River and shortnose suckers. Alternatively, massive differential over-wintering mortality of Lost River suckers could be the cause of this pattern in 1992. The near absence of Klamath largescale suckers in our field sampling in both 1991 and 1992 suggests that juveniles of this species are rare in Upper Klamath Lake.

Post-wintering distribution of suckers from the 1991 year class (age 1) was markedly different from the previous summer and fall distribution. A stratified, whole-lake cast net survey in late March captured no suckers. Although we are uncertain of the sampling efficiency of a cast net in deeper offshore sites, efficiency probably approaches 100% (within size-selective constraints of the mesh) in shallow shoreline habitats. Twenty six of the 48 sites sampled were onshore sites; thus, the importance of lakeshore habitat appears minimal in the spring or winter for age 1 suckers. Further, no suckers were captured in open-water sites with trawls, gill nets, or trammel net, and only 4 suckers were captured in lake habitats with trap nets.

In spring 1992, age 1 suckers were common in river mouth habitats, suggesting these habitats provide important refugia during the winter months. Pelican Bay, essentially a river mouth habitat of Recreation and Crystal Creek, provided important sucker refugia during a sucker die-off in August 1986 (Buettner and Scoppettone 1990). Vincent (1968) captured 23 suckers in 156 "sets" from 9 July to 27 December, 1964 near areas of "incoming water influence", but only captured 1 sucker in 141 sets "in other areas" presumably away from incoming water influence. A single Vincent "set" consisted of 2 floating gill nets, 1 sinking gill net, and a circular hoop net. Although Vincent (1968) does not state the time of year, location, or species of sucker catches, his data does lend support to the contention that age 1 and older suckers use river mouth habitat as refugia.

Recruitment and mortality estimates

The large numbers of age 0 suckers captured in our cast net samples 1991 as well as subsequent recaptures of this year class in 1991 and 1992 USBR canal salvage (for shortnose suckers) and in our trap net samples (for both species) appear to indicate year-class establishment. In contrast, our data suggest 1992 year classes of shortnose and Lost River suckers were complete failures. We captured no age 0 suckers in extensive fall sampling and 1992 canal sucker salvage operations by the USBR collected only 13 nominal age 0 suckers of 2611 suckers captured in the A-Canal between Upper Klamath Lake and Klamath Union High School (Buettner 1993). The latter contrasts markedly with 1991 canal sucker salvage in which age 0 suckers were the most abundant age class (D. Simon, pers. obs.) of 2247 suckers salvaged (Buettner 1993). Further, in 1992 canal salvage, age 1 suckers were the most abundant age class (D. Simon, pers. obs.) of the 2611 suckers salvaged from the A-Canal. Thus, sucker salvage data reflects our findings of an abundant 1991 year class and an absent 1992 year class.

Although the 1991 year class of suckers appears to be established, it is unclear when year-class strength is established. Although recruitment of suckers appears to have failed nearly every year since 1970 (with the exception of the 1977 and 1978 year classes of Lost River suckers (Buettner and Scoppettone (1990)), relative abundance of age 0 suckers has never been documented. Thus we cannot, as of yet, know if 1) 1991 was a "typical" year in that age 0 suckers are abundant and much of the mortality contributing to year-class failure is occurring between the first year of life and maturity, or 2) whether 1992 was a "typical" year indicative of massive early life mortality. If the first scenario is correct, then the abundance of age 0 suckers surviving to the first fall is insufficient to withstand mortality influences until reaching maturity. This may result from 1) insufficient reproductive effort (i.e., too few eggs and larvae produced), or 2) larval mortality rates are too high to allow for sufficient numbers of age 0 fish. Had beach seine samples been collected in summer 1992, we would have been able to focus in more closely on the timing of year-class failure in 1992.

Sizes and growth

The bi-modal length-frequency distributions in both age 0 Lost River and shortnose suckers appear to be real. We do recognize that some of the length-frequency data become weak with small sample sizes, but trends over time support two length modes. We could not attribute the modes to differences in size of suckers among sampling sites. Buettner and Scoppettone (1990) found bi-modal larval emigration patterns about 20 days apart in 1987 and in 1988 for shortnose suckers. If these patterns of larval emigration are annually similar, they may be reflected in our age 0 shortnose sucker length-frequency distributions. Lost River suckers produced at Sucker Springs may be represented, presumably, in the larger mode. The two modes of age 1 Lost River suckers in spring 1992 could be separated by mean number of precaudal vertebrae (Figure 40), suggestive of possible populational differences. Complimentary studies of otolith age, growth, and microchemistry of juvenile suckers will provide more insight into bi-modal length distributions.

Management issues

Our data seem to indicate that the recruitment of Klamath suckers differed dramatically in the two drought years, 1991 and 1992. The cause(s) of this difference in recruitment is not understood. If the 1991 year class, which seems to have persisted at least through its second summer, is well established, then factors operating in the first summer may be critical to understanding recruitment success.

In any fish population, most mortality will occur in larval stages. In a hypothetical model, Houde (1987) demonstrated that a change in instantaneous larval mortality rate per day from 0.100 to 0.125 could decrease the number of recruits by a factor of nearly three, and, if combined with a 25% increase in a larval stage duration, could decrease the number of recruits by a factor of more than twelve. Larval stage duration(s) might increase if spawning was earlier than normal and development took place at cooler temperatures than normal. Management activities that decrease larval mortality and increase larval growth may be important in reversing the declining trend in sucker populations. Other sources of juvenile mortality (e.g., over-wintering mortality or singular catastrophic fish kills) might also contribute to recruitment problems. However, the 1986 fish kill appeared selective for large, old adult Lost River suckers (96% of 190 suckers that were aged were 19-43 years old) (Buettner and Scoppettone 1990), further underscoring the critical need to increase age 0 and juvenile abundance.

Our beach seine and cast net surveys in 1991 and cast net surveys in 1992 indicate relative abundance of age 0 suckers can be monitored reliably during the summer and fall, and our results were corroborated by U.S. Bureau of Reclamation's canal salvage data. Ideally our goal would be the ability to quantify absolute abundance of age 0 suckers, but, at least for now, indices to abundance seem more feasible. Catch per unit of effort (CPUE) should be proportional to absolute abundance, although CPUE can vary with water level, season, location, turbidity, and other factors. Thus standardization of sampling programs (i.e., same gears, same places, same times, and for several years) is needed to reduce sampling variability. After the 1991 field season, we believed fall cast surveys would suffice. However our experiences with the 1992 year class failure indicate the need, in addition to fall cast netting, for early- and mid-summer beach seine surveys to focus in more closely on timing of mortality. Beach seine surveys would need to be designed to sample both Lost River and shortnose suckers, because their periods of vulnerability appear different.

ACKNOWLEDGEMENTS

We thank Daniel Logan, Erik Lesko, and Marcus Beck for their assistance with field sampling. Daniel Logan and Roger Nielsen performed the otolith microchemistry analyses which are reproduced herein. We thank many personnel at the U.S. Bureau of Reclamation Klamath Project, especially Mark Buettner and Bob Davis, and the staff at Pelican Marina for logistical support.

Literature Cited

Andreasen, J.K. 1975. Systematics and status of the family Catostomidae in Southern Oregon. Doctoral dissertation. Oregon State University, Corvallis.

Behnke, R.J. 1992. Native trout of western North America. Am. Fish Soc. Monograph 6, 1-275 pp., Bethesda, MD.

Bienz, C.S., and J.S. Ziller. 1987. Status of three lacustrine sucker species (Catostomidae). Klamath Tribe, Chiloquin, Oregon. Unpublished manuscript.

Buettner, M.E., and G.G. Scoppettone. 1990. Life history and status of Catostomids in Upper Klamath Lake, Oregon. Unpublished manuscript. National Fisheries Research Center, Reno Field Station, Nevada. 108 pp.

Buettner, M.E., and G.G. Scoppettone. 1991. Distribution and information on the taxonomic status of the shortnose sucker (Chasmistes brevirostris) and Lost River sucker (Deltistes luxatus) in the Klamath River basin, California. Completion Report for Cal. Dept. Fish Game, Contract FG-8304.

Buettner, M.E. 1993. Draft 1992 Klamath Project salvage report. U.S. Bureau of Reclamation, Klamath Project, Klamath Falls, Oregon.

Girard, C. 1856. Researches upon the cyprinoid fishes inhabiting the fresh waters of the United States, west of the Mississippi Valley, and from the specimens in the museum of the Smithsonian Institution. Proc. Acad. Nat. Sci., Phila. 1856, 8:165-213.

Harris, P.M. 1991 MS. Biochemistry and morphology of Upper Klamath Lake suckers. Final report to Oregon Department of Fish and Wildlife, 23 p.

Harris, P.M. and D.F. Markle 1991 MS. Quantitative estimates of fish transported from Upper Klamath Lake through the A-Canal, Klamath Project. Annual report to U. S. Bureau of Reclamation, contract number 0-FG-20-09630., 38 p.

Hennig, W. 1966. Phylogenetic systematics. Univ. Illinois Press,Urbana, 263 p.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symposium 2:17-29.

Jandel Scientific, 1991. TableCurve, version 3.10.Corte Madera, CA.

Kalish, J.M. 1989. Otolith microchemistry: validation of the effects of physiology, age, and environment on otolith composition. J. Exp. Mar. Biol. Ecol. 132:151-178.

Leary, R.F., F.W. Allendorf, and K.L. Knudsen 1983. Consistently high meristic counts in natural hybrids between brook trout and bull trout. Sys. Zoo. 32:369-376.

Logan, D.J., and D.F. Markle 1993 MS. Fish faunal survey of Agency Lake and northern Upper Klamath Lake, Oregon. Annual report to U. S. Bureau of Reclamation, contract number 0-FG-20-09630., 35 p.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill Book Co., New York, 428 p.

McPhail, J.D. 1984. Ecology and evolution of sympatric sticklebacks (Gasterosteus): morphological and genetic evidence for a species pair in Enos Lake, British Columbia. Can. J. Zool. 62:1402-1408.

Miller, R.R. and G.R. Smith 1981. Distribution and evolution of Chasmistes (Pisces: Catostomidae) in western North America. Occ. Pap. Mus. Zool. Univ. Mich, No. 696, 46 p.

Moyle, P.B. and W.J. Berg 1991. Population genetics of endangered catostomid fishes of Northern California. Final report to California Fish and Game, Contract FG-8143, 37 p.

Neff, N.A. and G.R. Smith 1979. Multivariate analysis of hybrid fishes. Sys. Zool. 28:176-196.

SAS Institute Inc., 1988. SAS/STAT Release 6.03. Cary, North Carolina.

Schluter, D. and J.D. McPhail 1992. Ecological character displacement speciation in sticklebacks. Am. Nat. 140:85-108.

Smith, G.R. and T.N. Todd 1984. Evolution of species flocks of fishes in north temperate lakes. pp. 45-68. In Echelle, A. E. and I. Kornfield, editors. Evolution of fish species flocks, Univ. Maine at Orono Press, 257 p.

Smith, G.R. 1992. Ecological causes of intralacustrine speciation of fishes. Amer. Soc. Ich. Herp. Annual Meeting at Univ. Illinois Urbana-Champaign, Abstract only.

STSC, Inc., 1991. Statgraphics Version 5.0. Rockville, Maryland.

Toole, C.L., and R.L. Nielsen 1992. Effects of microprobe precision on hypotheses related to otolith Sr:Ca ratios. Fish. Bull., U. S. 90:421-427.

Vincent, D.T. 1968. The influence of some environmental factors on the distribution of fishes in Upper Klamath Lake. M.S. thesis. Oregon State University, Corvallis.

Ward, F.J., J.A.T. Boubee, A.S. Meredith and T.G. Northcote 1989. Characteristics of common smelt, Retropinna retropinna (Richardson), of the Waikato River system. New Zealand J. Mar. Freshw. Res. 23:345-355.

Wiley, E.O., 1981. Phylogenetics, the theory and practice of phylogenetic systematics. John Wiley and Sons, New York, 439 p.

Table 1. Descriptions and abbreviations of measurements made on suckers. Unless noted, all length measurements are from the tip of snout and descriptions of measurements follow Hubbs and Lagler (1964).

Measurement	Abbreviation
Standard length	SL
Fork length	FL
Length to anterior edge of eye	LAE
Length to posterior edge of eye	LPE
Head length	HL
Width of interorbital	WINTERORB
Width of body at pectoral-fin base	WP1
Depth of body at pectoral-fin base	DP1
Depth of body at dorsal-fin base	DDO
Length to origin of pelvic fin	LOP2
Length to origin of dorsal fin	LOD
Length to insertion of dorsal fin	LID
Length to origin of anal fin	LOA
Length to insertion of anal fin	LIA
Length from dorsal-fin origin to anal-fin origin	LD_A
Length from dorsal-fin origin to base of caudal fin	LDO_C
Length from dorsal-fin insertion to base of caudal fin	LDI_C
Depth of caudal peduncle	DCAUDPED
Length of pectoral fin	LP1
Length of pelvic fin	LP2
Length from posterior edge of eye to dorsal-fin origin	LPE_OD
Length from pelvic-fin origin to anal-fin origin	LP_OA

Table 2. Descriptions and abbreviations of counts made on suckers. Unless noted, all counts follow Hubbs and Lagler (1964). Vertebral counts include the urostyle but do not include the Weberian apparatus. Counts of vertebrae to dorsal- and anal-fin origins include the centrum posteriad of a vertical from the origin if the fin origin lies between two centra.

Count	Abbreviation
Upper procurrent caudal-fin rays	UPCAUD
Upper primary caudal-fin rays	UPRICAUD
Lower primary caudal-fin rays	LPRICAUD
Lower procurrent caudal-fin rays	LOCAUD
Procurrent dorsal-fin rays	PROD
Primary dorsal-fin rays	D
Procurrent anal-fin rays	PROA
Primary anal-fin rays	A
Pectoral-fin rays	P1
Pelvic-fin rays	P2
Gill rakers on first arch	GR
Vertebrae anterior to dorsal-fin origin	VDO
Vertebrae anterior to anal-fin origin	VAO
Precaudal vertebrae	PRECAUDVER
Precaudal vertebrae without ribs	PCVW_ORIB
Caudal vertebrae	CAUDVER
Total vertebrae	TOTVER
Presence/absence	
Doubled neural spine on preural centrum 2	DUB_NS_PU2
Doubled neural spine on preural centrum 3	DUB_NS_PU3
Doubled haemal spine on preural centrum 2	DUB_HS_PU2
Doubled haemal spine on preural centrum 3	DUB_HS_PU3
Doubled neural/haemal spine on other centra	DUB_OTHERS

Table 3. List of size classes less than 85 mm and identifications of suckers collected in Upper Klamath Lake during 1991 sampling. Abbreviations are LRS, Lost River sucker; SNS, shortnose sucker; KLS, Klamath largescale sucker; and UNK, unidentified (presumed shortnose) sucker.

Size class (mm)	Number of specimens LRS	SNS	KLS	UNK
<29.9	3	4	0	54
30-34.9	3	18	0	133
35-39.9	7	16	0	108
40-44.9	0	7	0	46
45-49.9	6	1	0	12
50-54.9	2	0	0	7
55-59.9	2	1	0	9
60-64.9	1	19	0	7
65-69.9	3	44	2	15
70-74.9	10	58	0	9
75-79.9	13	26	1	1
80-84.9	36	31	0	1

Table 4. Summary of morphometric data for Klamath basin suckers: N is sample size, Min is minimum value, Max is maximum value and CV is coefficient of variation. See Table 1 for list of abbreviations.

	N	Average	Min	Max	CV
			SL		
Shortnose sucker	442	112.1	20.2	425	78.89
Klamath largescale sucker	161	133.9	21.8	475	89.12
Lost River sucker	378	100.9	25.6	680	68.92
			HL		
Shortnose sucker	266	19.8	8.40	62.4	38.85
Klamath largescale sucker	93	20.6	6.10	62.5	68.19
Lost River sucker	71	20.6	6.70	48.5	52.52
			LAE/HL		
Shortnose sucker	49	0.41	0.33	0.47	6.88
Klamath largescale sucker	89	0.40	0.29	0.48	8.64
Lost River sucker	33	0.42	0.33	0.48	7.78
			LPE/HL		
Shortnose sucker	49	0.60	0.55	0.65	4.27
Klamath largescale sucker	89	0.61	0.50	0.66	4.72
Lost River sucker	33	0.60	0.55	0.66	3.50
			WINTERORB/HL		
Shortnose sucker	49	0.39	0.34	0.47	6.94
Klamath largescale sucker	89	0.36	0.27	0.44	13.18
Lost River sucker	33	0.36	0.32	0.40	5.63
			WP1/HL		
Shortnose sucker	49	0.63	0.56	0.69	4.56
Klamath largescale sucker	89	0.57	0.47	0.70	9.19
Lost River sucker	33	0.56	0.45	0.64	8.70
			DP1/HL		
Shortnose sucker	49	0.75	0.62	0.85	5.22
Klamath largescale sucker	89	0.73	0.65	0.86	5.42
Lost River sucker	33	0.70	0.59	0.78	6.24
			DDO/HL		
Shortnose sucker	49	0.85	0.73	0.98	5.27
Klamath largescale sucker	89	0.78	0.59	1.00	10.11
Lost River sucker	33	0.78	0.64	0.87	7.58
			LOP2/SL		
Shortnose sucker	49	0.57	0.55	0.60	1.87
Klamath largescale sucker	89	0.58	0.55	0.62	2.37
Lost River sucker	33	0.55	0.53	0.57	2.38

Table 4. Continued.

	N	Average	Min	Max	CV
			LOD/SL		
Shortnose sucker	303	0.50	0.44	0.53	2.51
Klamath largescale sucker	93	0.51	0.48	0.54	2.81
Lost River sucker	212	0.49	0.43	0.58	3.24
			LID/SL		
Shortnose sucker	49	0.63	0.60	0.67	2.12
Klamath largescale sucker	30	0.65	0.62	0.68	2.16
Lost River sucker	33	0.62	0.58	0.65	2.40
			LPV/SL		
Shortnose sucker	49	0.77	0.73	0.80	1.75
Klamath largescale sucker	30	0.78	0.74	0.80	2.26
Lost River sucker	33	0.76	0.73	0.80	2.21
			LOA/SL		
Shortnose sucker	49	0.78	0.75	0.82	1.62
Klamath largescale sucker	89	0.78	0.76	0.82	1.79
Lost River sucker	33	0.78	0.74	0.80	1.91
			LIA/SL		
Shortnose sucker	49	0.85	0.82	0.89	1.63
Klamath largescale sucker	30	0.86	0.82	0.89	2.12
Lost River sucker	33	0.84	0.82	0.87	1.82
			LD_A/SL		
Shortnose sucker	49	0.36	0.29	0.38	4.54
Klamath largescale sucker	89	0.34	0.31	0.39	4.57
Lost River sucker	33	0.34	0.32	0.37	3.08
			LDO_C/SL		
Shortnose sucker	302	0.54	0.48	0.58	2.48
Klamath largescale sucker	93	0.52	0.46	0.55	3.15
Lost River sucker	212	0.53	0.41	0.57	3.40
			LDI_C/SL		
Shortnose sucker	49	0.39	0.35	0.42	3.82
Klamath largescale sucker	30	0.38	0.32	0.42	6.69
Lost River sucker	33	0.39	0.37	0.44	3.92
			DCAUDPED/SL		
Shortnose sucker	265	0.09	0.08	0.11	4.70
Klamath largescale sucker	93	0.09	0.08	0.10	7.11
Lost River sucker	71	0.08	0.07	0.10	6.82

Table 4. Continued.

	N	Average	Min	Max	CV
			LP1/HL		
Shortnose sucker	49	0.74	0.58	0.85	7.63
Klamath largescale sucker	30	0.76	0.44	0.96	13.01
Lost River sucker	33	0.70	0.56	0.78	8.11
			LP2/HL		
Shortnose sucker	48	0.55	0.45	0.65	7.60
Klamath largescale sucker	30	0.57	0.46	0.66	9.18
Lost River sucker	33	0.56	0.47	0.62	5.91
			LPE_OD/SL		
Shortnose sucker	268	0.36	0.34	0.39	2.78
Klamath largescale sucker	93	0.37	0.34	0.41	4.22
Lost River sucker	71	0.36	0.34	0.41	3.58
			LP_OA/SL		
Shortnose sucker	219	0.23	0.15	0.26	7.26
Klamath largescale sucker	72	0.22	0.19	0.24	6.08
Lost River sucker	38	0.23	0.20	0.27	7.60

Table 5. Summary of meristic data for Klamath basin suckers: N is sample size, Min is minimum value, Max is maximum value and CV is coefficient of variation.

	N	Average	Min	Max	CV
	Upper procurrent caudal-fin rays				
Shortnose sucker	75	12.2	10	15	8.5809
Klamath largescale sucker	84	12.1	10	14	6.6553
Clear Lake sucker	8	11.9	11	13	7.0275
Lost River sucker	60	10.1	5	13	13.6996
	Upper primary caudal-fin rays				
Shortnose sucker	74	9.0	8	10	1.8391
Klamath largescale sucker	24	9.0	8	9	2.2786
Clear Lake sucker	9	9.0	9	9	0
Lost River sucker	59	9.0	8	10	2.9179
	Lower primary caudal-fin rays				
Shortnose sucker	74	9.0	8	10	2.5911
Klamath largescale sucker	24	9.0	9	9	0
Clear Lake sucker	9	9.0	9	9	0
Lost River sucker	59	9.0	8	10	2.5246
	Lower procurrent caudal-fin rays				
Shortnose sucker	74	8.4	6	10	9.8316
Klamath largescale sucker	83	8.4	7	11	8.7110
Clear Lake sucker	8	8.2	7	10	12.5466
Lost River sucker	59	7.7	6	9	9.4668
	Procurrent dorsal-fin rays				
Shortnose sucker	75	1.9	1	3	23.0699
Klamath largescale sucker	82	2.1	1	3	21.5789
Clear Lake sucker	8	1.8	1	3	40.4061
Lost River sucker	64	2.2	1	3	23.3693
	Dorsal-fin rays				
Shortnose sucker	75	12.1	10	14	5.2285
Klamath largescale sucker	82	11.9	11	13	3.5676
Clear Lake sucker	8	11.9	11	12	2.9773
Lost River sucker	64	12.0	10	13	5.4610
	Procurrent anal-fin rays				
Shortnose sucker	77	1.0	1	2	21.2346
Klamath largescale sucker	80	1.0	1	2	15.3278
Clear Lake sucker	9	1.3	1	2	37.5000
Lost River sucker	66	1.1	1	3	32.2248

Table 5. Continued.

	N	Average	Min	Max	CV
	Anal-fin rays				
Shortnose sucker	77	8.0	7	9	2.8398
Klamath largescale sucker	80	8.0	7	8	2.4010
Clear Lake sucker	9	7.9	7	8	4.2254
Lost River sucker	66	7.9	7	8	3.6627
	Pectoral-fin rays				
	N	Average	Min	Max	CV
Shortnose sucker	50	15.8	11	19	10.3880
Klamath largescale sucker	30	15.8	10	18	12.5402
Lost River sucker	32	15.6	12	18	8.7163
	Pelvic-fin rays				
	N	Average	Min	Max	CV
Shortnose sucker	51	9.4	8	11	7.7215
Klamath largescale sucker	30	9.7	8	11	7.5994
Lost River sucker	33	9.6	8	11	7.8454
	Gill rakers on first arch				
	N	Average	Min	Max	CV
Shortnose sucker	416	34.6	22	46	11.8001
Klamath largescale sucker	138	30.0	20	38	12.7234
Clear Lake sucker	10	33.2	30	35	3.9656
Lost River sucker	154	26.0	20	31	8.6971
	Residual gillraker count				
	N	Average	Min	Max	CV
Shortnose sucker	416	1.1	-5.2	7.9	200.56
Klamath largescale sucker	138	-3.1	-8.0	1.6	-61.51
Clear Lake sucker	10	-3.1	-8.1	-1.6	-60.25
Lost River sucker	154	-8.5	-13.6	-1.0	-26.67
	Vertebrae to dorsal-fin origin				
	N	Average	Min	Max	CV
Shortnose sucker	78	12.8	10	16	6.5756
Klamath largescale sucker	94	13.4	11	15	5.1749
Clear Lake sucker	8	13.5	12	15	7.9188
Lost River sucker	67	13.6	13	15	4.6925
	Vertebrae to anal-fin origin				
	N	Average	Min	Max	CV
Shortnose sucker	77	31.4	28	33	2.4816
Klamath largescale sucker	83	31.7	30	33	1.8637
Clear Lake sucker	9	31.7	31	32	1.5789
Lost River sucker	67	33.1	32	35	2.5492

Table 5. Continued.

	N	Average	Min	Max	CV
	Precaudal vertebrae				
	N	Average	Min	Max	CV
Shortnose sucker	426	24.0	22	25	2.7098
Klamath largescale sucker	149	24.7	23	27	2.9769
Clear Lake sucker	11	24.4	24	25	2.0708
Lost River sucker	368	24.7	22	27	2.8500
	Precaudal vertebrae without ribs				
	N	Average	Min	Max	CV
Shortnose sucker	98	4.0	3	5	15.8906
Klamath largescale sucker	32	4.1	2	5	17.1420
Clear Lake sucker	9	4.1	3	5	14.6171
Lost River sucker	66	4.0	2	5	14.8102
	Caudal vertebrae				
	N	Average	Min	Max	CV
Shortnose sucker	427	19.0	17	21	3.8335
Klamath largescale sucker	149	18.4	17	20	3.8098
Clear Lake sucker	11	18.2	18	19	2.2249
Lost River sucker	368	20.8	19	23	3.5408
	Total vertebrae				
	N	Average	Min	Max	CV
Shortnose sucker	428	43.0	41	45	1.6648
Klamath largescale sucker	149	43.1	41	44	1.5466
Clear Lake sucker	11	42.5	42	43	1.2275
Lost River sucker	368	45.5	44	47	1.6439
	Doubled neural spine on PU2				
	N	Average	Min	Max	CV
Shortnose sucker	359	0.3	0	1	138.710
Klamath largescale sucker	102	0.6	0	2	83.973
Lost River sucker	332	0.3	0	1	137.574
	Doubled neural spine on PU3				
	N	Average	Min	Max	CV
Shortnose sucker	323	0.2	0	1	209.689
Klamath largescale sucker	82	0.3	0	1	143.603
Lost River sucker	314	0.2	0	1	201.928
	Doubled haemal spine on PU2				
	N	Average	Min	Max	CV
Shortnose sucker	296	0.01	0	1	855.847
Klamath largescale sucker	59	0.03	0	1	538.436
Lost River sucker	307	0	0	0	100.000

Table 5. Continued

	N	Average	Min	Max	CV
	Doubled haemal spine on PU3				
	N	Average	Min	Max	CV
Shortnose sucker	296	0.1	0	1	316.176
Klamath largescale sucker	66	0.1	0	1	292.545
Lost River sucker	307	0.1	0	1	283.825
	Doubled neural spine on other centra				
	N	Average	Min	Max	CV
Shortnose sucker	276	0.02	0	1	621.034
Klamath largescale sucker	58	0.03	0	1	533.772
Lost River sucker	313	0.01	0	1	1018.160

Table 6. Series number and calendar dates of sample series used during 1991 field sampling.

Series	Calendar dates Start	End
1	April 7	April 13
2	April 14	April 20
3	April 21	April 27
4	April 28	May 4
5	May 5	May 11
6	May 12	May 18
7	May 19	May 25
8	May 26	June 1
9	June 2	June 8
10	June 9	June 15
11	June 16	June 22
12	June 23	June 29
13	June 30	July 6
14	July 7	July 13
15	July 14	July 20
16	July 21	July 27
17	July 28	August 3
18	August 4	August 10
19	August 11	August 17
20	August 18	August 24
21	August 25	August 31
22	September 1	September 7
23	September 8	September 14
24	September 15	September 21
25	September 22	September 28
26	September 29	October 5
27	October 6	October 12
28	October 13	October 19

Table 7. Sample series, first date of series, sample size (N), and mean estimated number of fish per day and fish per series that entered the A-Canal at the headworks during 1991. Fish per series was calculated by multiplying fish per day times the number of days in a series (7). Grand total is the estimated total number of fish that entered the A-Canal during the study period. LCL and UCL represent lower and upper 95% confidence limits about the mean.

Sample Series	Date	N	LCL	Fish/Day	UCL	LCL	Fish/Series	UCL
1	4-07-91	9	0	0	0	0	0	0
3	4-21-91	18	0	1426	4348	0	9982	30436
4	4-28-91	18	0	0	0	0	0	0
5	5-05-91	18	0	0	0	0	0	0
6	5-12-91	18	0	5156	12258	0	36092	85806
7	5-19-91	18	0	0	0	0	0	0
8	5-26-91	18	0	5340	12910	0	37380	90370
9	6-02-91	18	25141	43887	62633	175987	307209	438431
10	6-09-91	18	4102	21682	39263	28714	151774	274841
11	6-16-91	18	0	0	0	0	0	0
12	6-23-91	18	0	32038	71691	0	224266	501837
13	6-30-91	18	12023	46690	81358	84161	326830	569506
14	7-07-91	18	181995	271696	361396	1273965	1901872	2529772
15	7-14-91	18	32385	74424	116463	226695	520968	815241
16	7-21-91	18	82202	121001	159800	575414	847007	1118600
17	7-28-91	18	25271	68168	110615	176897	477176	774305
18	8-04-91	18	4623	23261	41899	32361	162827	293293
19	8-11-91	6	0	45223	93343	0	316561	653401
Grand Total						2574194	5319944	8175839

Table 8. Sample series, first date of series, sample size (N),and mean estimated number of suckers per day and suckers per series that entered the A-Canal at the headworks during 1991. Sucker per series was calculated by multiplying the number of suckers per day times the number of days in a series (7). Grand total is the estimated total number of suckers that entered the A-Canal during the study period. LCL and UCL represent lower and upper 95% confidence intervals about the mean.

Sample Series	Date	N	LCL	Suckers/Day	UCL	LCL	Suckers/Series	UCL
1	4-07-91	9	0	0	0	0	0	0
3	4-21-91	18	0	0	0	0	0	0
4	4-28-91	18	0	0	0	0	0	0
5	5-05-91	18	0	0	0	0	0	0
6	5-21-91	18	0	3269	7111	0	22883	49777
7	5-19-91	18	0	0	0	0	0	0
8	5-26-91	18	0	5340	12910	0	37380	90370
9	6-02-91	18	25141	43887	62633	175987	307209	438431
10	6-09-91	18	4102	21682	39263	28714	151774	274871
11	6-16-91	18	0	0	0	0	0	0
12	6-23-91	18	0	4829	11854	0	33803	82978
13	6-30-91	18	0	0	0	0	0	0
14	7-07-91	18	0	21772	46029	0	152404	322203
15	7-14-91	18	0	7671	23374	0	53697	163618
16	7-21-91	18	0	0	0	0	0	0
17	7-28-91	18	0	0	0	0	0	0
18	8-04-91	18	0	0	0	0	0	0
19	8-11-91	6	0	0	0	0	0	0
Grand Total						204701	759150	1422248

Table 9. Sample series, first date of series, sample size, and mean estimated number of suckers per day that entered the A-Canal during night sampling (2400-0800 hours). LCL and UCL represent lower and upper 95% confidence intervals about the mean.

Sample Series	Date	N	LCL	Suckers/Day	UCL
3	4-21-91	6	0	0	0
4	4-28-91	6	0	0	0
5	5-05-91	6	0	0	0
6	5-12-91	6	0	1425	4765
7	5-19-91	6	0	0	0
8	5-29-91	6	0	0	0
9	6-02-91	6	8545	19249	29954
10	6-09-91	6	0	0	0
11	6-16-91	6	0	0	0
12	6-23-91	6	0	0	0
13	6-30-91	6	0	0	0
14	7-07-91	6	0	8159	27215
15	7-14-91	6	0	0	0
16	7-21-91	6	0	0	0
17	7-28-91	6	0	0	0
18	8-04-91	6	0	0	0

Table 10. Sample series, first date of series, sample size, and mean estimated number of suckers per day that entered the A-Canal during day sampling (0800-1600 hours). LCL and UCL represent lower and upper 95% confidence intervals about the mean.

Sample Series	Date	N	LCL	Suckers/Day	UCL
1	4-07-91	9	0	0	0
3	4-21-91	6	0	0	0
4	4-28-91	6	0	0	0
5	5-05-91	6	0	0	0
6	5-12-91	6	0	1846	4976
7	5-19-91	6	0	0	0
8	5-29-91	6	0	5354	13366
9	6-02-91	6	2890	14206	25522
10	6-09-91	6	0	11636	25764
11	6-16-91	6	0	0	0
12	6-23-91	6	0	0	0
13	6-30-91	6	0	0	0
14	7-07-91	6	0	6328	22122
15	7-14-91	6	0	7696	25670
16	7-21-91	6	0	0	0
17	7-28-91	6	0	0	0
18	8-04-91	6	0	0	0

Table 11. Sample series, first date of series, sample size, and mean estimated number of suckers per day that entered the A-Canal during evening sampling (1600-2400 hours). LCL and UCL represent lower and upper 95% confidence intervals about the mean.

Sample Series	Date	N	LCL	Suckers/Day	UCL
3	4-21-91	6	0	0	0
4	4-28-91	6	0	0	0
5	5-05-91	6	0	0	0
6	5-12-91	6	0	0	0
7	5-19-91	6	0	0	0
8	5-29-91	6	0	0	0
9	6-02-91	6	0	10460	25889
10	6-09-91	6	0	10097	23229
11	6-16-91	6	0	0	0
12	6-23-91	6	0	4840	12335
13	6-30-91	6	0	0	0
14	7-07-91	6	0	7286	24310
15	7-14-91	6	0	0	0
16	7-21-91	6	0	0	0
17	7-28-91	6	0	0	0
18	8-04-91	6	0	0	0
19	8-11-91	6	0	0	0

Table 12. Site location, number of times sampled, area sampled, number of age 0 Lost River suckers caught, weighted mean density per 10 m^2, and log_e transformed mean weighted density per 10 m^2 for each standardized seining station in Upper Klamath and Agency lakes in 1991.

Site	Times sampled	Area (m^2) sampled	LRS	Weighted mean density (per $10m^2$)	Log_e transformed weighted mean density (per $10m^2$)
U1	15	109.5	4	0.37	0.22
U2	13	94.9	0	0	0
U3	12	87.6	0	0	0
U4	14	102.2	4	0.39	0.23
U5	9	65.7	0	0	0
U6	10	73.0	3	0.41	0.21
U7	13	94.9	0	0	0
U8	14	102.2	0	0	0
U9	12	87.6	0	0	0
U10	6	43.8	0	0	0
Upper Klamath Lake totals	118	861.4	11	0.13	0.07
A1	6	43.8	0	0	0
A2	9	65.7	0	0	0
A3	3	21.9	0	0	0
A4	7	51.1	0	0	0
Agency Lake totals	25	182.5	0	0	0

Table 13. Site location, number of times sampled, area sampled, number of age 0 shortnose suckers caught, weighted mean density per 10 m^2, and $\log_e$ transformed mean weighted density per 10 m^2 for each standardized seining station in Upper Klamath and Agency lakes in 1991.

Site	Times sampled	Area (m^2) sampled	SNS	Weighted mean density (per $10m^2$)	Log_e transformed weighted mean density (per $10m^2$)
U1	15	109.5	9	0.82	0.51
U2	13	94.9	13	1.37	0.53
U3	12	87.6	0	0	0
U4	14	102.2	30	2.94	1.27
U5	9	65.7	42	6.39	1.05
U6	10	73.0	253	34.66	2.69
U7	13	94.9	5	0.53	0.33
U8	14	102.2	4	0.39	0.26
U9	12	87.6	2	0.23	0.13
U10	6	43.8	7	1.60	0.73
Upper Klamath Lake totals	118	861.4	365	4.24	0.70
A1	6	43.8	1	0.22	0.17
A2	9	65.7	0	0	0
A3	3	21.9	0	0	0
A4	7	51.1	0	0	0
Agency Lake totals	25	182.5	1	0.05	0.04

Table 14. Site location, number of times sampled, number of casts, total area sampled by the castnet, number of age 0 Lost River suckers caught, weighted mean density per 10 m^2, and $\log_e$ transformed weighted mean density for each cast net station in Upper Klamath Lake in 1991.

Site	Times sampled	Casts	Area (m^2) sampled	LRS	Weighted mean density (per $10m^2$)	Log_e transformed weighted mean density (per $10m^2$)
U1-onshore	1	10	54.0	0	0	0
U2-onshore	5	52	280.8	29	1.03	0.32
U3-onshore	1	10	54.0	0	0	0
U4-onshore	6	57	307.8	22	0.71	0.26
U5-onshore	4	39	210.6	10	0.47	0.17
U6-onshore	2	28	151.2	0	0	0
U8-onshore	1	17	91.8	2	0.22	0.12
U11-onshore	2	40	216.0	1	0.05	0.03
U14-onshore	1	6	32.4	0	0	0
U15-onshore	3	33	178.2	25	1.40	0.38
U18-onshore	2	54	291.6	5	0.17	0.06
U19-onshore	2	40	216.0	36	1.67	0.23
U21-onshore	1	10	54.0	12	2.22	0.48
SS-onshore	2	27	145.8	43	2.95	0.43
Onshore sub-total	33	423	2284.8	185	0.81	0.20
U2-offshore	4	41	221.4	30	1.36	0.31
U4-offshore	1	10	54.0	0	0	0
U5-offshore	6	135	729.0	5	0.07	0.04
U8-offshore	1	5	27.0	0	0	0
U12-offshore	1	13	70.2	0	0	0
U15-offshore	2	19	102.6	2	0.19	0.14
Offshore sub-total	15	223	1204.2	37	0.31	0.09
Grand total	48	646	3489.0	222	0.64	0.17

Table 15. Site location, number of times sampled, number of casts, total area sampled by the castnet, number of age 0 shortnose suckers caught, weighted mean density per 10 m^2, and $\log_e$ transformed weighted mean density for each cast net station in Upper Klamath Lake in 1991.

Site	Times sampled	Casts	Area (m^2) sampled	SNS	Weighted mean density (per $10m^2$)	Log_e transformed weighted mean density (per $10m^2$)
U1-onshore	1	10	54.0	0	0	0
U2-onshore	5	52	280.8	56	2.00	0.39
U3-onshore	1	10	54.0	0	0	0
U4-onshore	6	57	307.8	45	1.46	0.33
U5-onshore	4	39	210.6	47	2.23	0.30
U6-onshore	2	28	151.2	0	0	0
U8-onshore	1	17	91.8	2	0.22	0.12
U11-onshore	2	40	216.0	0	0	0
U14-onshore	1	6	32.4	0	0	0
U15-onshore	3	33	178.2	7	0.39	0.19
U18-onshore	2	54	291.6	4	0.13	0.07
U19-onshore	2	40	216.0	6	0.28	0.12
U21-onshore	1	10	54.0	4	0.74	0.31
SS-onshore	2	27	145.8	38	2.60	0.42
Onshore sub-total	33	423	2284.8	209	0.91	0.19
U2-offshore	4	41	221.4	9	0.41	0.18
U4-offshore	1	10	54.0	1	0.19	0.13
U5-offshore	6	135	729.0	22	0.31	0.10
U8-offshore	1	5	27.0	0	0	0
U12-offshore	1	13	70.2	0	0	0
U15-offshore	2	19	102.6	0	0	0
Offshore sub-total	15	223	1204.2	32	0.27	0.10
Grand total	48	646	3489.0	241	0.70	0.16

Table 16. Site location, number of times sampled, total minutes trawled, number of age 0 Lost River suckers caught, weighted mean catch per 10 minutes, and $\log_e$ transformed weighted mean catch per 10 minutes for each trawling station in Upper Klamath Lake in 1991.

Site	Times sampled	Minutes trawled	LRS	Weighted mean catch (per 10 min.)	Log_e transformed weighted mean catch (per 10 min.)
U13	12	139	0	0	0
U14	5	54	6	1.11	0.39
U16	9	97	3	0.31	0.20
U17	8	118	18	1.53	0.49
U20	19	365	16	0.44	0.24
Total	53	773	43	0.56	0.24

Table 17. Site location, number of times sampled, total minutes trawled, number of age 0 shortnose suckers caught, weighted mean catch per 10 minutes, and $\log_e$ transformed weighted mean catch per 10 minutes for each trawling station in Upper Klamath Lake in 1991.

Site	Times sampled	Minutes trawled	SNS	Weighted mean catch (per 10 min.)	Log_e transformed weighted mean catch (per 10 min.)
U13	12	139	0	0	0
U14	5	54	1	0.18	0.14
U16	9	97	0	0	0
U17	8	118	6	0.51	0.24
U20	19	365	2	0.05	0.03
Total	53	773	9	0.11	0.06

Table 18. Site location, number of trap net samples (N), total hours sampled, mean hours per trap net sample, number of Klamath largescale suckers (KLS), number of Lost River suckers (LRS), number of shortnose suckers (SNS), and weighted mean number of suckers per hour captured during trap net surveys in Upper Klamath Lake, Agency Lake, and river mouth habitats in spring 1992.

Site	N	Total hours	Mean set time	KLS	LRS	SNS	Suckers/hr
Williamson River	9	258.5	28.7	1	37	25	0.24
Thomason Creek	2	44.0	22.3	0	3	6	0.20
Crystal Creek	1	99.0	99.0	0	1	3	0.04
Recreation Creek	1	18.5	18.5	0	0	0	0
River mouth sub-totals	13	420.0	32.3	1	41	34	0.18
Straights	1	22.0	22.0	0	1	0	0.05
Upper Klamath Lake	5	274.0	54.8	0	3	0	0.01
Agency Lake	8	188.0	23.5	0	0	0	0
Lake habitat sub-totals	14	484.0	34.6	0	4	0	<0.01

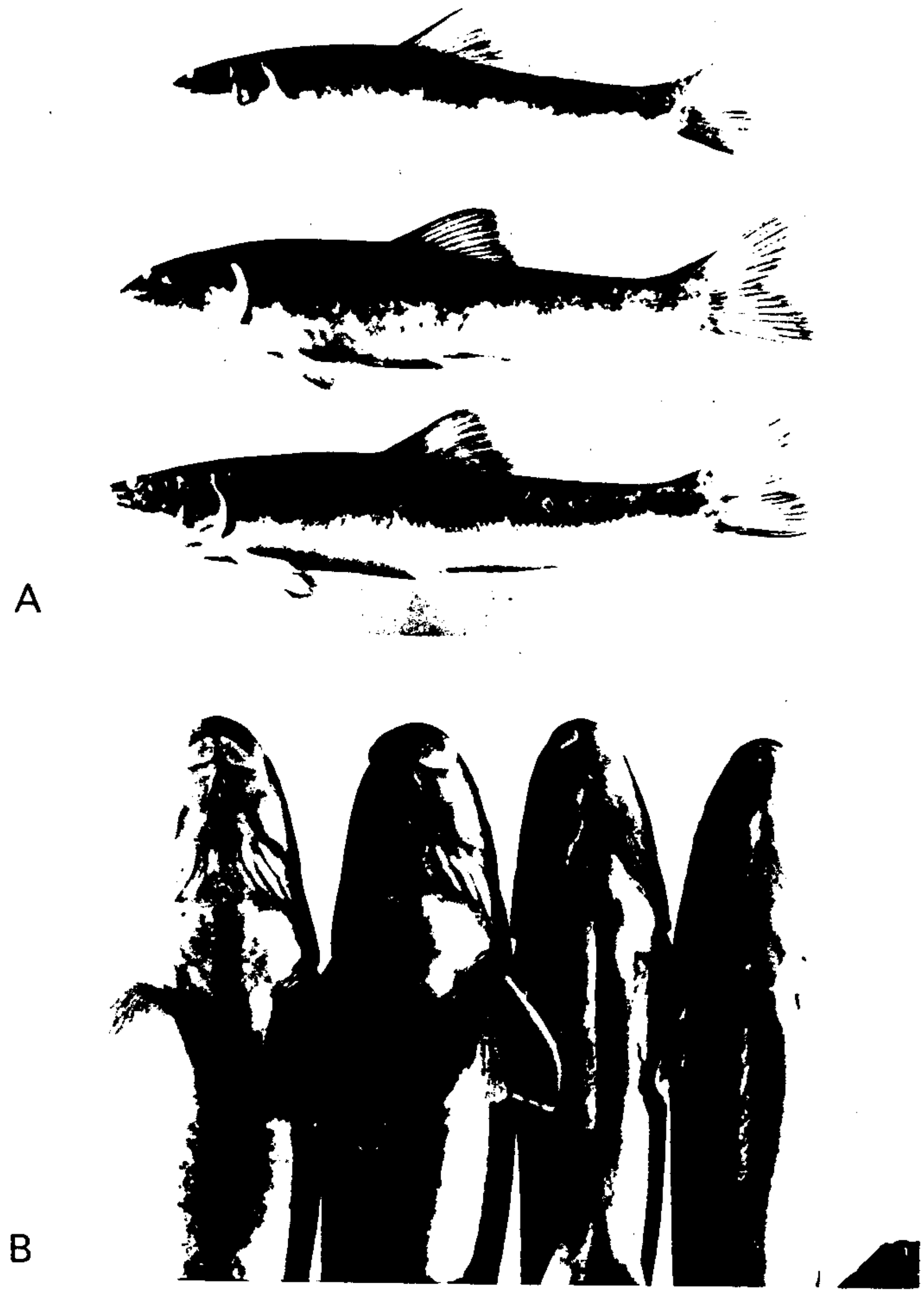


Figure 1. A. Left lateral view of (top) shortnose sucker, 92.4 mm SL, A92072-5, (middle) Klamath largescale sucker, 105.7 mm SL, OS 13739, (bottom) Lost River sucker, 110.1 mm SL, A92072-24. B. Ventral view of head of (left) two Klamath largescale suckers, OS 13739, and (right) two shortnose suckers, A92072.

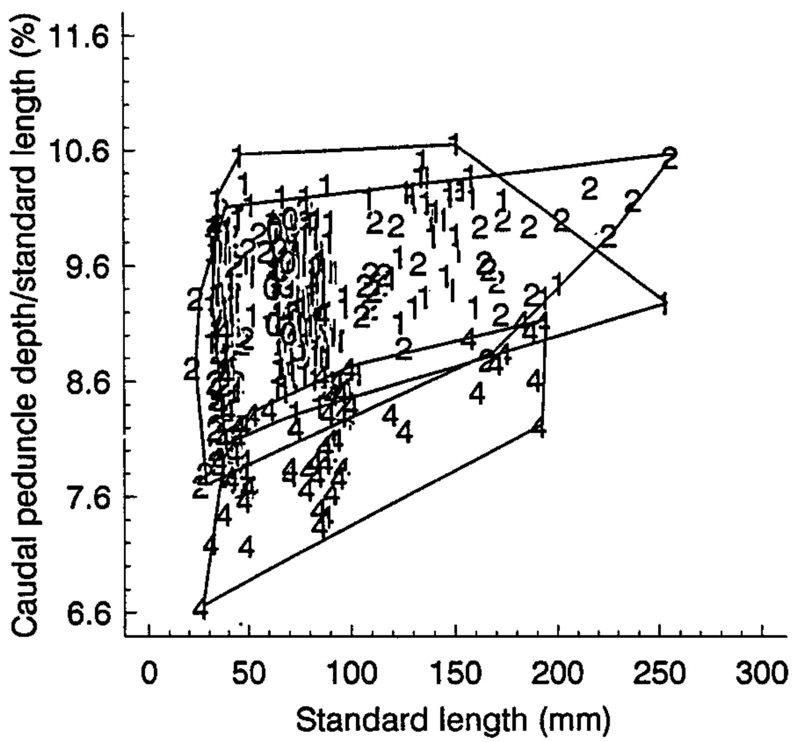


Figure 2. Relationship between caudal peduncle depth (as a per cent of standard length) and standard length in mm. Species codes are: 0=unknown, presumed shortnose sucker; 1=shortnose suckers; 2=Klamath largescale suckers; and 4=Lost River suckers. Lines connect outer bounds of each species.

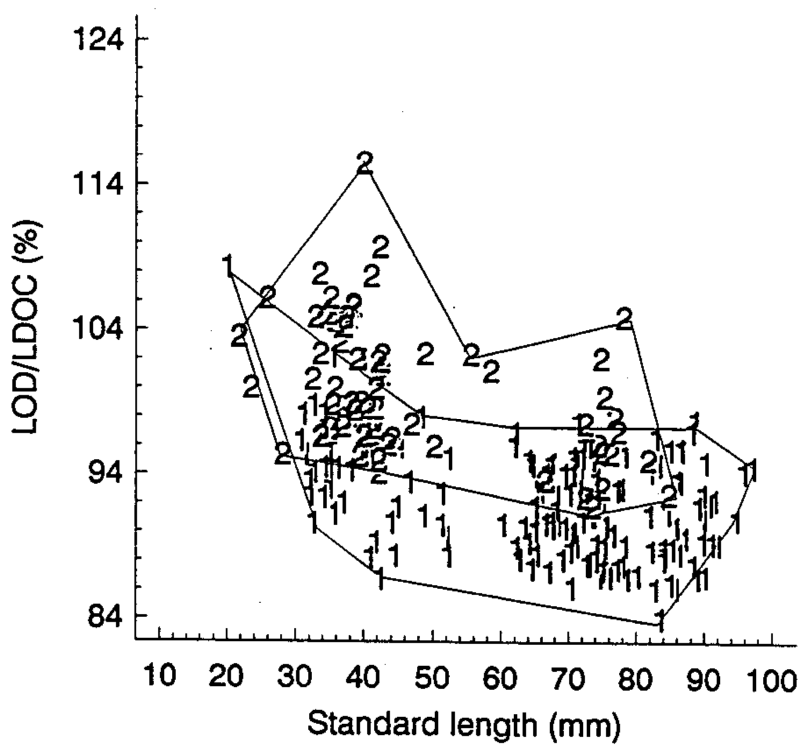


Figure 3. Relationship between LOD/LDOC and standard length in mm for shortnose sucker (code=1) and Klamath largescale suckers (code=2). Lines connect outer bounds of each species

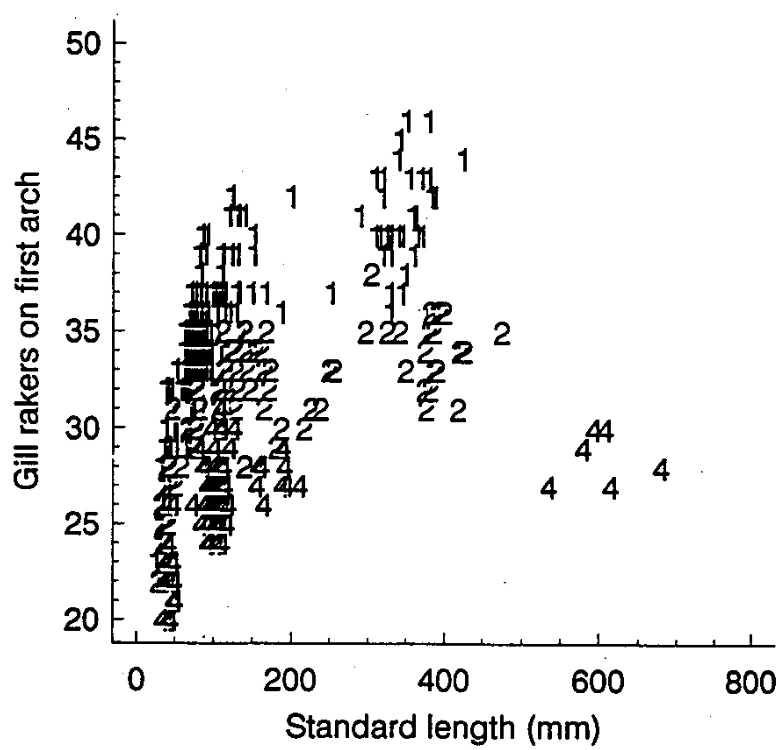


Figure 4. Relationship between number of gillrakers on the first arch and standard length in mm. Species codes are: 1=shortnose suckers; 2=Klamath largescale suckers; and 4=Lost River suckers.

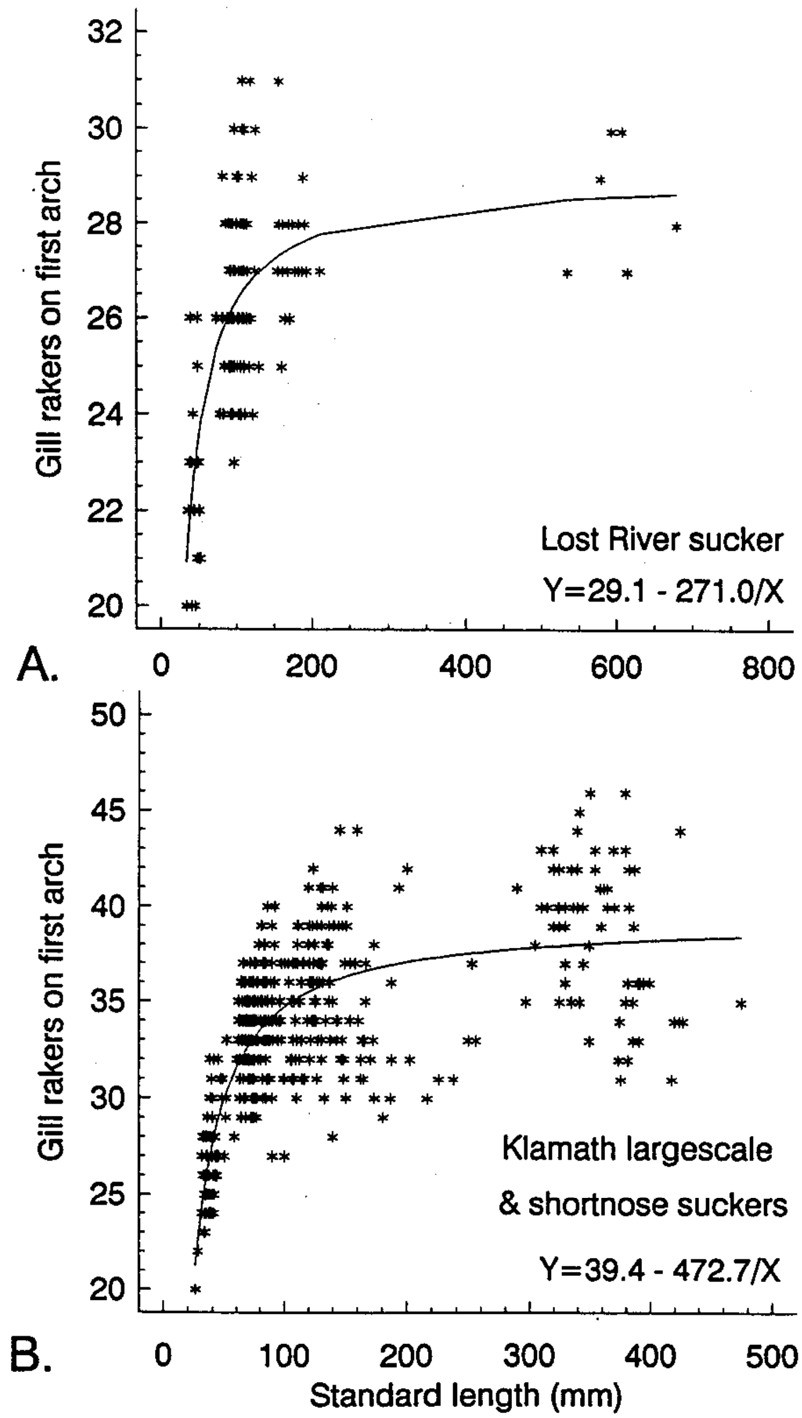


Figure 5. Relationship between number of gillrakers on the first arch and standard length in mm. A. Lost River suckers fitted to the curve Y=29.1-(271.0/X). B. Klamath largescale and shortnose suckers fitted to the curve Y=39.4-(472.7/X).

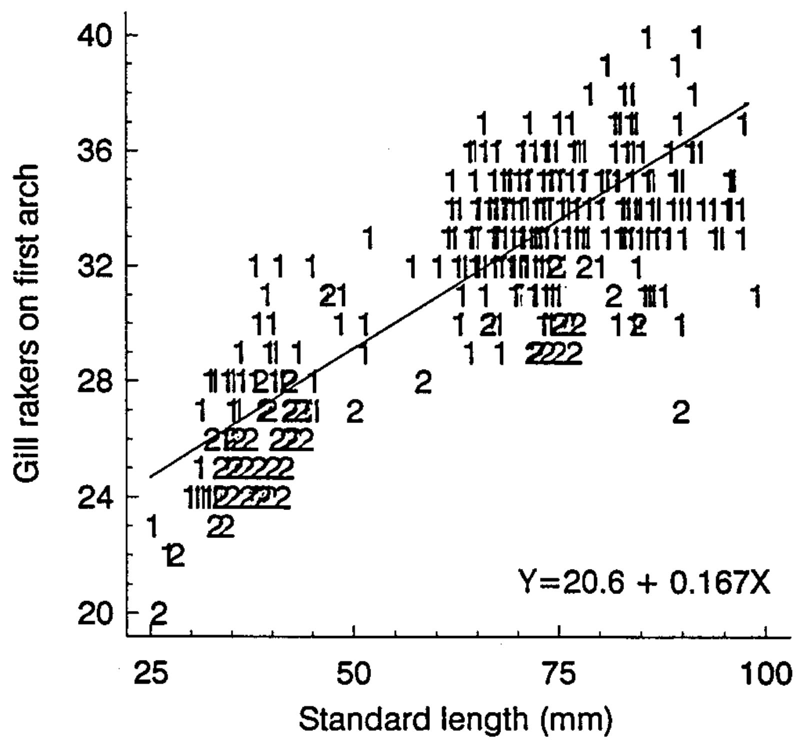


Figure 6. Relationship between number of gillrakers on the first arch and standard length in mm for shortnose suckers (code=1) and Klamath largescale suckers (code=2) less than 100 mm SL. Data fitted to the curve Y=20.6+0.167(X).

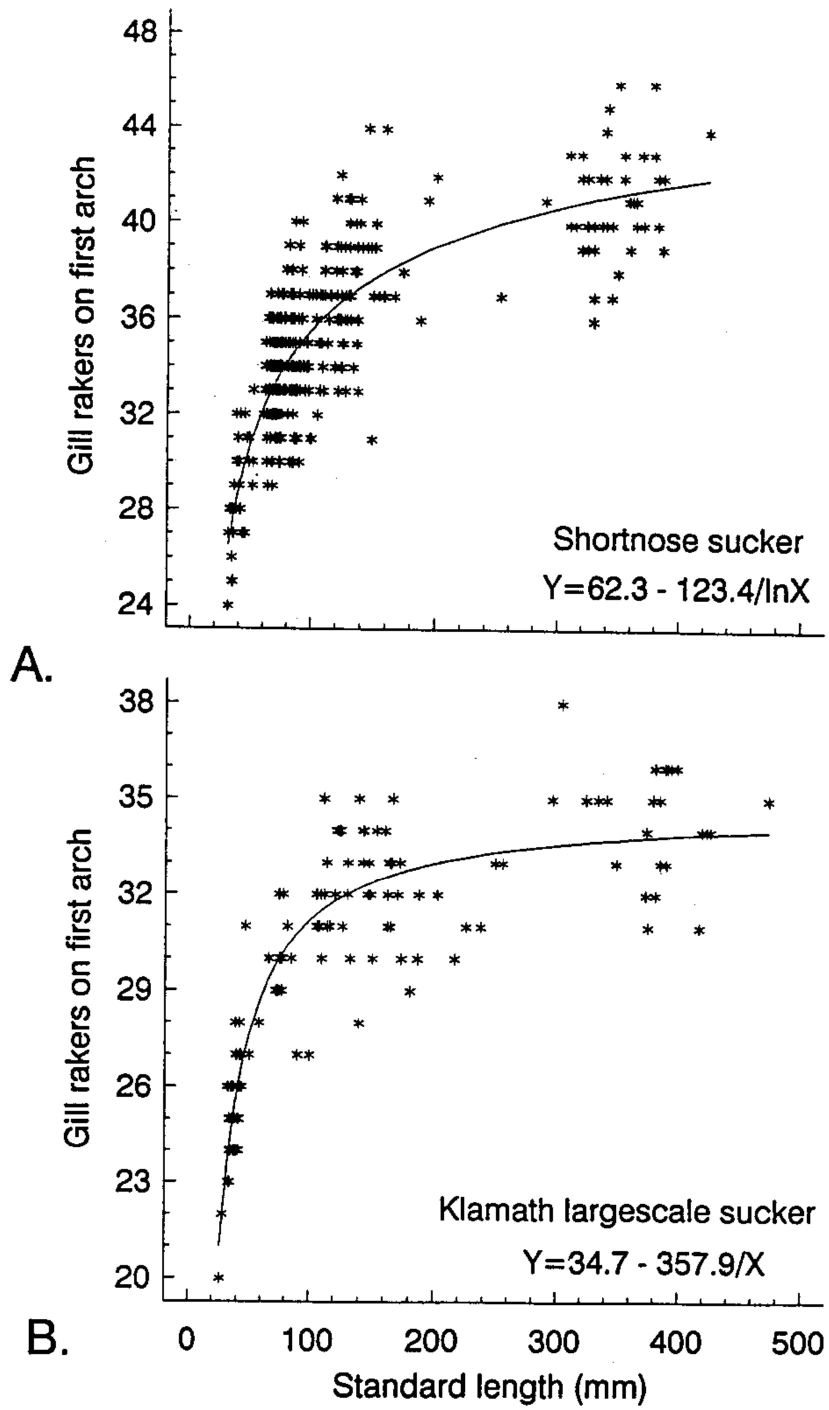


Figure 7. Relationship between number of gillrakers on the first arch and standard length in mm. A. Shortnose suckers fitted to the curve Y=62.3-(123.4/lnX). B. Klamath largescale suckers fitted to the curve Y=34.7-(357.9/X).

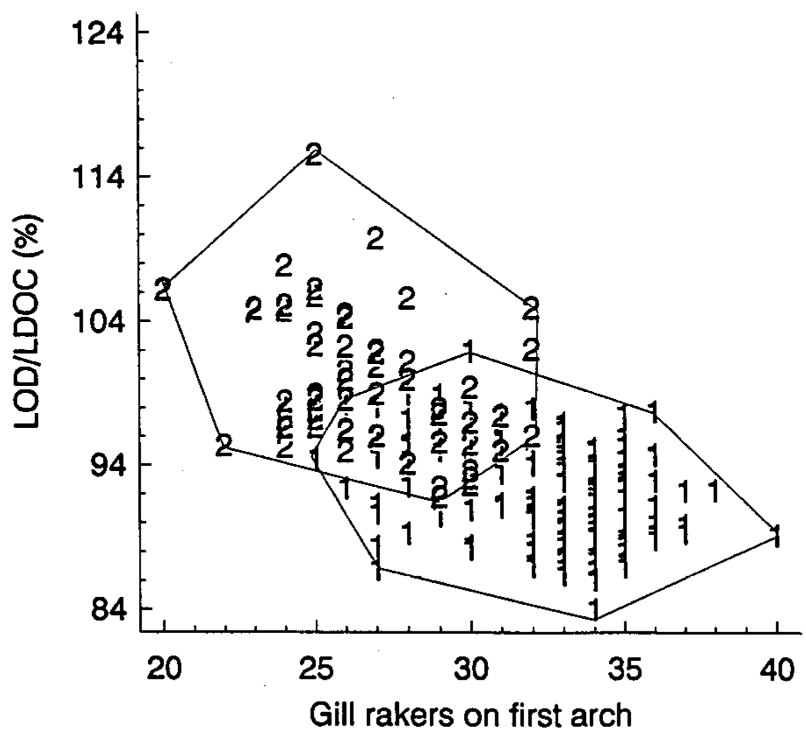


Figure 8. Relationship between LOD/LDOC and gillrakers on the first arch for shortnose suckers (code=1) and Klamath largescale suckers (code=2) less than 100 mm SL. Lines connect outer bounds of each species.

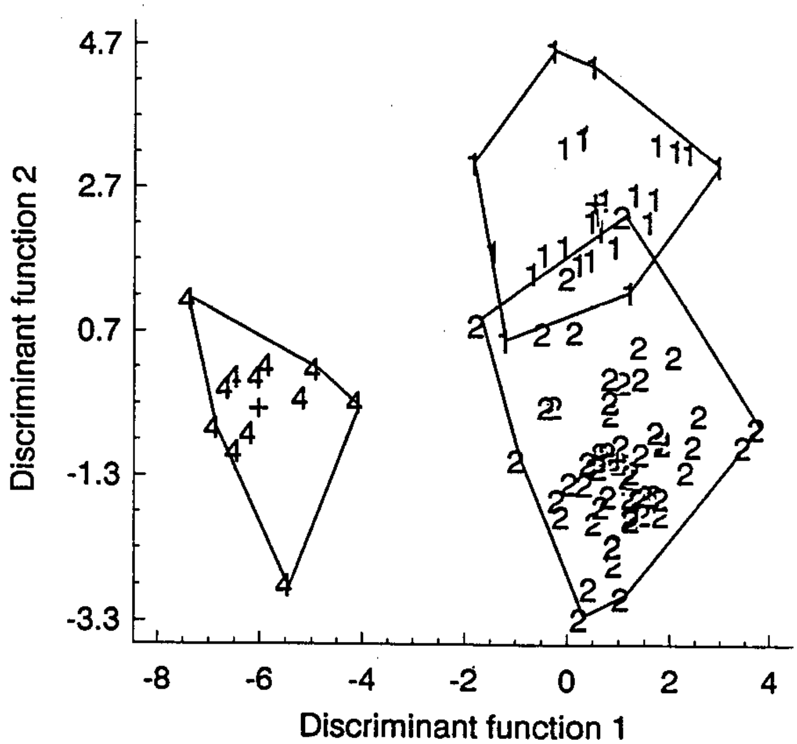


Figure 9. Multigroup discriminant function axes for continuous variables (GRRESID, LDOC, DP1, LAE, HL, DCAUDPED) in specimens less than 100 mm SL. Species codes are: 1=shortnose suckers; 2=Klamath largescale suckers; and 4=Lost River suckers. Lines connect outer bounds of each species.

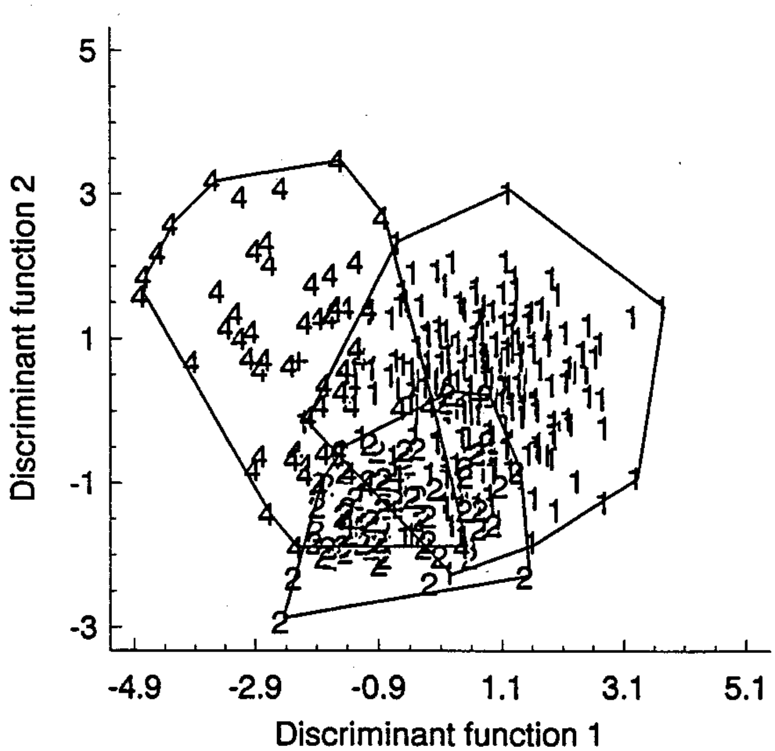


Figure 10. Multigroup discriminant function axes for continuous variables (SL, LOD, LDOC and DCAUDPED) in available specimens. Species codes are: 1=shortnose suckers; 2=Klamath largescale suckers; and 4=Lost River suckers. Lines connect outer bounds of each species.

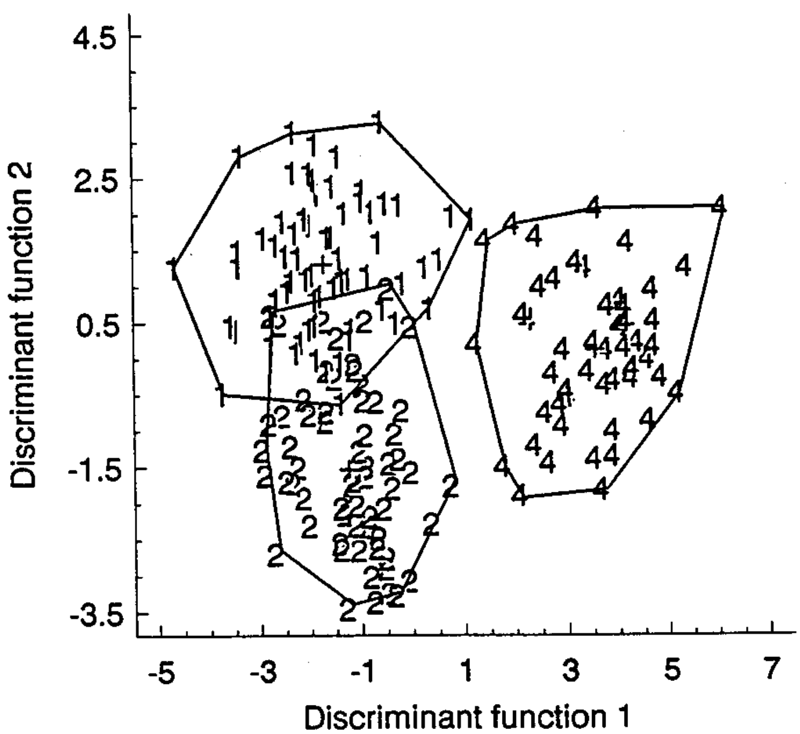


Figure 11. Multigroup discriminant function axes for selected discrete variables (GR, PRECAUDVER, UPCAUD, VDO, VAO, CAUDVER) in available specimens. Species codes are: 1=shortnose suckers; 2=Klamath largescale suckers; and 4=Lost River suckers. Lines connect outer bounds of each species.

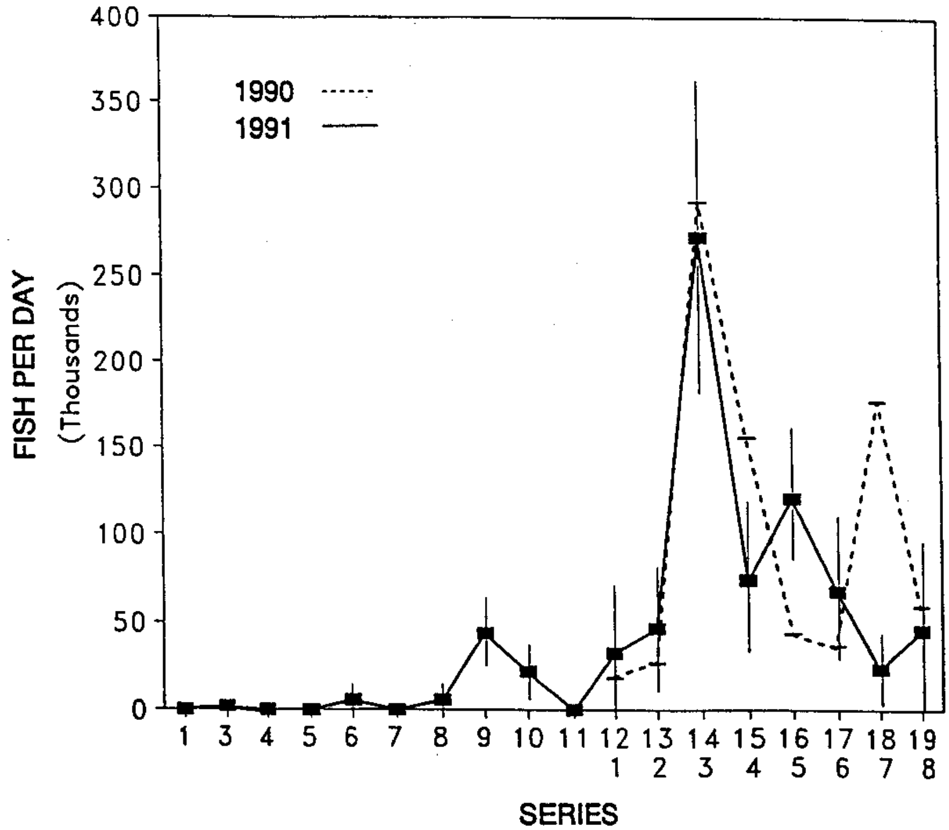


Figure 12. Estimated number of fish per day by series that entered the A-Canal in 1991, and estimated number of fish per day that entered the headworks between series 1-8 in 1990. Series 1-8 in 1990 (bottom) corresponded with series 12-19 in 1991.

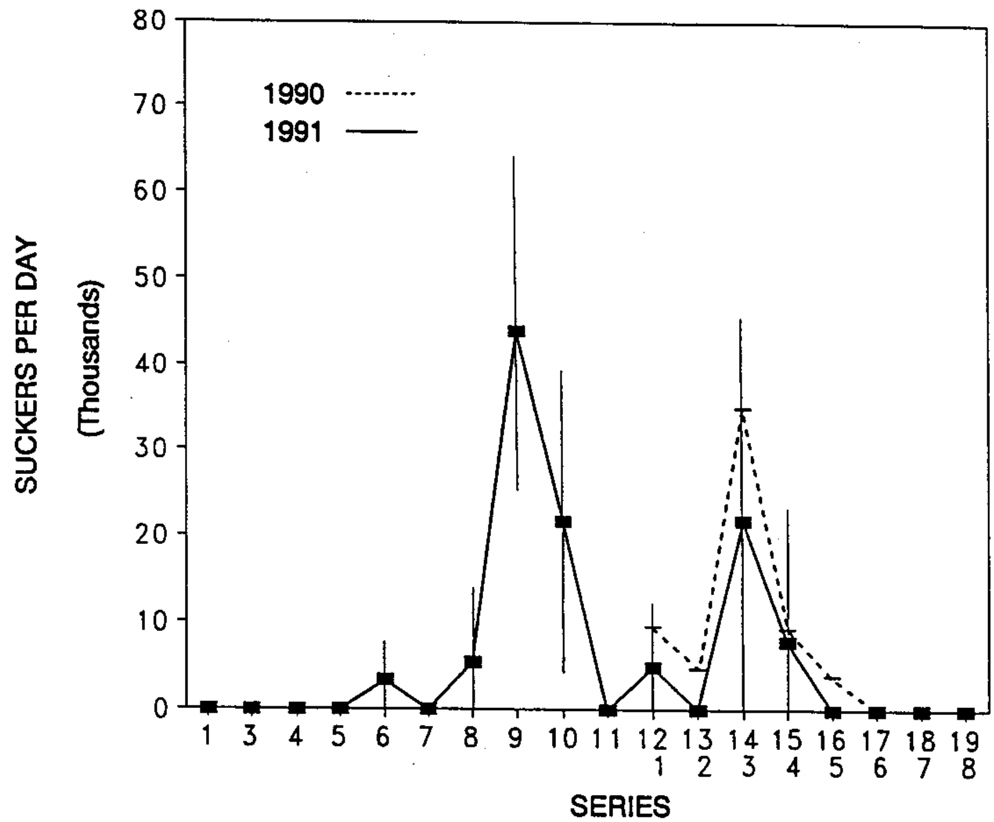


Figure 13. Estimated number of suckers per day by series that entered the A-Canal in 1991, and estimated number of suckers per day that entered the headworks between series 1-8 in 1990. Series 1-8 in 1990 (bottom) corresponded with series 12-19 in 1991.

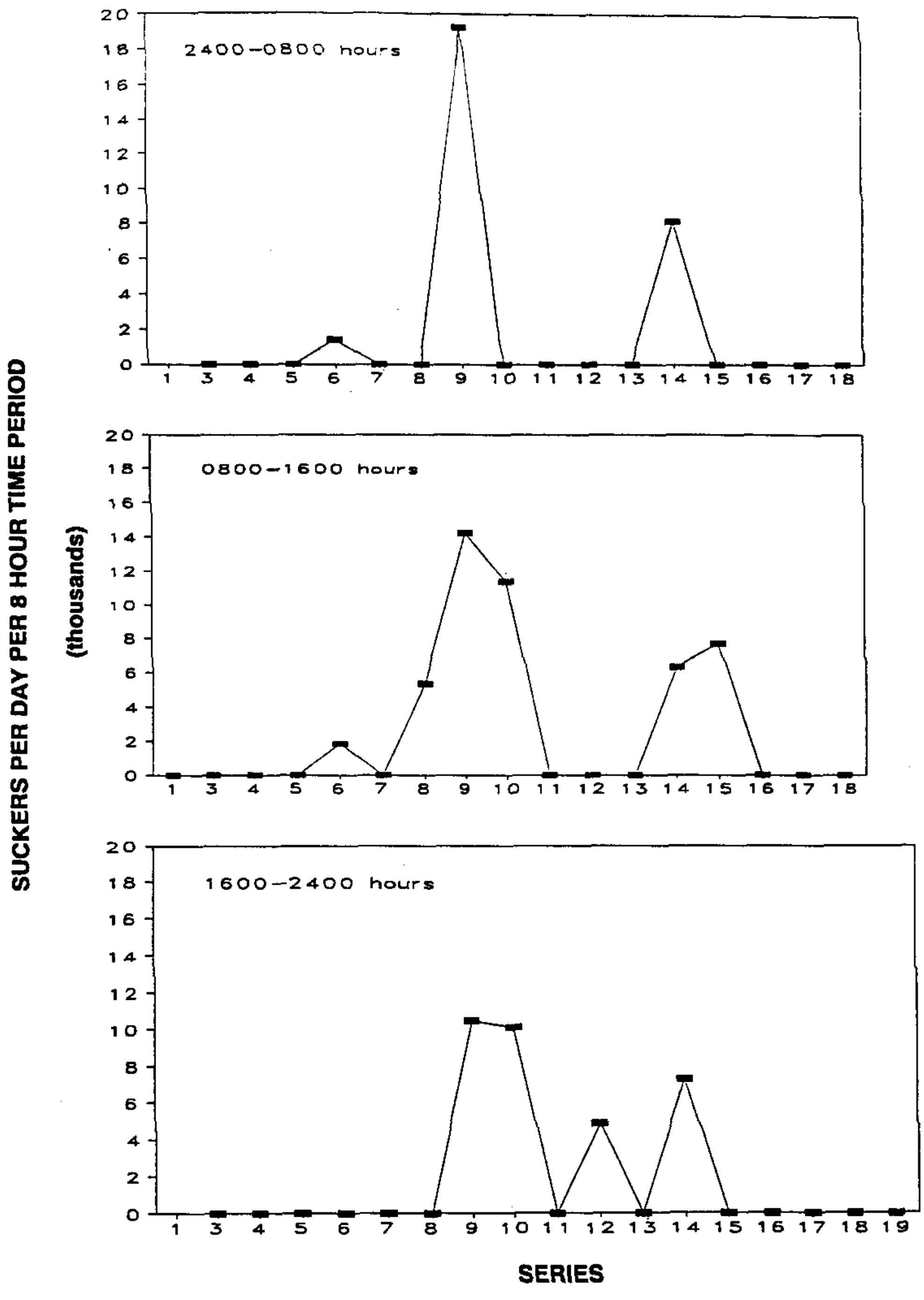


Figure 14. Estimated number of suckers per day per 8 hour time period that entered the A-Canal during night (2400-0800 hours), day (0800-1600 hours), and evening (1600-2400 hours) sampling in 1991.

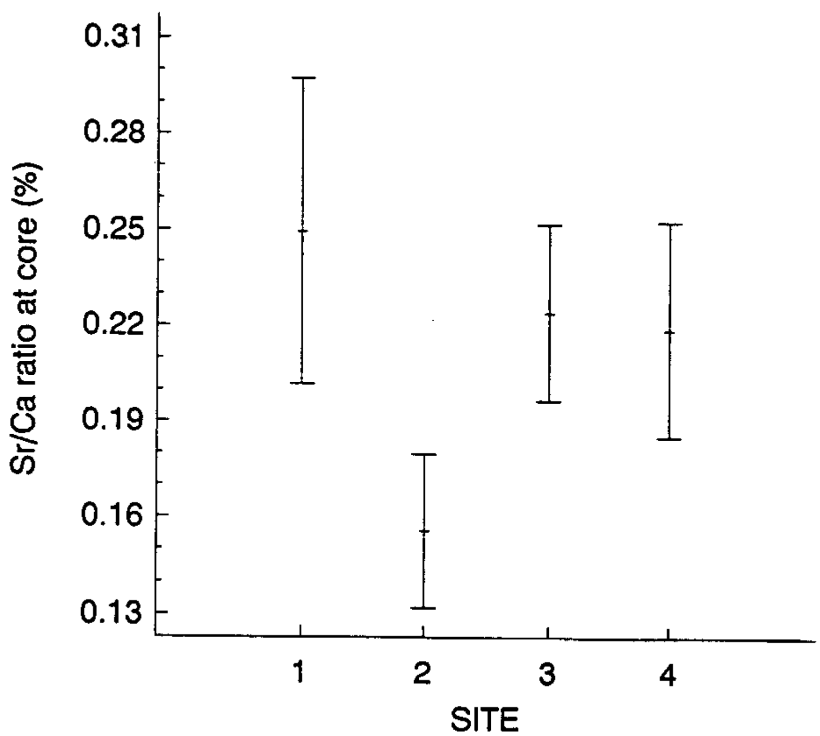


Figure 15. Strontium:calcium ratio from otolith cores. Site numbers and sample sizes are as follows: 1=Crooked Creek (2); 2=Sucker Springs (12); 3=Williamson River (7); and 4=Wood River (6).

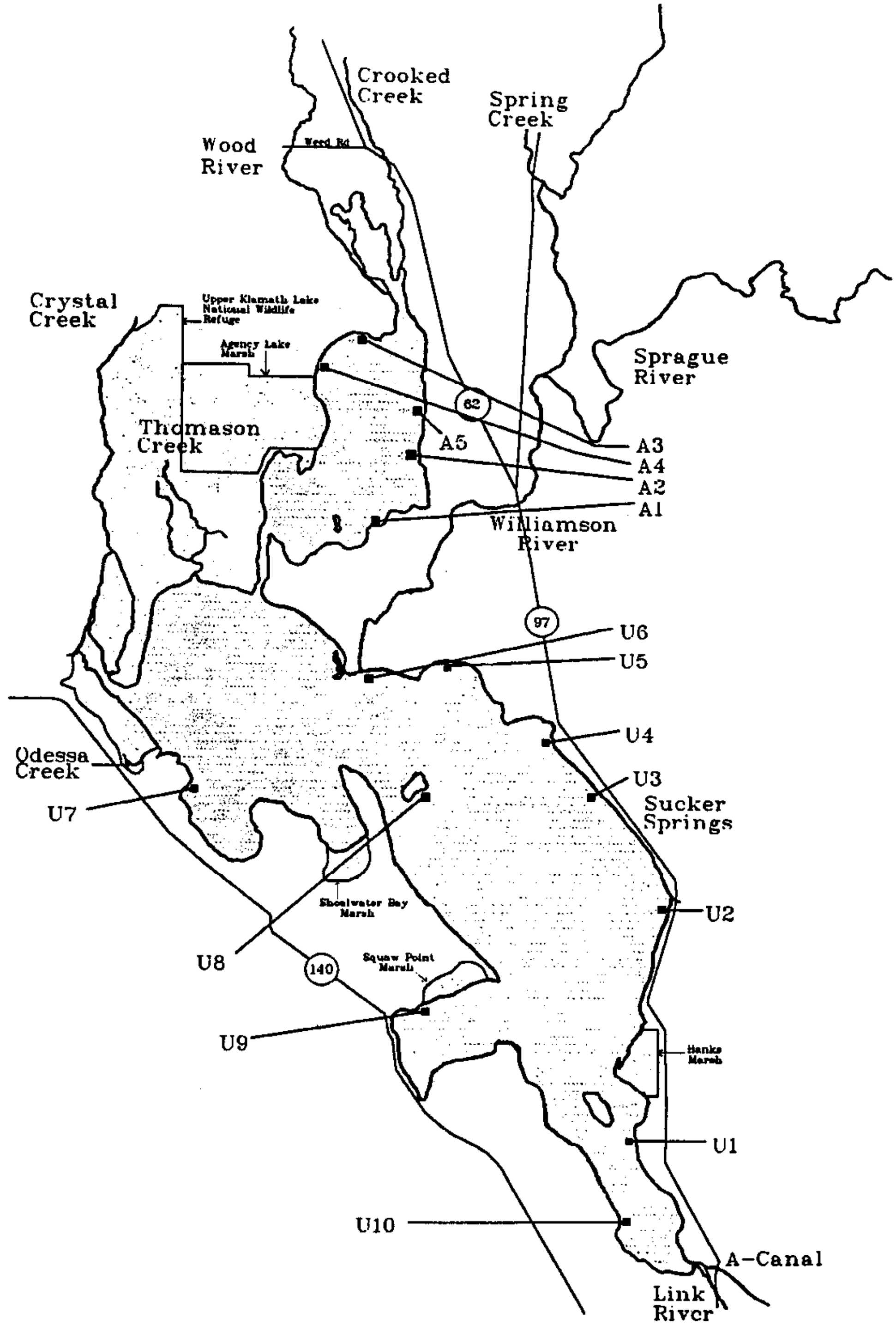


Figure 16. Beach seine sampling sites in Upper Klamath and Agency lakes, 1991.

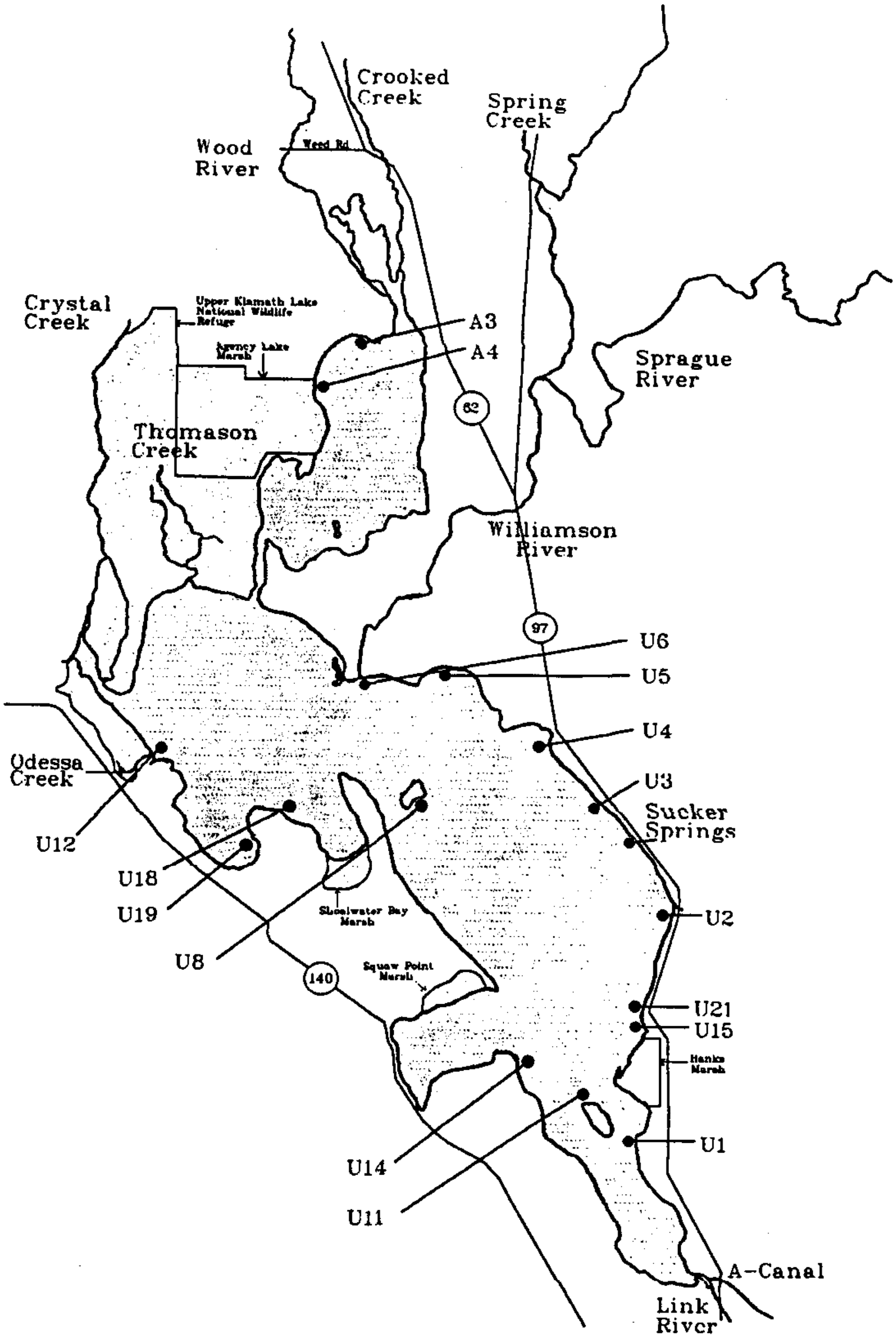


Figure 17. Cast net sampling sites in Upper Klamath and Agency lakes, 1991.

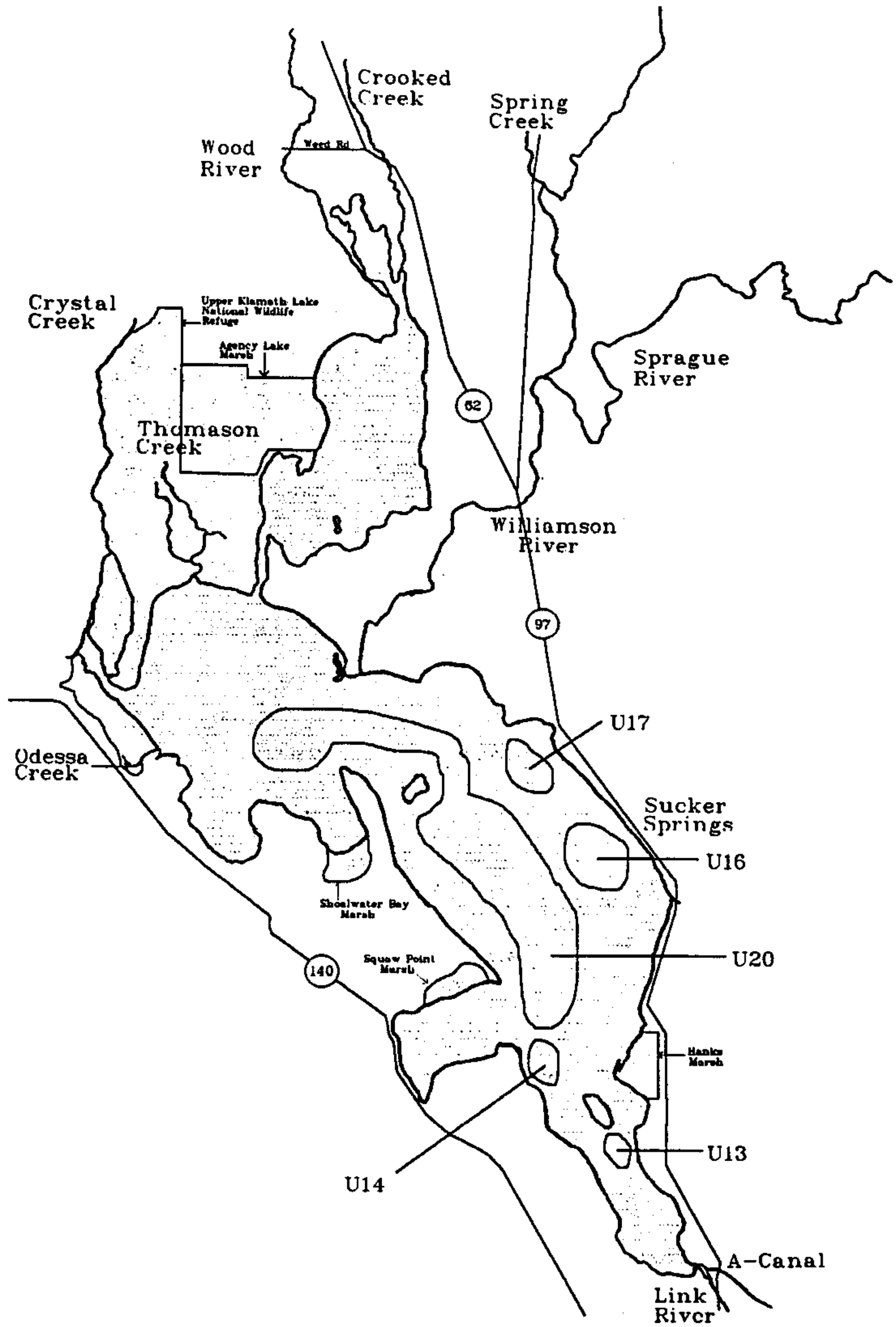


Figure 18. Trawl sites in Upper Klamath Lake, 1991.

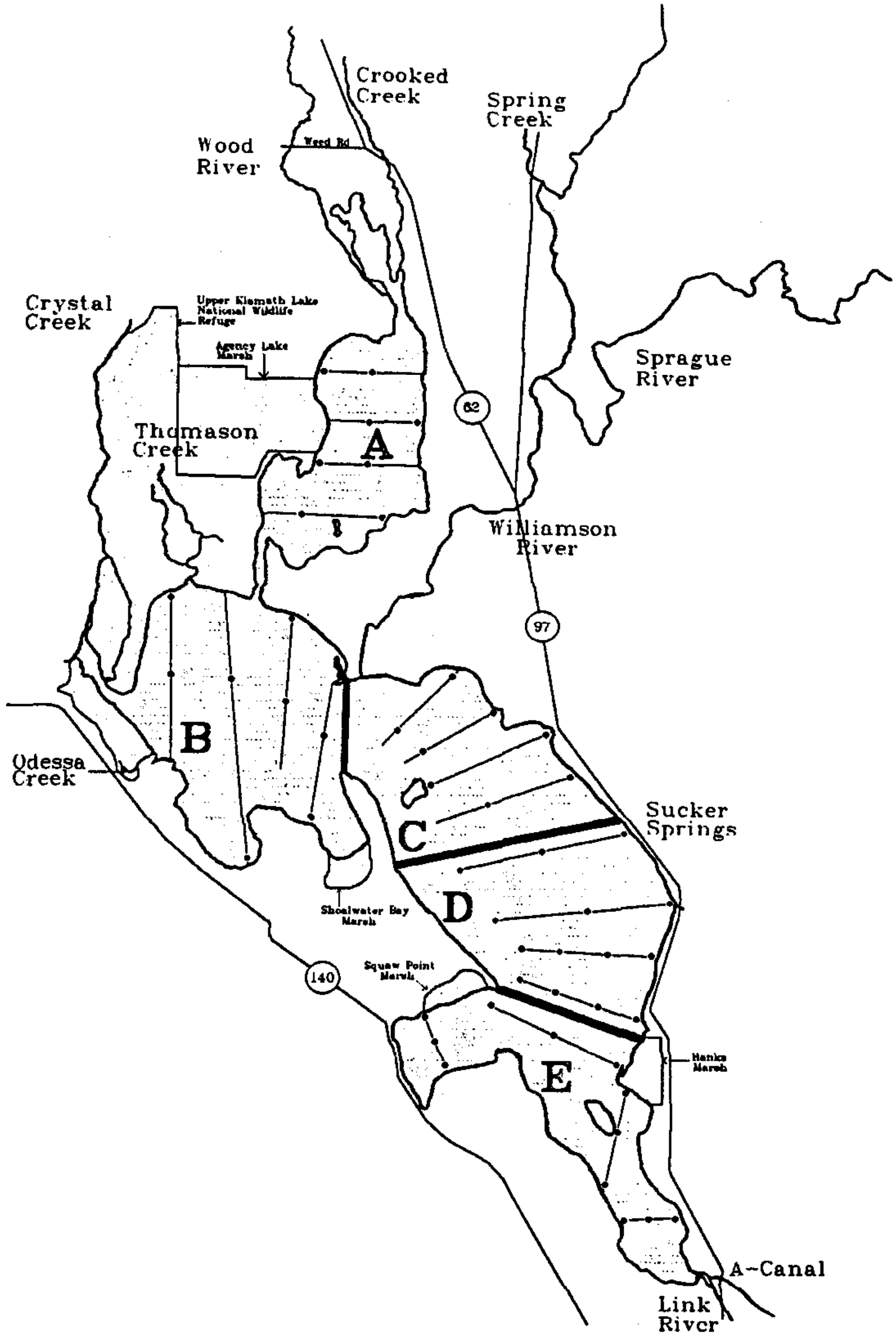


Figure 19. Whole-lake stratified sampling design used in spring 1992 cast net survey.

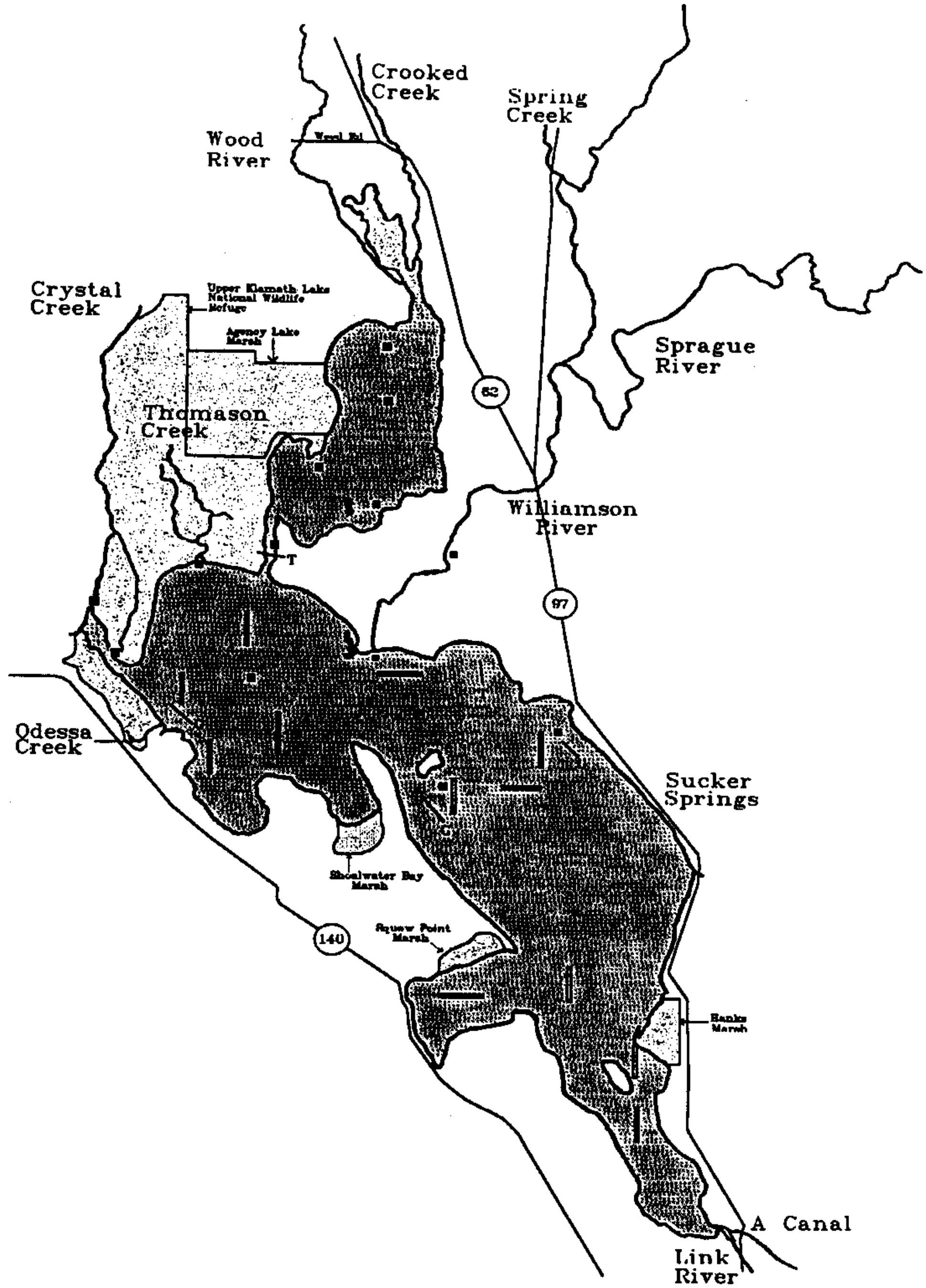


Figure 20. Trap net (squares), trawl (open rectangles), and gill net and trammel net (lines; G=gill net, T=trammel net) sampling sites in spring 1992.

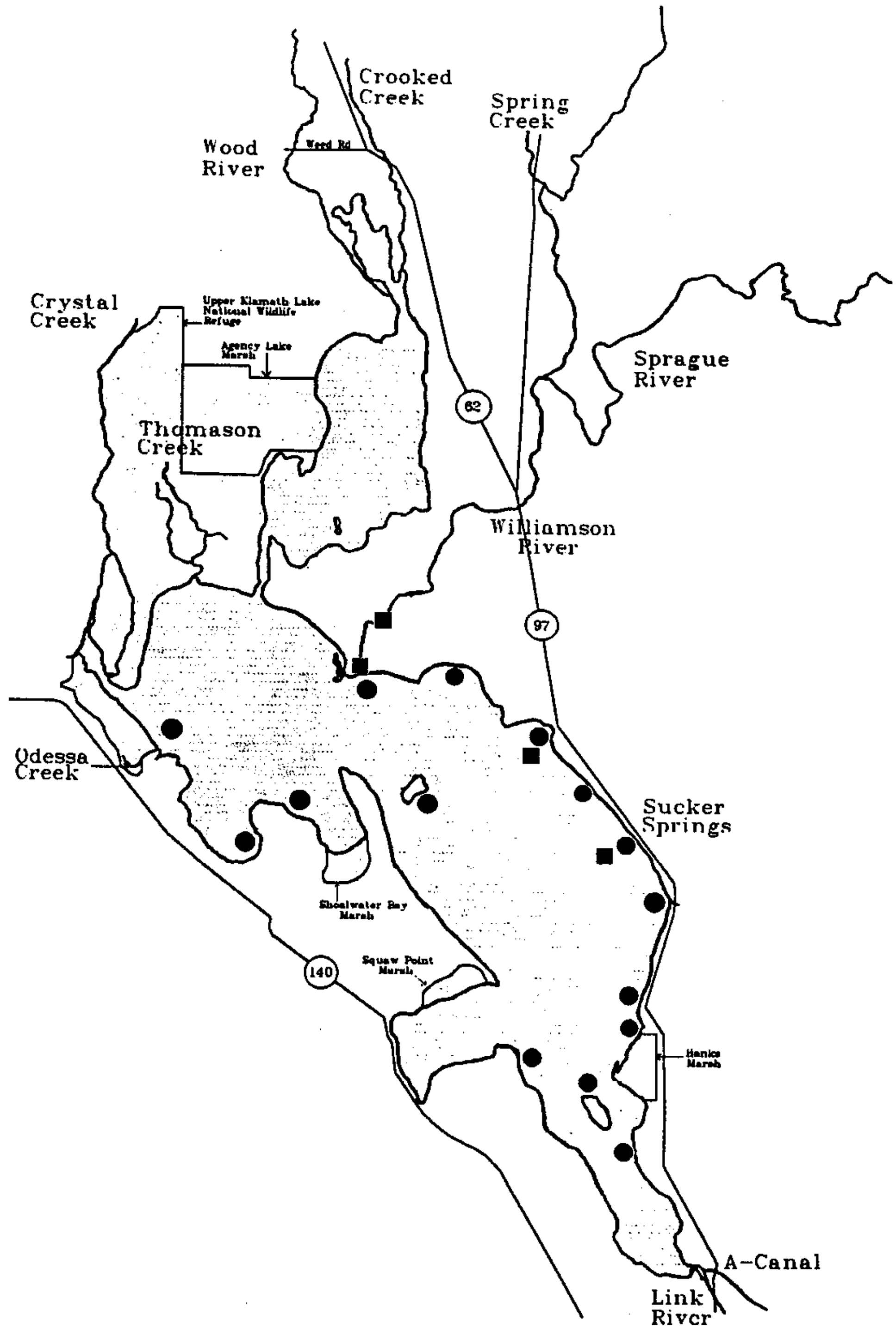


Figure 21. Cast net (circles) and trap net (squares) sampling sites in fall 1992.

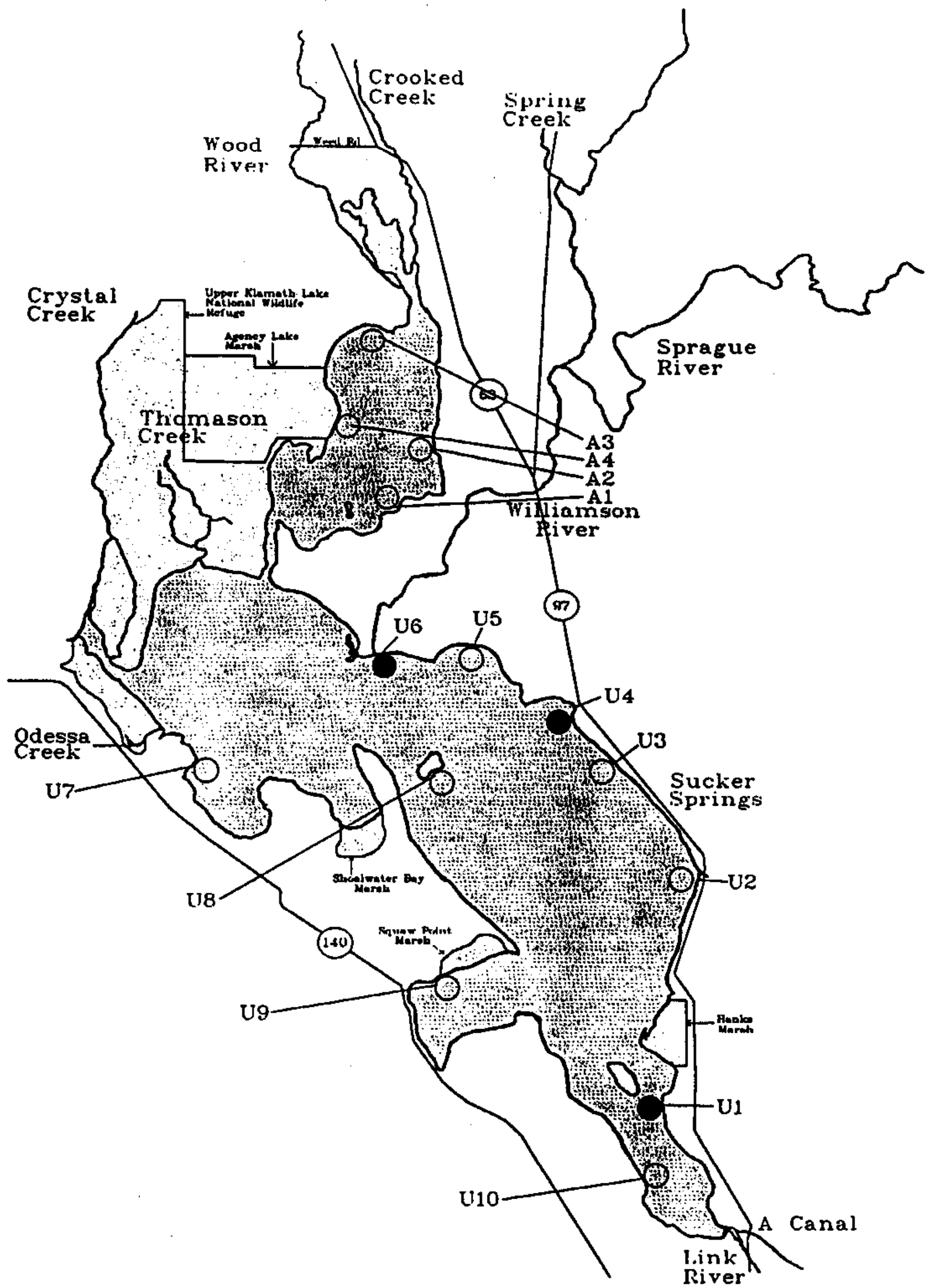


Figure 22. Age 0 Lost River sucker weighted mean density estimates (from Table 12) for each standardized seining station in 1991. Large solid circles=high densities (>1.00 per 10 m^2), medium solid circles=medium densities (0.20-0.99 per 10 m^2), small solid circles=low densities (<0.20 per 10 m^2), and empty circles=none captured.

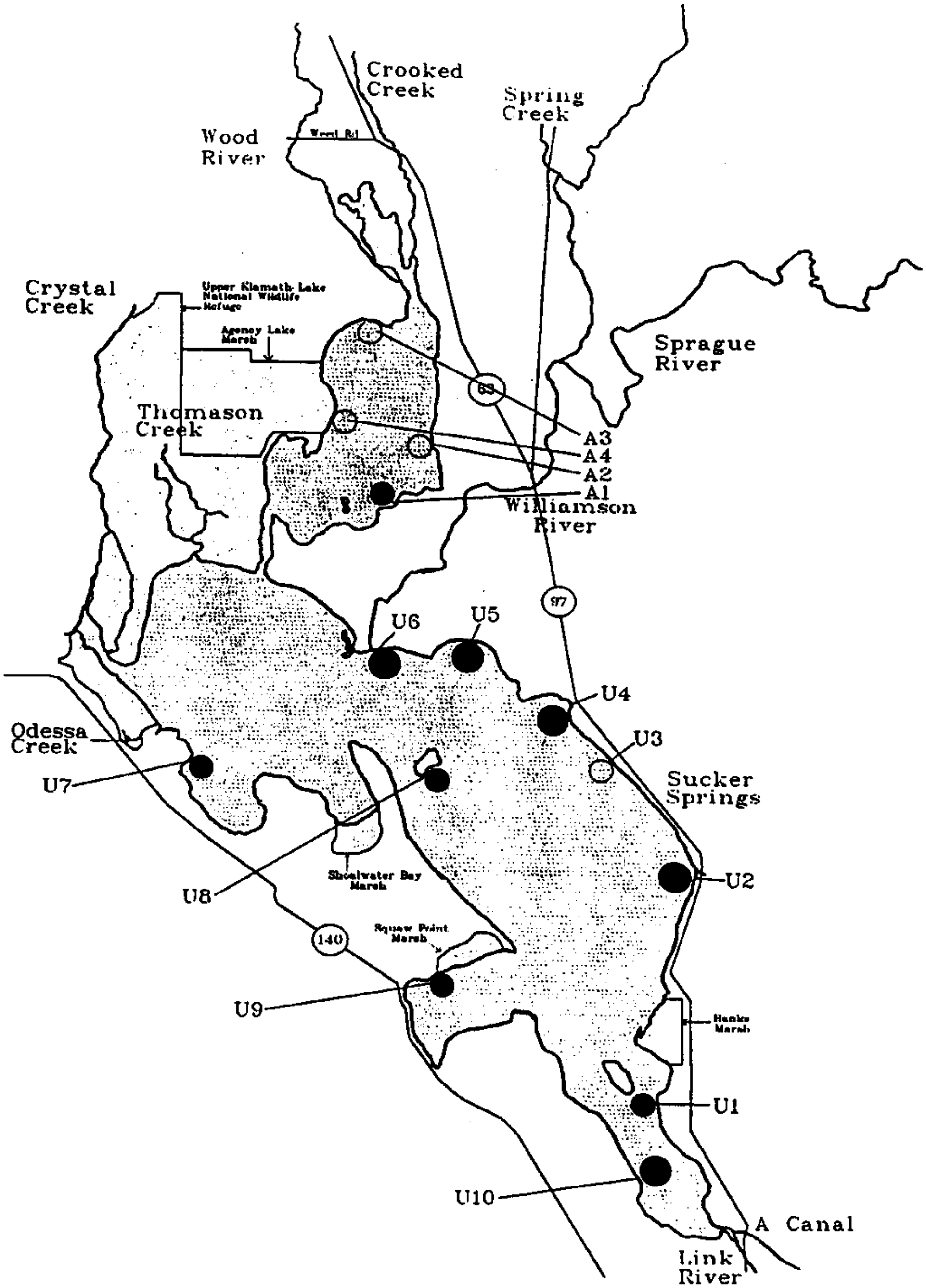


Figure 23. Age 0 shortnose sucker weighted mean density estimates (from Table 13) for each standardized seining station in 1991. Large solid circles=high densities (>1.00 per 10 m^2), medium solid circles=medium densities (0.20-0.99 per 10 m^2), small solid circles=low densities (<0.20 per 10 m^2), and empty circles=none captured.

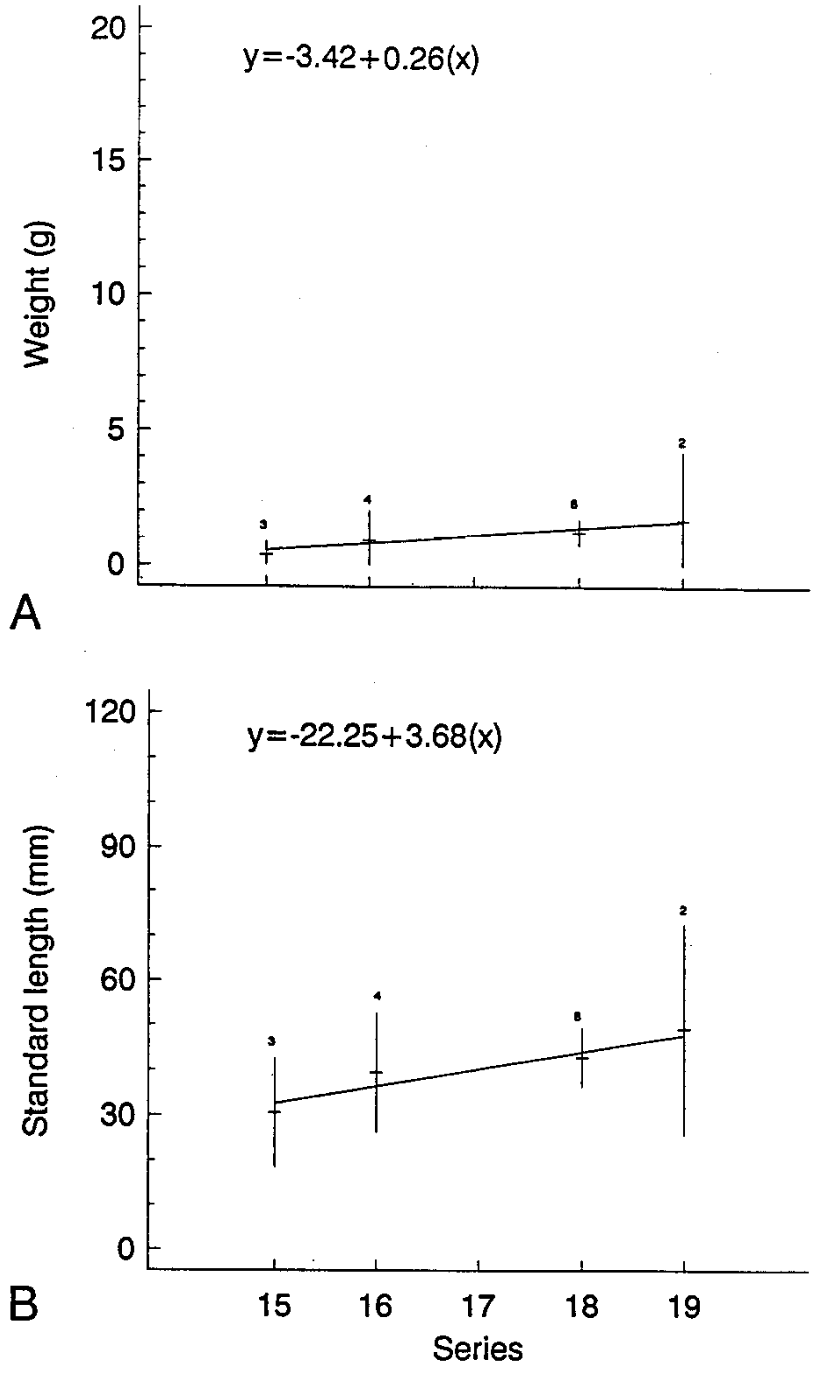


Figure 24. Mean and 95% confidence intervals by series of (A) weight and (B) standard length of age 0 Lost River suckers from beach seine collections. Slope of the regression line estimates weekly growth rate. Sample sizes indicated above confidence interval bars.

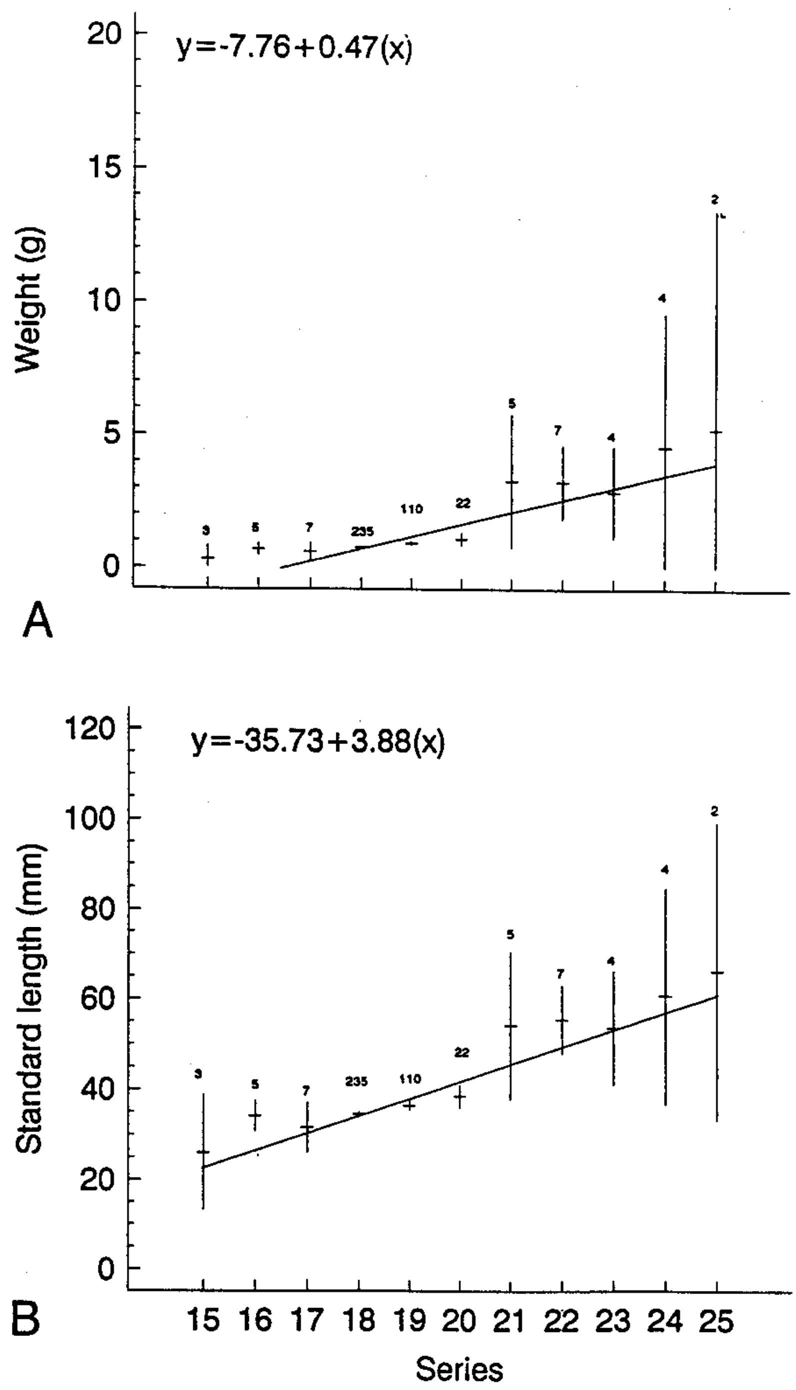


Figure 25. Mean and 95% confidence intervals by series of (A) weight and (B) standard length of age 0 shortnose suckers from beach seine collections. Slope of the regression line estimates weekly growth rate. Sample sizes indicated above confidence interval bars.

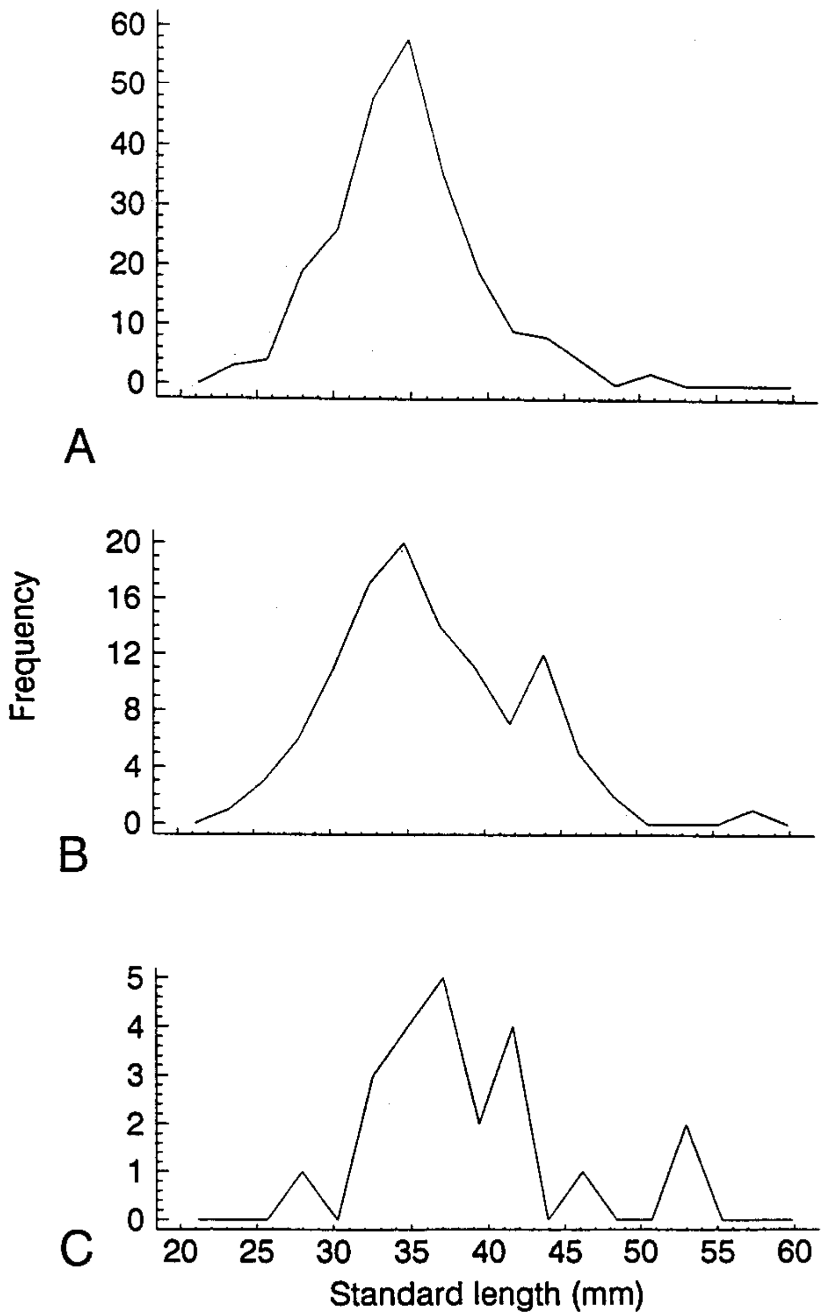


Figure 26. Length-frequency distribution of age 0 shortnose suckers from beach seine collections during (A) series 18, (B) series 19, and (C) series 20. Data points are grouped by 2.3-mm groups.

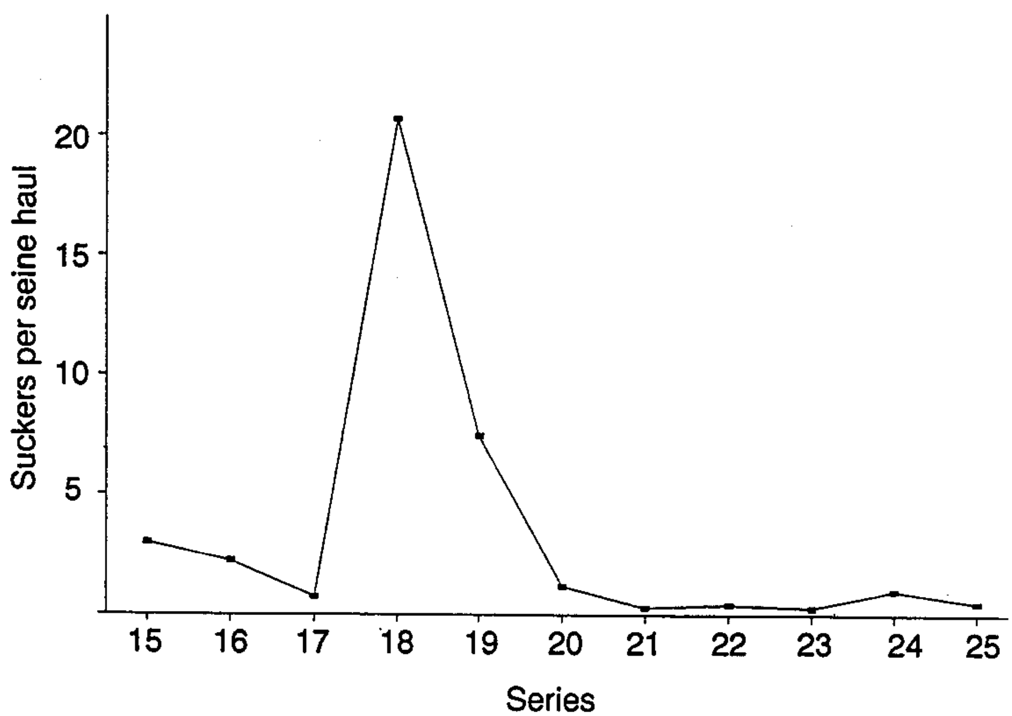


Figure 27. Mean number of suckers per seine haul during each series in Upper Klamath Lake, 1991.

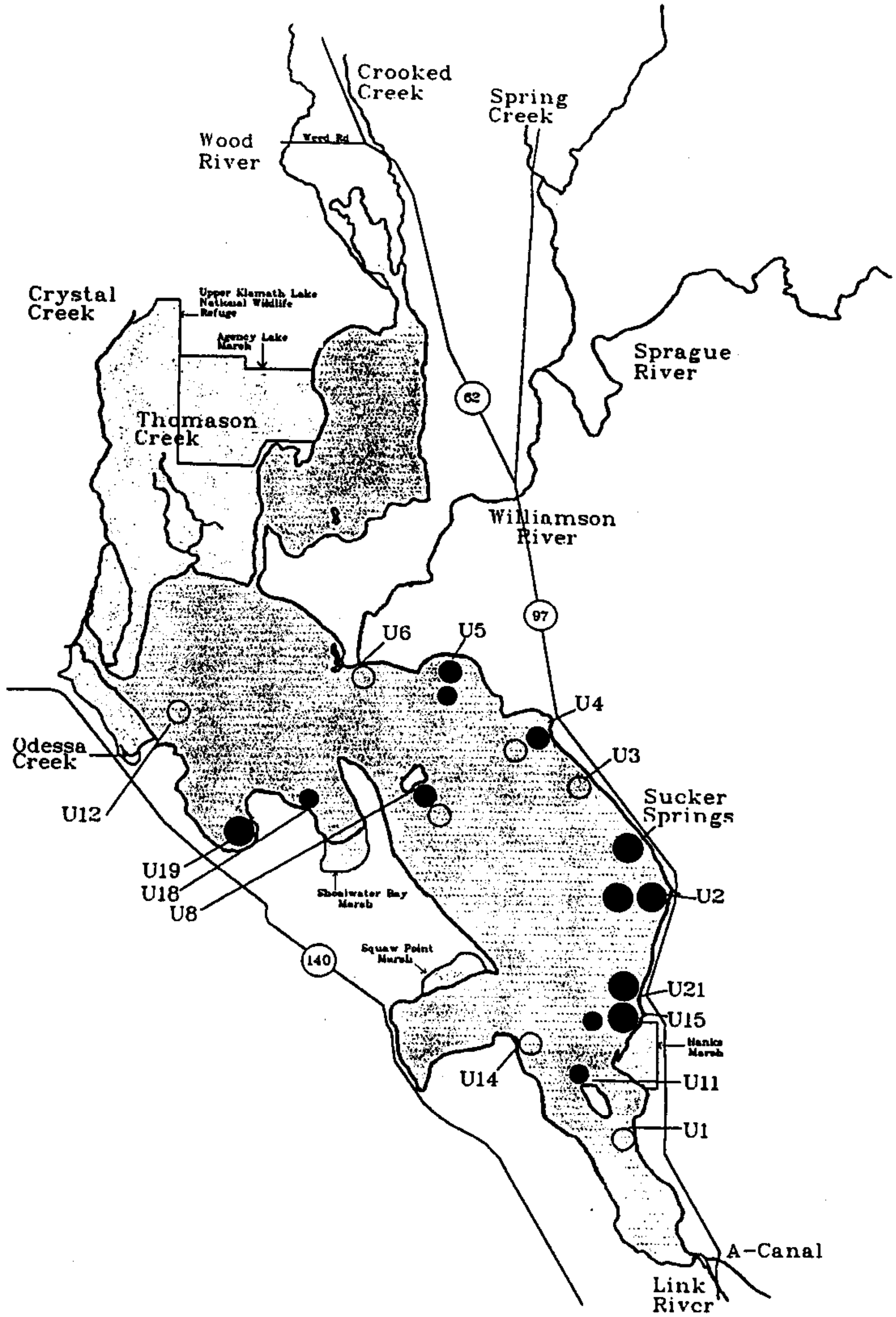


Figure 28. Age 0 Lost River sucker weighted mean density estimates (from Table 14) for each cast net station in 1991. Large solid circles=high densities (>1.00 per 10 m^2), medium solid circles=medium densities (0.20-0.99 per 10 m^2), small solid circles=low densities (<0.20 per 10 m^2), and empty circles=none captured.

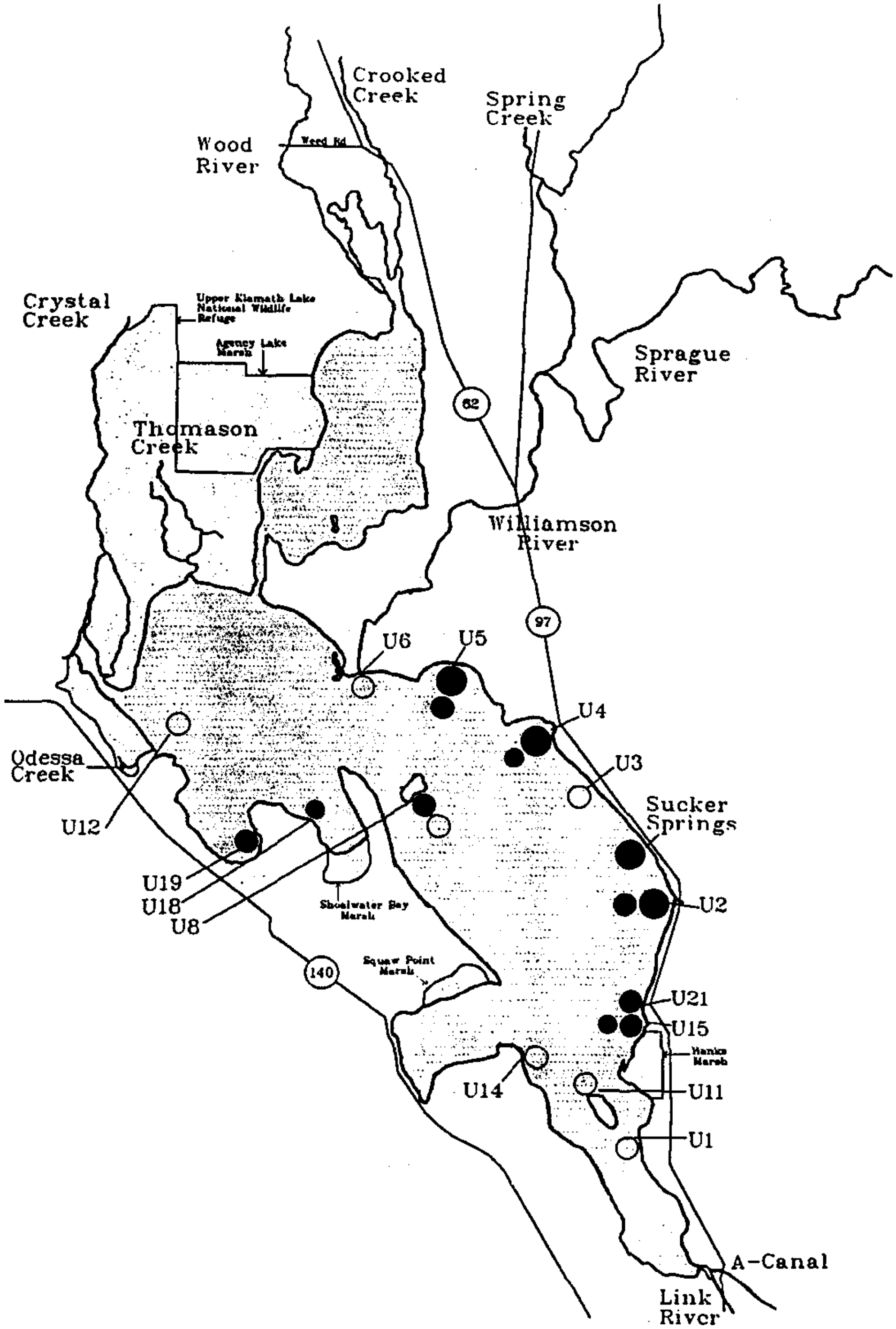


Figure 29. Age 0 shortnose sucker weighted mean density estimates (from Table 15) for each cast net station in 1991. Large solid circles=high densities (>1.00 per 10 m^2), medium solid circles=medium densities (0.20-0.99 per 10 m^2), small solid circles=low densities (<0.20 per 10 m^2); and empty circles=none captured.

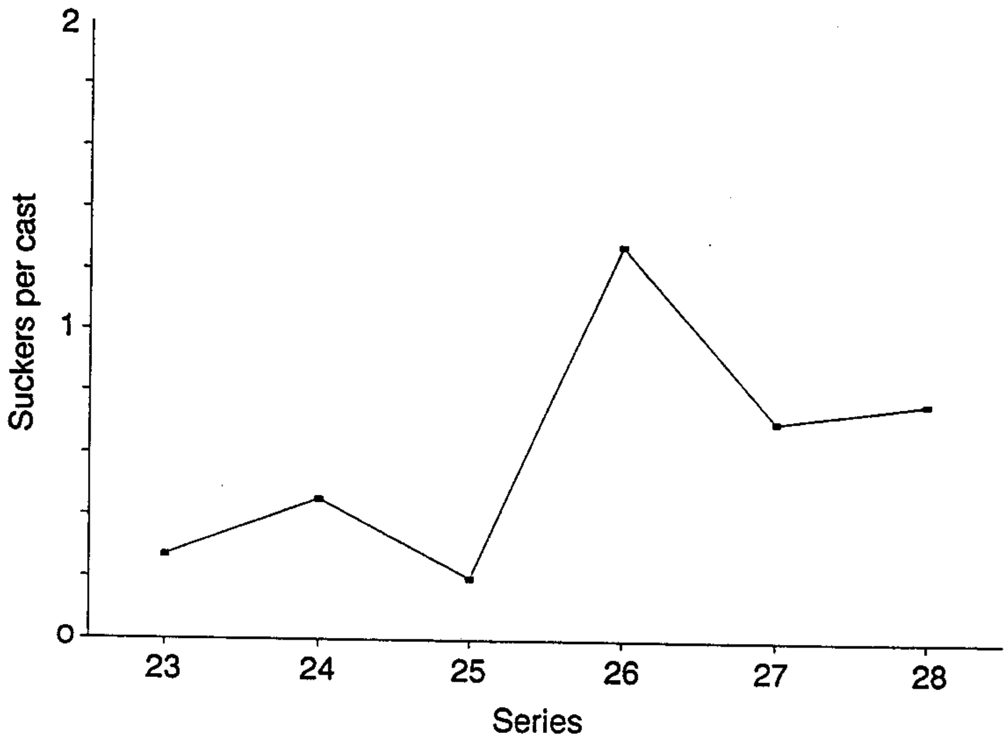


Figure 30. Mean number of suckers per cast during each series in Upper Klamath Lake, 1991.

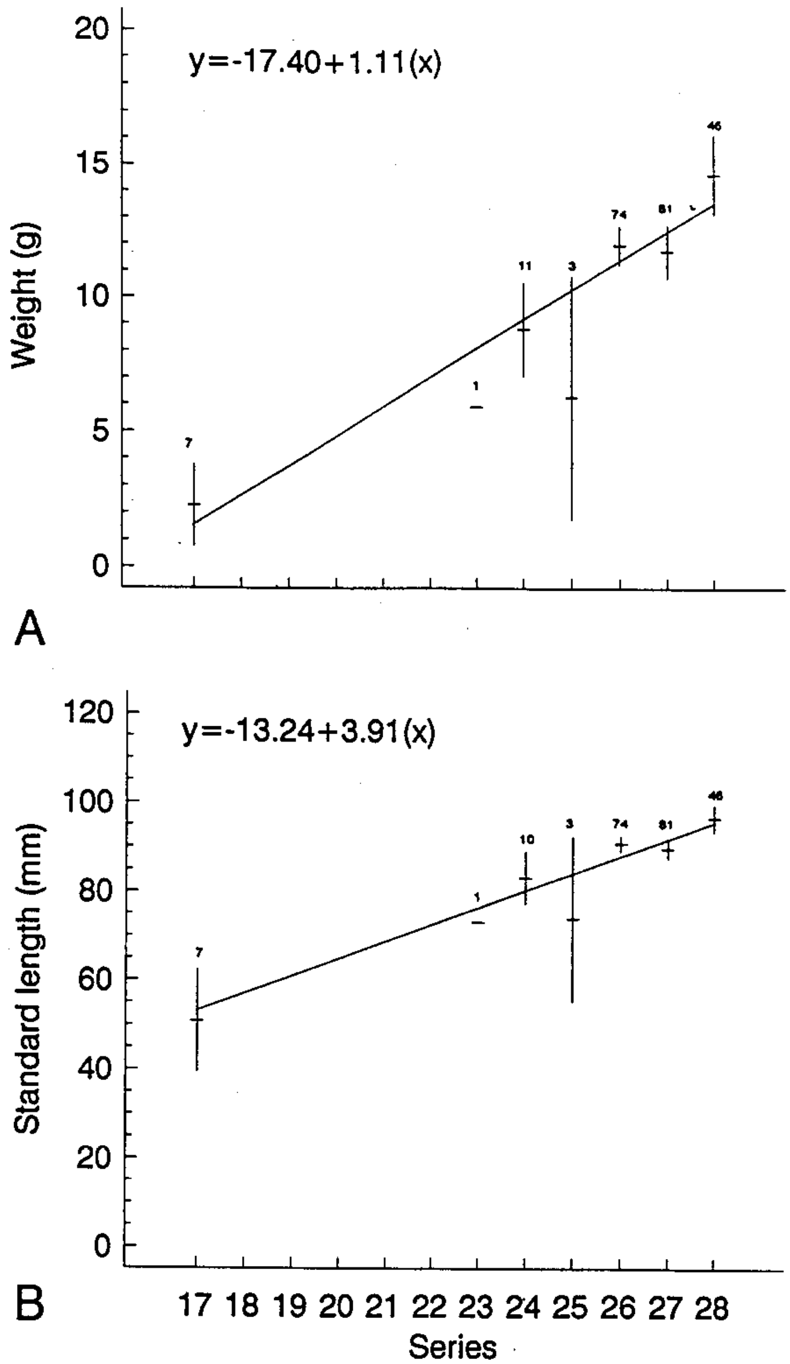


Figure 31. Mean and 95% confidence intervals by series of (A) weight and (B) standard length of age 0 Lost River suckers from cast net collections. Slope of the regression line estimates weekly growth rate. Sample sizes indicated above confidence interval bars.

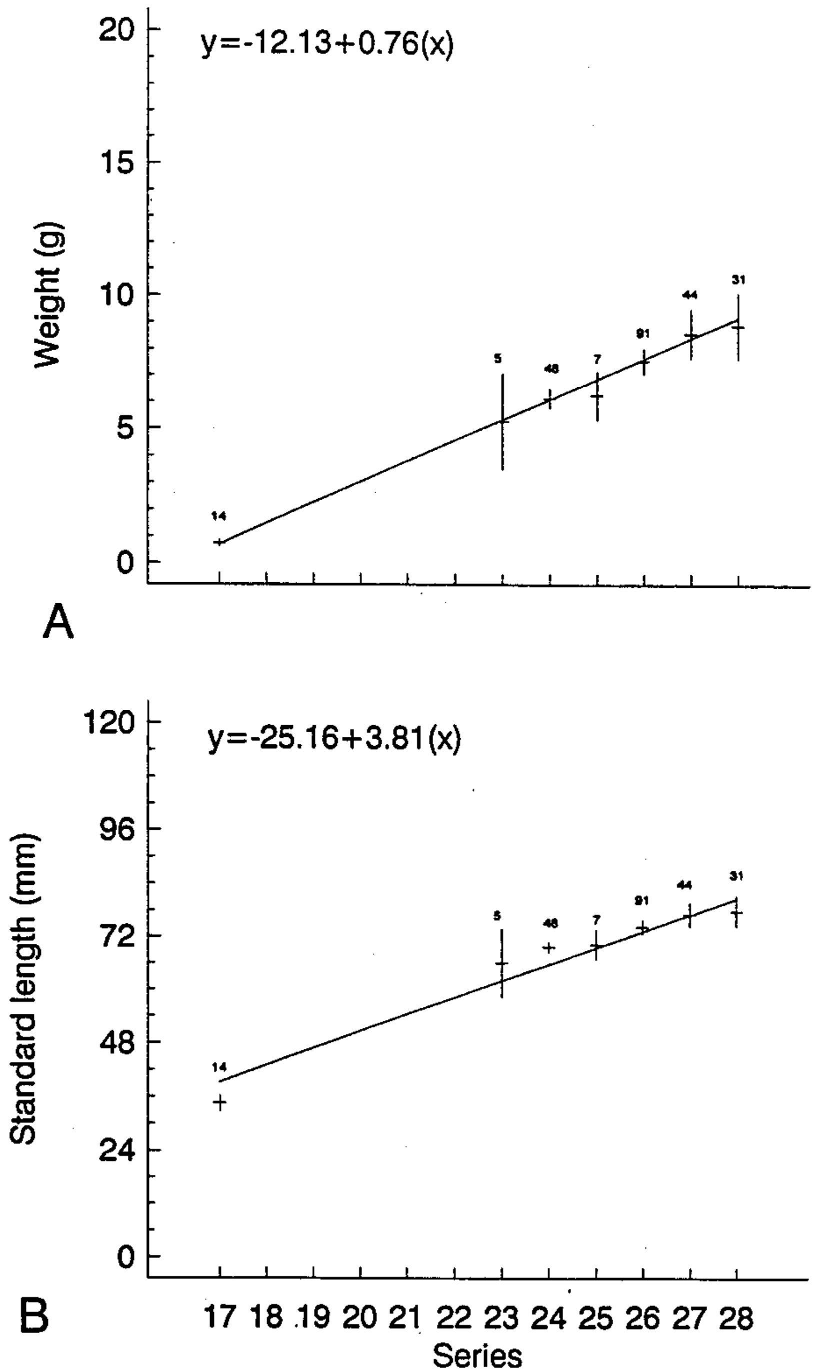


Figure 32. Mean and 95% confidence intervals by series of (A) weight and (B) standard length of age 0 shortnose suckers from cast net collections. Slope of the regression line estimates weekly growth rate. Sample sizes indicated above confidence interval bars.

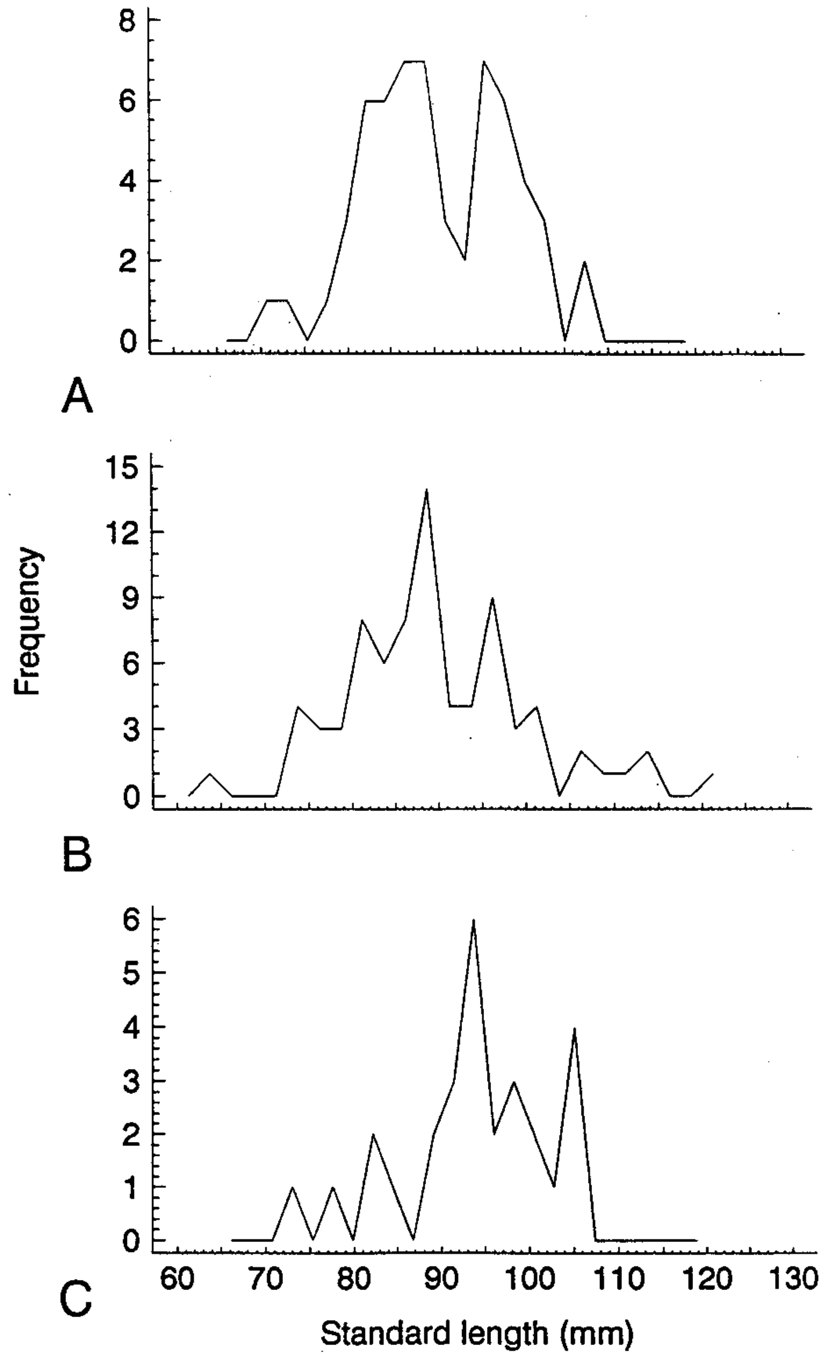


Figure 33. Length-frequency distribution of age 0 Lost River suckers from cast net collections during (A) series 26, (B) series 27, and (C) series 28. Data points are grouped by 2.3-mm groups.

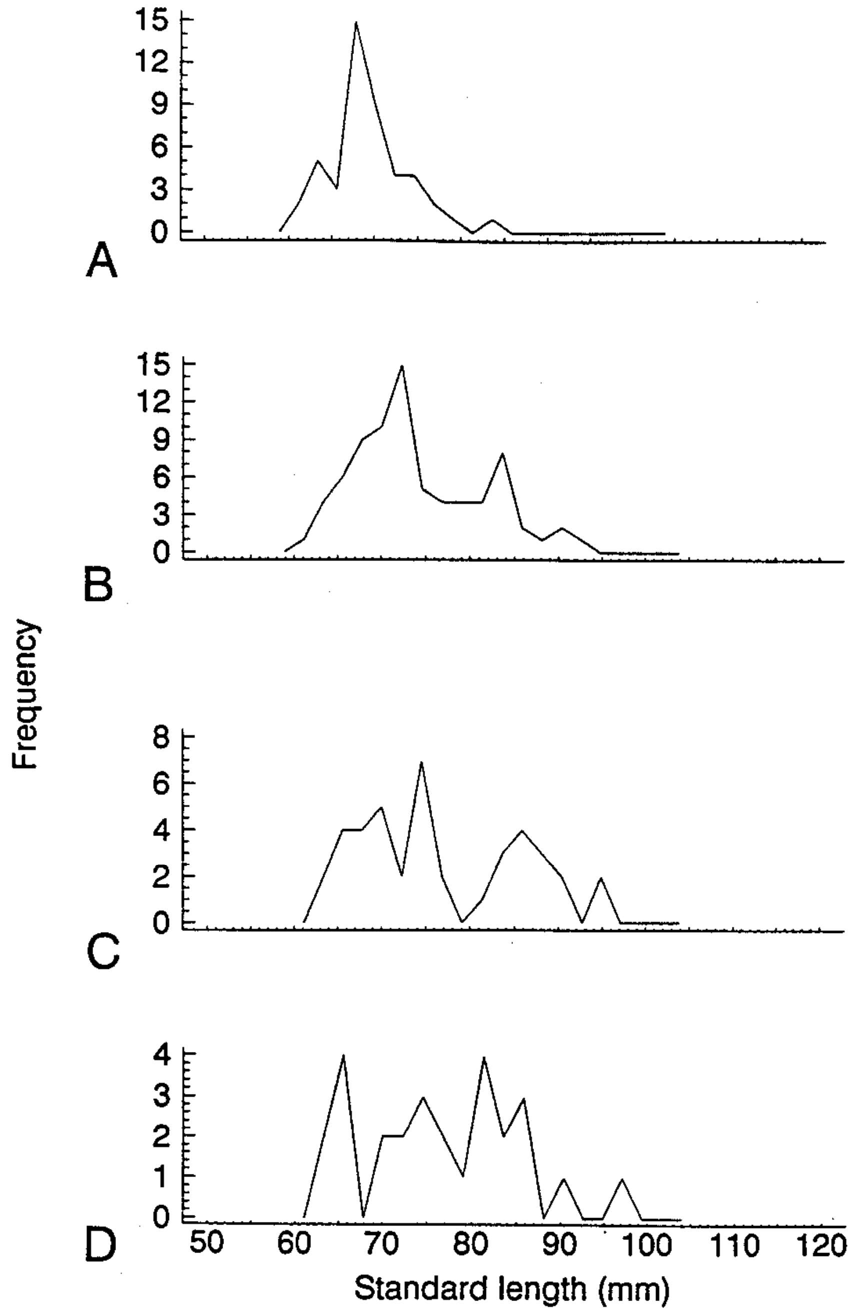


Figure 34. Length-frequency distribution of age 0 shortnose suckers from cast net collections during (A) series 24, (B) series 26, (C) series 27, and (D) series 28. Data points are grouped by 2.3-mm groups.

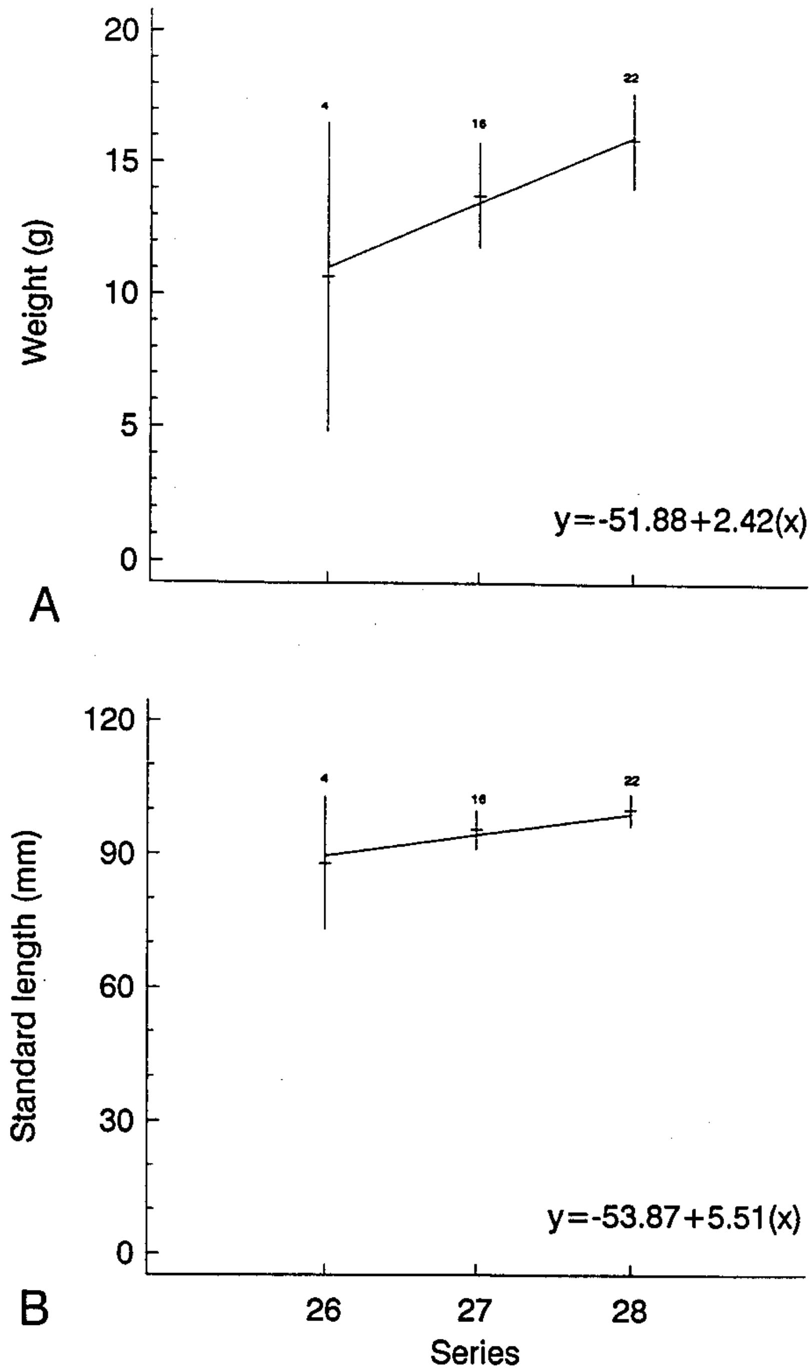


Figure 35. Mean and 95% confidence intervals by series of (A) weight and (B) standard length of age 0 Lost River suckers from trawl collections. Slope of the regression line estimates weekly growth rate. Sample sizes indicated above confidence interval bars.

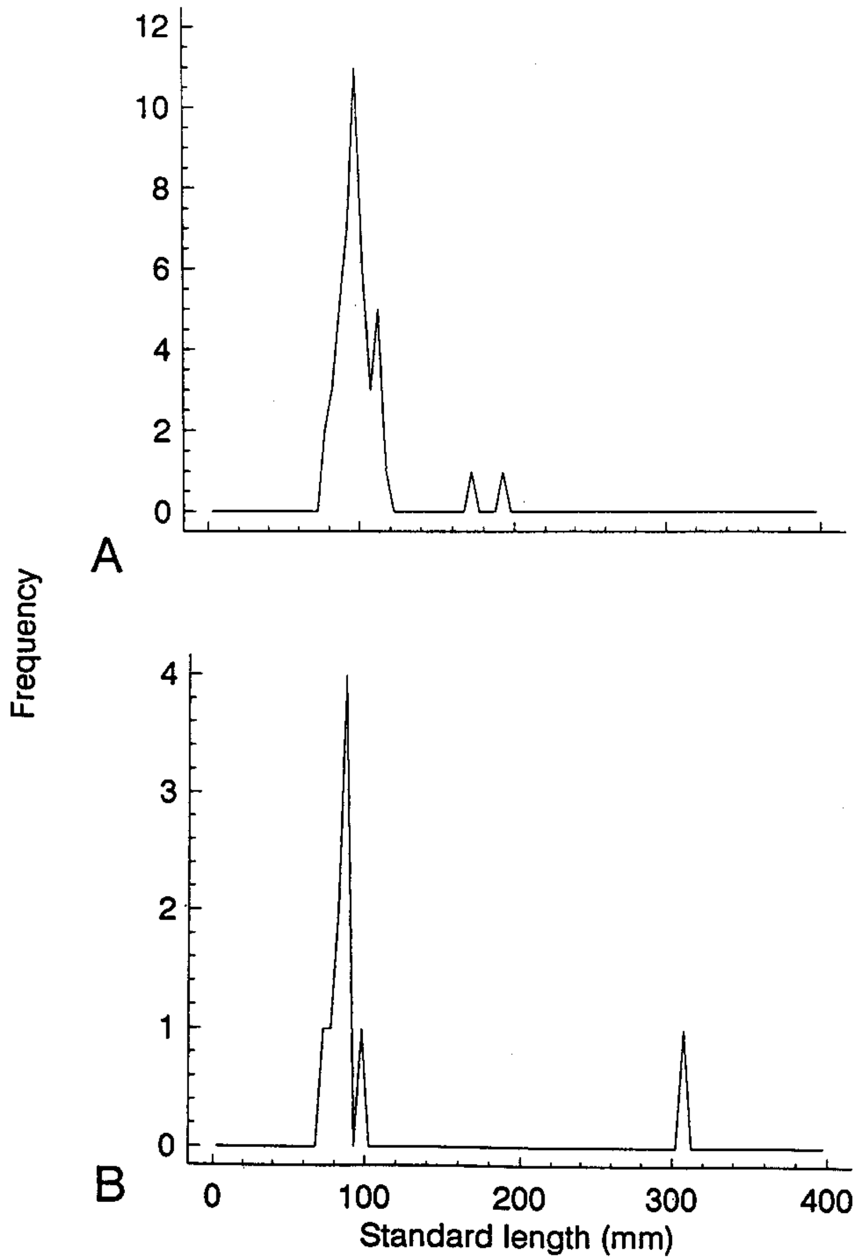


Figure 36. Length-frequency distribution of (A) Lost River and (B) shortnose suckers from trawl collections from 2 October to 17 October, 1991. Data points are grouped by 5-mm groups.

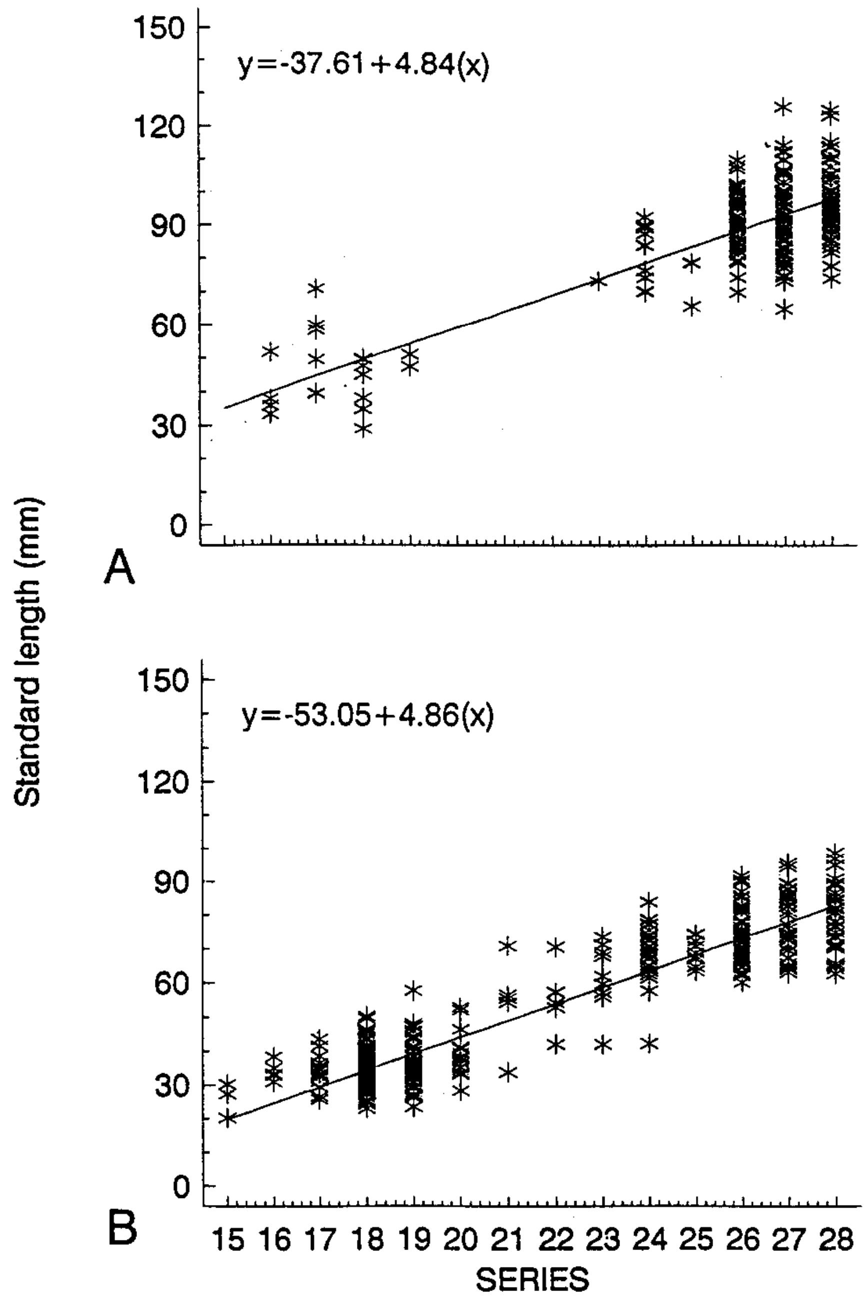


Figure 37. Regression of standard length on time for age 0 (A) Lost River suckers and (B) shortnose suckers from combined seine, cast net, and trawl collections. Slope of the regression line estimates weekly growth rate. Stars represent individual data points.

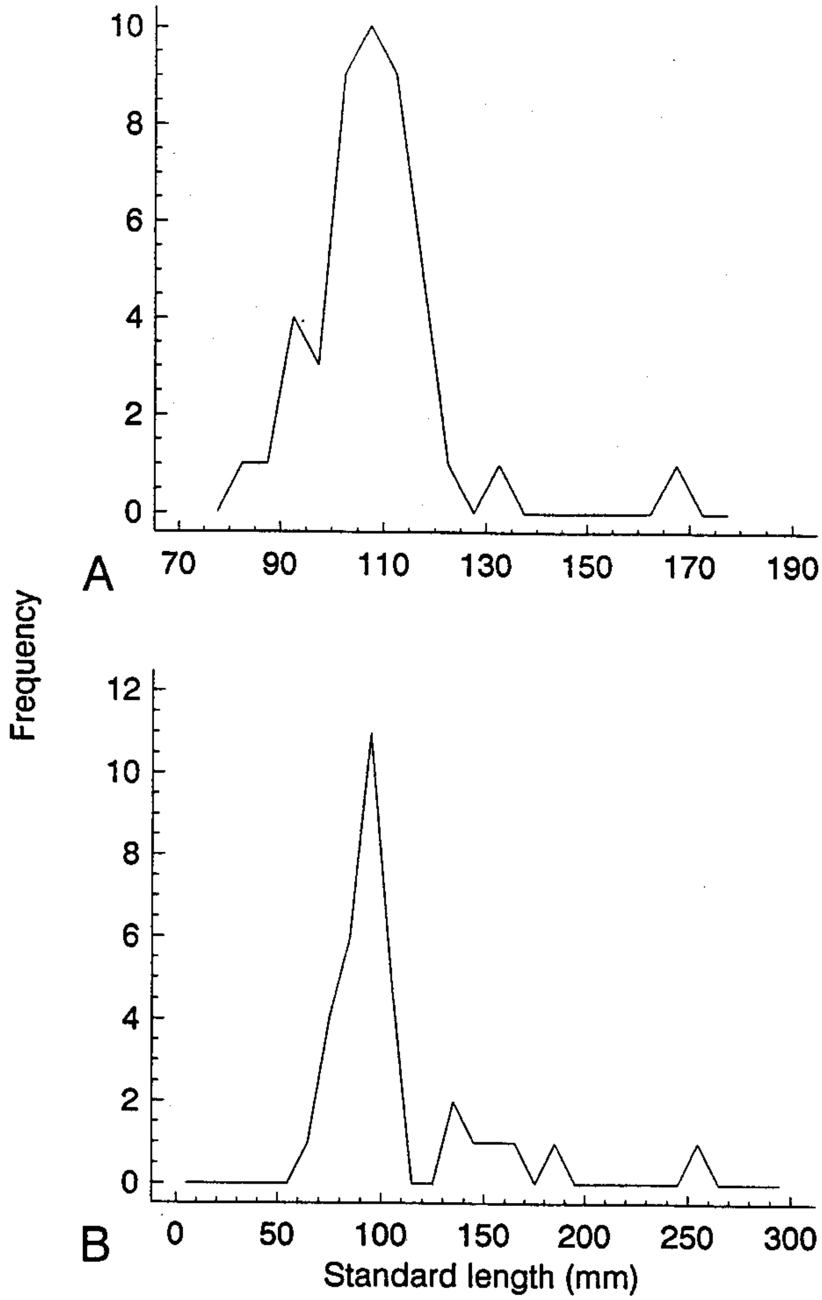


Figure 38. Length-frequency distribution of (A) Lost River suckers and (B) shortnose suckers from trap net collections in April and May, 1992. Data points are grouped by 5-mm groups. Note x-axes are different.

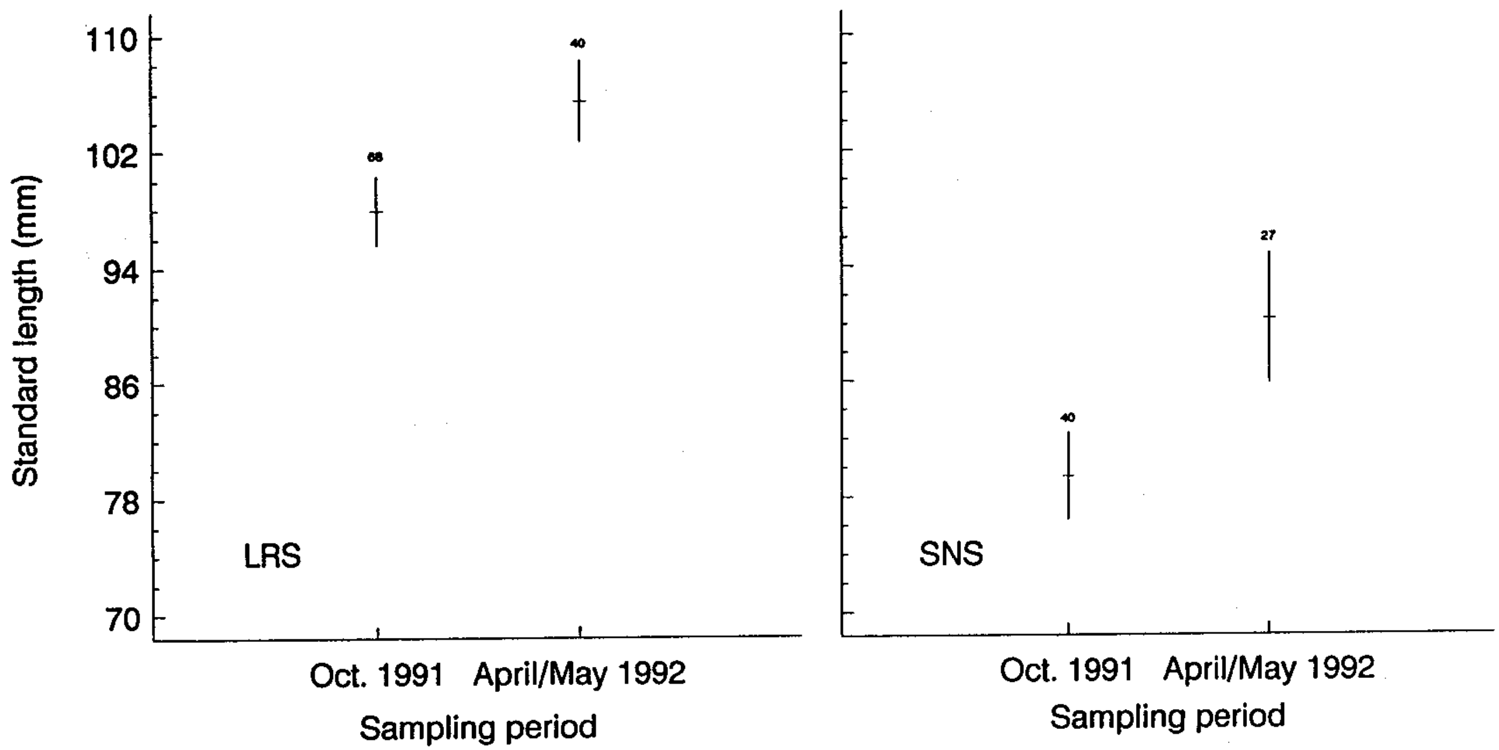


Figure 39. Mean and 95% confidence intervals of age 0 Lost River and shortnose sucker standard length from cast net and trawl collections during series 28 in 1991 and trap net collections during April and May 1992. Sample sizes indicated above confidence interval bars.

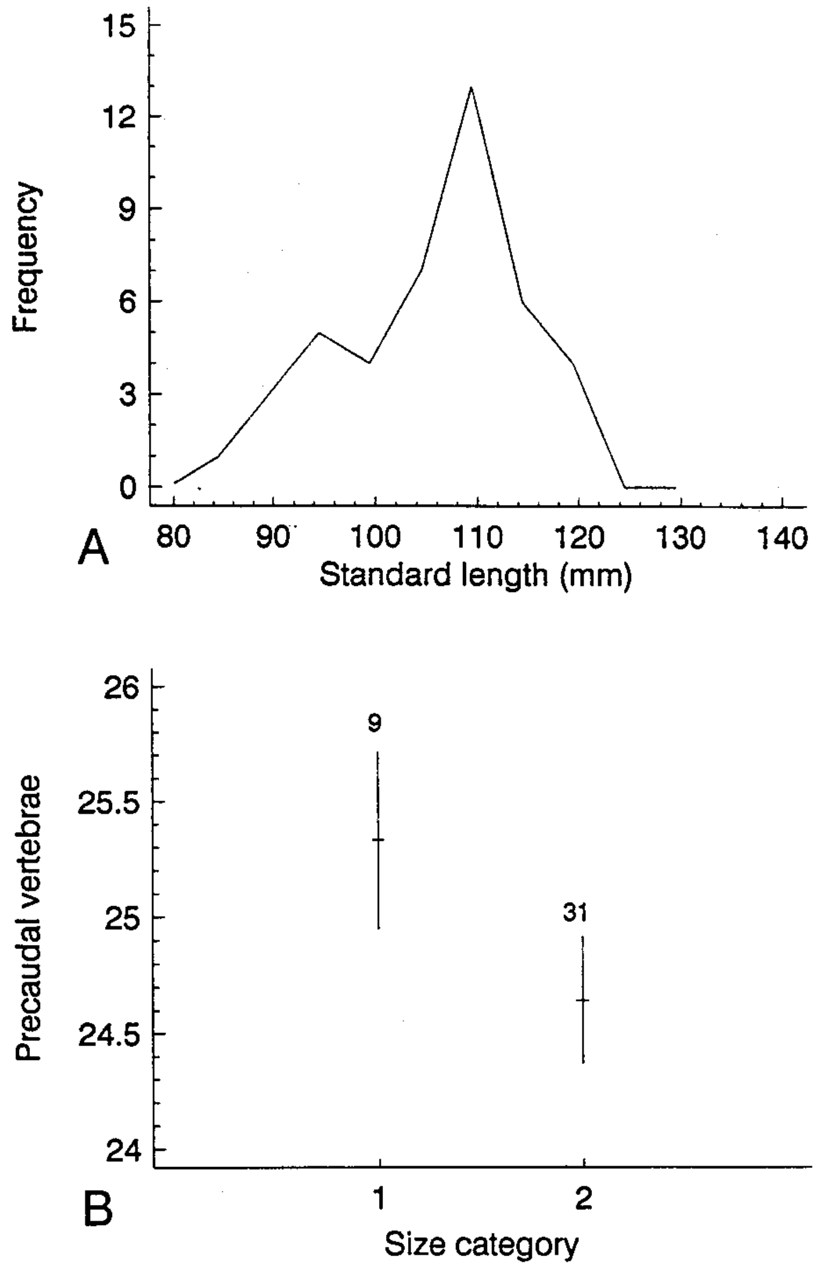


Figure 40. (A) Length-frequency distribution of age 0 Lost River suckers from trap nets in April and May 1992. Data points are grouped by 5-mm groups. (B) Mean and 95% confidence interval of number of precaudal vertebrae of the first mode (size category 1, <100 mm) and second mode (size category 2, >100 mm). Samples sizes indicated above confidence interval bars.