Exxon Valdez Oil Spill
Restoration Project Annual Report

Sockeye Salmon Overescapement

Restoration Project 95258
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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Study History: Restoration Project 95258 continues the studies initiated in 1992 with Fish/Shellfish 27 (same title), which continued until 1992. The studies continued in 1993 with Restoration Project 93002 and in 1994 Restoration Project 94258 (same title throughout).

Abstract: We continue to examine the effects of large escapements of sockeye salmon into the Kenai River, and Red and Akalura Lakes (Kodiak Island). Seasonal variability of the dominant copepod, *Cyclops columbianus*, coupled with variation in adult escapement, provides a high degree of predictability of fall fry recruitment in Skilak and Kenai Lakes. Fall fry abundance provides a high degree of predictability of adult recruitment to Kenai River. Cropping by juvenile sockeye of a cohort of *Cyclops* is hypothesized to be an important factor affecting the recruitment of juvenile sockeye from the subsequent year class. The positive relationship of spring age-1 *Cyclops* biomass to fall fry recruitment and the negative relationship of spring *Cyclops* biomass to previous year's fall fry abundance gives a plausible basis to the one year lag in the apparent compensatory response of adult returns to high escapements in 1987–1989. We further hypothesize that large year classes of sockeye salmon fry reduce *Cyclops* recruitment by decreasing the age-1 cohort. Smolt studies on Akalura and Red Lakes indicate continued poor production. Failure to meet escapement goals on Akalura Lake is of particular concern, as reduced smolt production suggests a long term decline in productivity of this lake.

Key Words: Escapement, juvenile salmon rearing, Kenai River, Kodiak Island, lake ecosystems, limnology, *Oncorhynchus nerka*, overescapement, sockeye salmon.

Project Data: Data used in the studies are stored electronically at the Alaska Department of Fish and Game area offices of each project component (Soldotna and Kodiak). Data formats are EXCEL, D:BASE (limnological data only), and ASCII. Copies of the data or specific data sets are available only upon request from the principal investigators: Dana Schmidt or Ken Tarbox, Alaska Department of Fish and Game, 34828 Kalifornsky Beach Road , Soldotna, Alaska 99669, (907) 262-9368.

Citation:
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REPORT NOTE: This is a report of studies that are in progress. All data and analyses provided are incomplete and preliminary. This report, as well as the data and analyses contained in the report, should not be cited without an express statement of the incomplete and preliminary nature of the information.

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contained less fat that Tustumena Lake fry. Vertical bars are standard errors of the least squares means.

EXECUTIVE SUMMARY

This status report is the sixth in a series describing studies conducted on the production of sockeye salmon from selected major rearing lakes impacted by the Exxon *Valdez* oil spill.

Kenai River Studies

This year's investigation examined the limnological evidence for the relationship of zooplankton to the recruitment of fall sockeye salmon fry in Skilak and Kenai Lakes. Our analyses suggested that much of the variability in fall fry abundance can be attributed to spring biomass of the dominant copepod, *Cyclops columbianus*. Assessment of length frequency distributions strongly indicates a two year life cycle of this zooplankton species. Survivors from the age-0 cohort in the spring strongly influence recruitment of the next generation of juvenile sockeye salmon. This creates an interaction between adjacent sockeye salmon year classes. Further, spring *Cyclops* survivors provide the reproductive potential for the next generation. Hence additional density dependent effects may be observed in the recruitment of *Cyclops*, providing for the potential of an additional two year lag in the response of the recruitment rate of salmon to top-down control from earlier cohorts of sockeye salmon juveniles. This feature of the life history of *Cyclops* coupled with the typical five year life history of sockeye salmon in the Kenai River glacial lakes may create a response in the population one to two years after the initial impact of large escapements on the zooplankton community. This should manifest itself in decreased production in the 1996 adult sockeye salmon return from the 1991 brood year. The poor recruitment anticipated from the 1991 year-class has a positive value, however, on the 1997 adult return, which will be predominantly from the 1992 brood year. Three years of poor recruitment should result in minimal brood year interaction (1991 and 1992) and the modest 1990 escapement should minimize impacts of large escapements on the recruitment of *Cyclops* in 1992. These combined effects should result in a relatively large return of adult sockeye salmon in 1997. This model suggests that production patterns of the 1987, 1992, and 1997 year classes are indicative of the development of cyclic dominance in Kenai River sockeye salmon. This study is probably unique in determining the probable biological basis of these cycles in glacial lakes.

Predictions of adult sockeye salmon returns from fall fry have been quite reliable, although only six years of data are currently available. However, the 1987 brood year produced an above average return (based on a linear model) which suggests a depensatory relationship between fall fry and adults. This observation is counter to what we would predict from decreased size of fall fry and the limited data that we have on decreased fall to spring fry survival. Because the single data point for 1987 is driving this relationship, we require the 1996 and 1997 adult returns to determine if the relationship holds. Consequently, we recommend continued monitoring of fall and spring fry in Skilak and Kenai lakes through 1997 and continued monitoring of seasonal variation of copepods.

These data have been used to assess the biological escapement goal for the Kenai River and were used in the Board of Fisheries process during January 1996. The key to restoration of Kenai River sockeye salmon involves understanding the recruitment process and density related affects

of sockeye salmon escapements on the ecosystem of the major rearing lakes. Determining the costs and benefits of large escapements is essential for managers and public policy makers to respond intelligently to fisheries closures caused by oil spills or other factors. Concluding these studies by resolving the importance of management actions in regulating sockeye salmon population cycles is an important legacy that the EVOS studies can contribute, not only to the Kenai River population, but by providing an understanding of the proper role of fisheries management in maintaining sustained yields in other sockeye salmon stocks throughout the Pacific Northwest.

Kodiak Island Studies

Smolt studies from Red Lake indicated poor sockeye salmon smolt production (341,490), about 48% below the 1990 to 1994 average. Limnological data did not indicate the reason for the lowered smolt numbers. Adult return analysis suggested that smolt traps (mark-recapture estimates) provided a negative bias prior to 1992 and that run reconstruction may have problems with catch assignment. The 1996 run forecast is 722,000 fish.

In 1995 smolt migration from Akalura Lake was an estimated 134,000. Smolt length and weight estimates are both below the values observed in 1994. Adult escapement in 1995 was 2,010 (early and late runs combined), far below the escapement goal of 40,000 fish. The escapement failure was not a function of harvests, given run reconstruction estimates of the effects of harvest, although harvest rates were most likely similar to Upper Station Lake. Smolt production failure is the most likely cause, given the weak production from the 1990 and 1991 brood years.

Frazer Lake, which is being used as a reference for these nearby systems, produced over 8 million smolt in 1995, the second largest smolt count since 1991.

INTRODUCTION

Following the Exxon *Valdez* oil spill (EVOS) in 1989, the presence of oil in the waters of traditional fishing areas in the Gulf of Alaska resulted in the closure of many commercial fisheries. This closure resulted in escapement of large numbers of sockeye salmon (*Oncorhynchus nerka*) into some systems. EVOS funded investigations of the impact of large escapements on future production were initiated in 1990. Specifically, these investigations assessed impacts on the production and ecology of major sockeye salmon rearing lakes on Kodiak Island and the Kenai Peninsula (Figures 1 and 2).

In the Kodiak Island area, Red Lake sockeye salmon escapement was 768,000 in 1989, more than twice the management goal of 200,000 to 300,000. At Akalura Lake, the escapement was 116,000, about twice the 40,000 to 60,000 goal. However, not all systems received higher-than-average escapements. For example, nearby Upper Station Lake had a 286,000 escapement, which is reasonably close to the 200,000 to 275,000 goal.

The Kenai Peninsula in South-central Alaska contains several major glacial lakes that have produced large runs of sockeye salmon over the past decade. From 1987 to 1989, escapements of adults into the Kenai River system were approximately double those of previous years, and double the Alaska Department of Fish and Game's management goal of 550,000 (Figure 3). However, escapement into the Kasilof River from 1987 to 1989 averaged about 195,000, which is within the escapement goal range of 125,000 to 225,000 (Figure 4).

The first three years of study (1990 to 1992) were designed to characterize the population parameters of sockeye salmon smolts resulting from escapements before and during 1989, when oil on the fishing grounds curtailed fishing. Smolt sizes, ages, and numbers reflect the density-dependent effects of escapements consistent with established goals, and thus help to establish pre-impact conditions. The limnological assessment characterized the conditions during the initial impact of large numbers of rearing fish and the effects of large nutrient additions to the lakes from salmon carcasses. Because high densities of planktivorous fish can exert top-down control over lower trophic levels, measurable ecosystem changes within the affected lakes were expected to occur. For example, major forage items within the zooplankton community may be reduced or eliminated, prey item body-sizes may be reduced, and preferred food items may be replaced by forms resistant to predation. Kyle et al. (1988) found that large sockeye escapements into Frazer Lake on Kodiak Island resulted in subsequent reductions in smolt size that was correlated with a depressed zooplankton community. The resulting reduction in the number of migrating smolt may foretell a significant reduction in the commercial, sport, and subsistence harvests on affected stocks of salmon in Cook Inlet and on Kodiak Island.

Investigations on the Kenai River system have examined in much more detail the effects of seasonal changes of the zooplankton population on the recruitment of fall fry into the system. These data have been interpreted with respect to trends observed in adult spawner-recruit data. We have used these new insights to develop a hypothesis describing the processes that regulate

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adult returns to the Kenai system. Understanding these processes is the key to restoration of Kenai River sockeye salmon populations and the future management of this system.

OBJECTIVES

The following objectives of this study were developed to assess impacts of large escapements on the production of sockeye salmon. The term "overescapement" has lead to misunderstandings of study objectives in the past. Overescapement has been defined as allowing an excess of fish to spawn in a river system, beyond the range or target value previously established by the management agency to provide for maximum sustained yield. Since failure of the management system to regulate escapements in 1989 was a consequence of the EVOS, these investigations were initiated to define what effect, either positive or negative, large escapements would have on subsequent production of sockeye salmon. The following objectives were defined in the initial stages of this project to address potential impacts of EVOS and to suggest restoration and harvest regulation strategies in the event of future fisheries closures.

Study objectives:

1. Measure critical biological attributes (number, age, and size) of juvenile sockeye salmon in nursery lakes on the Kenai Peninsula and Kodiak Island.

2. Determine effects on smolt production and subsequent adult returns of large escapements resulting from fishery closures after the EVOS. These effects will be inferred by studying changes in the rearing capacity of selected nursery lakes which were either affected or unaffected by the oil spill. Data used for these studies include:

   (a) abundance, age, and growth of sockeye salmon juveniles and smolt;
   (b) nutrient budgets, plankton populations, and other physical and chemical parameters; and
   (c) sockeye salmon adult recruitment data.

This report provides observations and some analytically derived conclusions as to changes and resulting impacts that have occurred in biological, physical, and chemical properties. We also provide analyses of some of these data with the intent to demonstrate our current understanding of ecosystem related processes that effect sockeye salmon production in the Kenai River.

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METHODS

Adult Sockeye Salmon Assessment

Escapements of sockeye salmon were estimated by weirs at Red, Upper Station, and Akalura lakes. Escapement into the Kenai and Kasilof rivers was estimated by sonar counters using fish wheels for capturing samples of the escapement for species apportionment, sex ratios, and size data (King and Tarbox 1991). Potential egg deposition (PED) was defined as 3500 times the estimated abundance of female spawners. Spawners in the Kenai River were estimated from the sonar counts minus the estimated sport fishing harvests above the counting sites. Kasilof River sport fishing harvests were considered negligible; therefore sonar counts are considered equal to spawners. Kenai River spawner estimates were further adjusted by removing escapement estimates from the Russian River and Hidden Lake (weir counts). Adult scales were collected for age analysis from the fishery and fish collection devices near the sites where escapements were enumerated.

An analysis of Kenai River spawner-recruit (S-R) data was conducted to determine the status of adult production subsequent to the first overescapement event in 1987. The analysis consisted of an attempt to fit compensatory, depensatory, and density independent models to the S-R data using methods described in Hilborn and Walters (1992). This was followed by an assessment of recruitment rate (recruit-per-spawner) data using statistical process control methods (Grant and Leavenworth 1974).

Juvenile Sockeye Salmon Assessment

For each of the three lake studies on the Kenai Peninsula, and from three lakes on Kodiak Island, the abundance, size, and freshwater age of juveniles from the 1989 escapement were estimated using hydroacoustic surveys and tow net sampling. The tow net sampling was conducted to determine species composition and to collect specimens for size and age data. Fish lengths and weights were measured after preservation in 10% formalin. Occasionally, frozen or unpreserved fish were measured.

Since 1992, hydroacoustic surveys were conducted only on the Kenai Peninsula lakes. Detailed survey methods are documented for the Kenai River lakes in Tarbox and King (1992), for Tustumena Lake in Kyle (1992), and for the Kodiak Island lakes in Honnold (1993). Freshwater growth and age of juvenile sockeye salmon from all study systems were determined from scale and otolith measurements made either by direct visual analysis of scales or for otoliths with an optical pattern recognition system.

Tow net sampling at alternative depth strata using a closing net system designed by Biosonics Inc. was deployed in the summer and fall of 1993 and throughout the season in 1994 and 1995. These data provided size and age data at different depths and areas and were used to provide stratified sampling estimates in addition to the usual surface tows. Fry were also collected in Skilak and Tustumena lakes from 1992 to 1995 and analyzed for lipid content; in the current

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report we present analyses of lipid data obtained from August, 1993 to April, 1994. Lipid content analyses were conducted by the University of Alaska Palmer Laboratory using methods described by Randall (1974).

Sockeye Salmon Smolt Enumeration

The total number (with 95% confidence intervals) of sockeye salmon smolt migrating from each of the lake systems in 1990 to 1995 was estimated by a mark-recapture technique (Rawson 1984). Estimated size and age of sockeye salmon smolts was compared by brood year. Smolt were collected from traps of various designs. At weekly intervals, a sample of fish was marked with Bismark Brown dye and released upstream. Recovery rates of the dyed fish were used to estimate trap efficiency. The efficiency rate was then applied to estimate the total smolt migration. Methods deviated slightly each year but specific details of sampling are available in Barrett et al. (1993a) for the Kodiak lakes, in King et al. (1991, 1994a) for the Kenai River, and in Kyle (1992) for the Kasilof River. King et al. (1994b) describe the procedures used to estimate smolt abundance in the years prior to 1993. Subsamples of smolts from Kodiak Island were stored frozen and sent to the University of Alaska in Fairbanks to determine the relative levels of marine versus terrestrial nitrogen from selected Kodiak Island systems. These samples were taken to determine the effects of carcass nutrient additions in maintaining the productivity of Red Lake. The Kenai River smolt program was discontinued in 1994 (King et al. 1996).

Limnological Studies

Limnological sampling has been conducted in Tustumena Lake at three stations since 1981. Two stations were sampled from Skilak and Kenai lakes from 1986 to 1989, and beginning in 1990 three stations were used to collect limnological parameters. Zooplankton data were collected from Skilak Lake at five stations in 1990, 10 stations in 1991, and three stations in 1992 to 1995. Zooplankton samples from Kenai Lake were collected at three stations from 1990 to 1995. Limnological data were collected from three stations in Red Lake, two stations in Akalura Lake, and two stations in Upper Station Lake. Samples were collected at about three week intervals on each lake during May to October. Study site locations, sampling dates, physical, chemical and biological parameters, and data summaries are provided in Appendix A of Schmidt and Tarbox (1993). Water nutrients and basic physical parameters, chlorophyll a, and zooplankton samples were analyzed at the State of Alaska's Limnology Laboratory located in Soldotna. Analytical procedures followed standardized laboratory and quality assurance methods (Koenings et al. 1987). In cases where data from prior years were available, limnological parameters during residence of juveniles from the 1989 escapement were compared to parameters during prior years.

To collect quantitative data representative of the vertical distribution of the zooplankton community, a closing zooplankton net was utilized. The net is constructed of 153-μ Nitex mesh with a 0.5-m stainless steel ring at the mouth and a 200-ml collection bucket. Essentially, this netting procedure is identical to the methods used for collecting water column zooplankton samples used for biomass estimates. The net is vertically lowered to the desired depth as measured with a tow line marked in 1-m increments. After vertically retrieving a 5 m or 10 m tow, the line is sharply pulled triggering the release of a closure mechanism at the opening of the net. Triggering this mechanism causes the net to fold over on itself stopping any further collection of zooplankton. After the collection bucket is thoroughly rinsed with distilled water, the release mechanism is reset and the net lowered to the depth at which collection had previously been halted and the process is repeated.

RESULTS AND DISCUSSION

Kenai River System Investigations

Adult Returns and Escapement

Adult returns during 1995 (primarily from brood-year 1990) were relatively low for the Kenai River system despite statewide record or near record harvests of sockeye salmon (Figure 5). Recruit-per-spawner trends from the Kenai River were evaluated to determine if the most recent runs reflected a statistically defined departure from the historic patterns (Figure 6). Recruitment rate from the 1988 to 1990 brood years were clearly anomalous, suggesting that a pattern of decreased production has been established. Despite this recent pattern, an investigation of the spawner-recruit relationship showed that a density independent model best describes the data and that recent trends do not substantially affect the relationship (Personal comm., S. Carlson and D. Schmidt 1995, Soldotna, AK).

Fry and Smolt Investigations

The smolt program was terminated in 1994 in the Kenai River and summaries of findings were provided in previous reports. We evaluated the relationship between fall fry abundance and PED of female spawners in the Skilak/Kenai lake system from 1985 to 1995 (Figure 7). Note that the relationships, which is a density independent (linear) model, although statistically significant ($P = 0.03$), is not particularly strong ($r^2 = 0.48$).

In the Kasilof River, escapement and smolt production continued the pattern observed in 1994 (Table 1). Age-1 smolt remained the dominant migrant from the Kasilof River (Table 2). The smolt lengths in 1995 remained approximately the same size as observed in 1994 (Table 3).

Juvenile sockeye salmon production within Kenai and Skilak lakes as reflected by mainstem spawners and fall fry abundance is shown in Figure 8.

Mean length and weight of fall fry from Skilak, Kenai, and Tustumena lakes are presented in Table 4. Fall fry in Skilak Lake and Kenai Lake are generally smaller than in Tustumena Lake. Figure 9 illustrates the relationship between mean fall fry weight and estimated mainstem spawner abundance and fall fry abundance for Skilak Lake. Figure 10 shows a comparison of percent lipid content of fry collected in Tustumena and Skilak lakes from August, 1993 to April, 1994. Overall, Tustumena Lake fry contained significantly more fat than Skilak Lake fry ($P < 0.001$). Tustumena Lake fry also exhibited a consistent pattern of decreasing fat content with the most loss occurring over winter (November to April). Skilak Lake fry, on the other hand, exhibited little or no change in lipid content over time, a pattern that may be indicative of fall to winter and over-winter mortality. Figure 11 presents a comparison of the relationship between wet weight and percent fat of Tustumena Lake and Skilak Lake fry for the August, 1993 to April, 1994 sampling periods. No significant relationship ($P > 0.05$) was found between wet weight and fat content for Tustumena Lake fry. However, Skilak Lake fry exhibited a significant

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positive relationship which became less pronounced over time; this is suggestive of competitive interactions that became less important in winter and spring, possibly due to mortality.

Limnological Studies

Figure 12 illustrates the trend in biomass of the two dominant copepod species in Skilak Lake from 1986 to 1995. We observed an increase in relative copepod biomass (mg fry^{-1}) in Tustumena Lake in 1993 and 1994, exceeding Skilak Lake for the first time since 1986 (Table 5), which also corresponded to an increase in fall fry wet weight (Table 4). A comparison of Tustumena and Skilak lakes in the relationship between fall fry weight and relative copepod biomass is shown in Figure 13. Tustumena Lake exhibited a significantly steeper slope than Skilak Lake ($P = 0.008$) indicating a differential response to the availability of copepod prey between the two lakes.

We have further examined the seasonal abundance of zooplankton in Skilak Lake. The lack of a significant trend ($P > 0.05$) in the copepod data (Figure 12), despite large variations in fall fry abundance (Figure 8), suggests that major changes have occurred in the recruitment of fry to the pelagic zone of the lake. Consequently, examination of the seasonal changes in abundance of zooplankton in these lakes may suggest some relationship to the observed variability in recruitment.

Figure 14 illustrates the seasonal changes in mean length of *Cyclops* and *Diaptomus* during 1994 in Skilak Lake. The change in mean length in July and the striking difference in the size of ovigerous *Cyclops* compared to the entire population suggests that multiple cohorts were present. Figure 15 illustrates the length frequency distribution of *Cyclops* observed throughout the summer in 1994, clearly indicating the presence of two age-class cohorts beginning in July. The mean length of ovigerous *Cyclops* essentially duplicates that of the larger cohort and that the May and June lengths indicates that only *Cyclops* held over from the previous fall (Figures 15 and 16). These data clearly indicated that this species has a two year life cycle with no individuals reaching sexual maturity during the first summer and very few surviving to the third year.

The temporal variation in *Cyclops* biomass was examined in more detail. Seasonal biomass was estimated as the mean of all dates sampled from Stations A and C, during May and June (spring), July and August (summer), and September and October (fall). These dates correspond to the relative changes in cohort dominance illustrated in Figure 15. Samples taken in November and December showed marked decrease in abundance and biomass indicating that the zooplankton were not available to the sampling gear. This decrease most likely reflects dispersion into deeper areas of the lake as a result of winter diapause. The seasonal biomass of *Cyclops* is quite variable (Figure 17), compared to the lack of variability illustrated by seasonal means (Figure 12). Two major factors may contribute to this variability. Spring abundance of *Cyclops* is a result of midsummer recruitment from the previous year and cropping (by fry) during late summer and fall. Fall biomass reasonably reflects spring biomass, suggesting that overwinter mortality is most likely minimal (Figure 18).

To examine the importance of seasonal variability of these prey items, we analyzed variation in fall fry abundance as a function of seasonal *Cyclops* abundance and brood year mainstem spawner abundance using stepwise multiple regression (Table 6, Figures 19 and 20). Besides mainstem spawners, Spring *Cyclops* biomass was a highly significant variable in the model. Including summer *Cyclops* biomass further improved the ability to predict fall fry abundance (Table 6). Because spring *Cyclops* abundance is affected by the previous year's fall sockeye salmon fry, we would expect an interaction between adjacent year classes to affect recruitment. This interaction also corresponds to the lag observed in the response of recent year's recruit per spawner values to high escapements in the late 1980's.

Discussion

The 1995 investigations have provided insight into the trophic interactions of glacial lake ecosystems. These studies were developed upon premises established by investigations on clear water systems (Kyle et al. 1988), particularly Frazer Lake on Kodiak Island. Large escapements provide top down controls on the zooplankton population, particularly the cladoceran component. This resulted in large decreases in juvenile salmon recruitment and was expressed by very low adult returns from the affected brood years. These effects have been observed to continue beyond the immediate year (Koenings and Kyle 1996) and is associated with a failure of the zooplankton population to recover. In the glacial systems on the Kenai River, previous evaluations (Schmidt and Tarbox 1993; 1995; 1996) have not suggested a limnological basis for the variation in fall fry abundance observed in the lake. Nutrients, temperature, turbidity, and mean annual zooplankton biomass have been examined as a potential cause, but only adult escapements provided a significant relationship with fall fry mean weight and abundance. Although we examined the response of zooplankton mean length to potential cropping effects early in these studies (Schmidt and Tarbox 1993), the apparent lack of response in seasonal changes in size suggested that cropping effects were either not related to size or were masked by growth. A re-evaluation of the length frequency data by season provides definitive evidence that the species of *Cyclops* in Kenai and Skilak lakes, *Cyclops columbianus* Lindberg, 1956 (Personal Comm., Janet Reid, Smithsonian Institute, Washington DC) has a multiple year life cycle. (Note that this species is very closely related *Cyclops scutifer* (Reed 1963) whose life history has been defined as encompassing multiple years in certain environments (Elgmork, 1981;1985). This species has a fecundity of 20 to 40 eggs per female with little or no survival beyond the second year of life and sexual maturity being reached only during the second summer (Figures 15 and 16). Consequently, the reproductive capacity of this species is extremely limited and we would expect high predation rates to adversely affect future recruitment. Since recruitment does not occur until mid-July, juvenile sockeye salmon are dependent upon survivors from the previous year's cohort of *Cyclops*. The other common copepod, *Diaptomus pribilofensis*, Juday and Muttkowsky, (Personal Comm. T.E. Bowman, Smithsonian Institute, Washington, DC) has an annual life cycle with recruitment occurring somewhat earlier than *Cyclops*. Spring stomach samples from pre-smolt sockeye salmon (Schmidt and Tarbox 1995) indicated age-1 *Cyclops* were exclusively the preferred diet. Figure 17 illustrates the high degree of seasonal and interannual variability of *Cyclops*. This variability can be attributed to several

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causes; spring abundance reflects cropping from the previous year's juvenile fall sockeye salmon while summer abundance reflects recruitment and the abundance of age-1 survivors from the previous year. The strong relationship between spring *Cyclops* biomass and the fall fry numbers (Table 6) suggests that recruitment of juvenile salmon occurs before the July *Cyclops* bloom. Since these are survivors of predation from the previous year's rearing juvenile sockeye salmon, a delay of one year in the density dependent response of large escapements can be explained. Further, since the reproductive component of the population are the age-1+ *Cyclops* that survive the previous summer and fall predation and the current year's spring predation, we expect a density dependent lag in the response of the *Cyclops* population which may affect the recruitment of juvenile sockeye salmon two years later. Unfortunately, the spatial segregation of cohorts of *Cyclops*, coupled with continued cropping during recruitment in July, has limited the use of our data in accurately measuring *Cyclops* recruitment. As this time series of juvenile sockeye salmon abundance and seasonal copepod abundance increases, we anticipate obtaining sufficient resolution to determine if *Cyclops* recruitment can be affected by the cropping of the previous year's sexually mature animals. More precise measurement of *Cyclops* cohort strength can be expected to be obtained by an increase in the number of sampling stations in the lake.

Sockeye salmon run timing is usually thought to provide for optimal emergence timing of juveniles from their natal spawning areas. The observation that emergence timing precedes the main summer *Cyclops* bloom in Kenai and Skilak lakes, with apparently detrimental effects on recruitment, is an apparent contradiction to this conventional wisdom. Our earlier investigations (Schmidt and Tarbox 1995) provide some insight into this problem. We obtained ample evidence from age, weight, length, and lipid analysis, during the fall and spring, supporting the hypothesis that winter mortality was relatively high and related to size and condition in the fall. The combined effects of cold water temperatures and the relatively predation resistant copepod zooplankton community most likely provide sockeye salmon with a limited survival window. The diel vertical migration behavior examined in earlier reports (Schmidt et al. 1994) is an example of this predator avoidance behavior which limits the emergence timing window for juvenile sockeye salmon. A prolonged feeding period, even with a decreased probability of sufficient food in the spring, may be preferable to recruitment during the July *Cyclops* bloom and lacking a sufficient growth window to reach a condition to successfully overwinter. This also suggests that, depending upon the spring availability of surviving *Cyclops* from the previous year, early emerging juveniles would have a distinct advantage and can most likely recruit and survive at high rates, even if they are abundant, thus creating very large returns and recruit-per-spawner values exhibited from 1987 and most likely from the 1992 brood years.

The strong evidence for adjacent year interaction of juvenile sockeye salmon competing for a single cohort of *Cyclops* provides the basis for the one year lag observed in the recruit-per-spawner data for the Kenai River, following the 1987, 1988, and 1989 large escapements. Adult returns are reasonably predicted from fall fry abundance for those brood years that have adult return data (Figure 21). The 1987 brood year may be an anomaly but also may suggest that marine survival increases as a function of high abundance, indicating depensatory mortality. Density independent and compensatory fits to the data are possible only if 1987 is excluded, although data is limited at this time. This counters evidence we have on

overwintering mortality and fall fry condition (Schmidt and Tarbox 1995; 1996). An alternative hypothesis explaining this contradiction may be that initial hydroacoustic estimates of 1987 fall fry were biased low. If this were the case, the seasonal *Cyclops*-escapement model presented here would most likely have a decreased fit to the data. Alternatively, enhanced survival caused by high numbers of smolt may be much more important in increasing overall survival than the effects of food, competition, and small fall fry size on decreasing overwinter survival and the resulting small smolt size effects on subsequent marine survival. We have also observed a five year pattern developing in the Kenai River sockeye salmon returns (Figures 5 and 22), suggesting that this interactive effect may have regulated the strength of sockeye salmon runs throughout the recent history of the Kenai River, with 1977, 1982, 1987 and 1992 having a consistently strong recruitment. Based on the juvenile fall fry data from Skilak and Kenai lakes in 1993, we expect this trend to continue with a large run in 1997. This pattern of one or two year classes dominating returns is usually referred to as "cyclic dominance" and is a common feature of sockeye salmon systems in Alaska and Canada. This information was provided to the Alaska Board of Fisheries at their 1996 meeting to develop a management plan for the Kenai River. Further investigations on the Kenai system will be designed to further define escapement and juvenile predation on subsequent recruitment of *Cyclops* and to develop a method of incorporating zooplankton dynamics into a yield model so that alternative harvest strategies can be examined. The strength of the relationships described has had the fortunate benefit of limiting the utility of exploring alternative hypothesis, and can result in a much more focused study on the important variables affecting sockeye salmon recruitment. The ultimate legacy that can be provided by these studies is a predictive model that will allow future policy makers, when faced with fishery closures caused by oil spills or other actions, to have a reasonable estimate as to the costs associated with alternative harvest options. These studies also have the benefit of defining a baseline as to the causes of population variation when the lake rearing habitats and spawning areas of the Kenai River have been only marginally affected by habitat destruction.

Kodiak Lake Investigations

The following information was taken from Swanton et al. (1996), and is condensed for this report. The complete report is included in Appendix A.

Adult and Juvenile Studies

Red Lake

During 1995, 341,490 smolt (95% CI = 315,923 to 367,056) were estimated to have emigrated from Red Lake. The 1995 smolt migration was 221,200 less than in 1994 and about 48% less than the 1990–1994 average. This is the second consecutive year that the migration from Red Lake has been comprised of over 90% age-2. smolt . The mean length and weight of age-1., -2., and -3. smolts increased in 1995 compared to 1994. Mean length and weight of age-1. and -3. smolts in the 1995 migration are comparable to the average values measured since project inception.

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The 1995 Red Lake smolt migration completes the 1991 BR. An estimated 0.8 million sockeye smolts were produced from the 0.37 million 1991 escapement. This level of production is about half of what was estimated for the 1989 BR and nearly 4 times larger than for the 1990 BR. Smolt population estimates for the 1987 and 1988 brood years should be considered relative indices, as the population estimates for these years are marginal. The lack of confidence in these estimates is based upon age-2. smolt numbers which were adjusted using a 30% smolt to adult survival rate (Koenings et al. 1993) that was 4.5 times lower than the number of age-2. adult returns. We believe error in this estimate is centered around using a single smolt trap during 1990 that experienced substantial avoidance by age-2. smolts. Although two traps were used during 1991, trap avoidance still appeared to be a problem. Age-1. and -2. smolt estimates after adjusting for marine survival were 2.0 and 4.3 times lower, respectively than the numbers of freshwater age-1. and -2. returning adults. During 1992, trap configuration was modified, a smolt weir operated, and resulting smolt population estimates evaluated (Barrett et al. 1993b).

It appears based upon sockeye smolt migrations during 1995, 1994, and 1993, that the adult return from the 1991 BR will be significantly better than anticipated from the 1990 BR. Assuming 30% ocean survival (mean length 108.6 mm) the 520,000 age-2. smolts from the 1991 BR will result in about 156,000 age-2.2 adults. The smolt sizes from the 1991 BR suggest that experiencing greater than 30% smolt-to-adult survival from these BR's is not anticipated.

The diminished index of littoral zone rearing fry numbers observed in 1995 indicates that the 1996 and 1997 smolt migrations may decline from the present level. However, the pattern of catches observed in 1995 suggests that fry may have moved offshore and become unavailable to the beach seine earlier than in previous years. We observed no apparent differences in the length of age-0. rearing fry between years or within a year; however, rearing fry generally begin pelagic rearing at 35–40 mm (Barrett 1989). Therefore, fry lengths are probably a biased index of littoral zone rearing conditions. In addition, this premise is supported by the relatively static fry length observed.

An adult pre-season run forecast of 325,000 fish was derived for 1995. Most of the run (70%) was projected to be age to be 2 and 3 ocean fish. The actual run was an estimated 884,134 sockeye salmon comprised of a 317,832 escapement and 566,302 commercial catch. The difference represents over 100% forecast error. It has become clear that the present run reconstruction methods for the Ayakulik system are problematic in terms of catch assignment from the Inner and Outer Ayakulik sections (ADF&G 1993). Preliminary assignment of the catches to stock of origin using scale patterns has shown that other stocks are contributing to the June sockeye salmon catches within these sections (ADF&G, unpublished data). This could be responsible for confounding both our smolt production estimates and also be partially responsible for the high forecast error.

The 1996 pre-season run forecast is 722,000 fish, which if accurate, will allow a harvest of approximately 422,000. The 1996 run is projected to be about 36% 2.2 fish, 20% 1.2 fish, and 19% 1.3 fish.

Akalura Lake

The 1995 smolt migration was an estimated 134,117 smolts (95% CI 125,523 to 142,712) which is about 30% less than the 1994 smolt migration of 170,172. Age-2. smolts were the most abundant age class comprising 53% (1992 BR) of the total, followed by age-1. at 47% (1993 BR), and age-3. at less than 1% (1991 BR). The 1995 smolt migration had the smallest age-3. contribution since 1990. Both age-1. and age-2. smolt were of smaller mean length and weight during 1995 than in 1994. The mean length and mean weight of all age classes of smolt from the 1995 migration were larger than the 1990–1994 averages. Age-1. smolts averaged about 6.5 mm larger and weighed 1 g more than age-1. smolts from 1990–1994, and age-2. smolts were 7.9 mm larger and weighed 1.4 g more than age-2. smolts from 1990–1994.

Tow net sampling was reinitiated at Akalura Lake in 1995 after a 3 year hiatus. Sockeye fry CPUE during 1995 (2.2 fish/min.) was slightly higher than 1991 (2.1 fish/min.), but lower than observed in 1990 (3.4 fish/min.). The stickleback CPUE observed during 1995 (14.8 fish/min.) was greatly reduced from both 1991 (153.8 fish/min.) and 1990 (60.7 fish/min.).

Based on 1990–1995 smolt run estimates, the 1987, 1988 and 1989 BR's produced over twice the number of smolt as the 1990 and 1991 BR's. Overall, Akalura Lake has shown a steady decline in smolt production. However, the shift in age composition to fewer age-1. smolts and more age-3. smolts, which has been evident in past years, was less prevalent in the 1995 migration.

In 1995, Akalura Lake received an escapement of 2,010 fish for both the early and late runs combined. This exceedingly low escapement was far below the minimum goal of 40,000. Preliminary run reconstruction numbers for 1994–1995 indicate that the minimum escapement goal would not have been met given the complete absence of a commercial fishery in the Alitak Bay District for either year. This fishery is managed from late July throughout August for sockeye salmon returning to the Upper Station system and secondarily for coho salmon escapements into district streams. We believe that the escapements experienced at Akalura are in part a function of the commercial fishery. However, we do not believe that there is a major difference between the Akalura and Upper Station harvest rates. The poor escapements for the last two years are likely a function of the depressed sockeye smolt production from the associated broods. The 1996 sockeye run is not expected to meet minimum escapement requirements based upon smolt numbers produced from the 1990 and 1991 BR's and no commercial fishing time is expected within the Inner and Outer Akalura Sections (ADF&G 1993) in 1996.

Frazer Lake

The total sockeye smolt migration was an estimated 8,386,087 (95% CI = 7,595,899 to 9,176,275), which was the second largest observed run since 1991. Age-2. (98%) smolt dominated the 1995 migration as compared to age-1. (0.7%) smolt. In comparison, during 1991 age-1. (40%) and -2. (59%) smolts represented most of the estimate, whereas in 1993 the smolt

age composition was evenly divided between ages-2. and -3. In 1995, age-2. smolts averaged about 91.2 mm which was nearly 5 mm less than the 1990–1994 average of 96.1 mm. Age-2 smolt during 1995 weighed an average of 5.6 g as compared to the 1990–1994 average weight of 7.3 g. The 1995 tow net survey catches showed markedly fewer rearing sockeye fry in 1995 than in surveys conducted during 1990–1993. A total of two fry were caught during 1995 which may in-part have been due to poor survey conditions. Similar catches were observed during 1994 and 1993 when catches were 2 and 16 respectively. The 1995 stickleback CPUE of 3.9 fish per min. was approximately two thirds of the 1990–1994 average of 6.1 stickleback per min.

Based on the 1992–1995 smolt estimates, the 1990 BR produced an estimated 5,753,179 smolts from an escapement of 226 thousand adults. This is significantly below the 13 million smolts produced from the 1989 BR but similar to the 1991 BR (4.7 million, incomplete). The 1988 (incomplete), 1990, and 1991 (incomplete) BR's have produced roughly 50% fewer smolts than the 1989 BR, when the attendant escapement levels were about 20% less than in 1989. Overall, age-1. smolt production has dramatically decreased (1989-93 BR's), whereas age-2. smolt numbers appear to be relatively stable or increasing (1988–1992). Age-3. abundance increased markedly (1987–1989), but the 1990 and 1991 BR's indicate a declining trend.

The 1996 pre-season Frazer Lake sockeye forecast is 1.48 million fish which is approximately 50% larger than the actual 1994 run of 952 thousand. The 1996 run is projected to be comprised of 75% two ocean fish and about 25% three ocean fish.

Limnological Studies

The zooplankton biomass by taxa for the three lake systems is provided in Tables 6–8 and Figure 23. As stated in Schmidt and Tarbox (1993), the preferred prey of sockeye fry (cladocerans) in Red Lake apparently demonstrated a density-dependent response to the large escapement of 1989, as indicated by a 5- to 10-fold decrease in *Bosmina* and *Daphnia* in 1990 compared to 1986 (Table 6). In 1991, the total biomass decreased further despite the lower escapement in 1990 (371,000), but the majority of smolt produced from the 1989 BR held over an additional year and were rearing in the lake during 1991. In 1992, both *Bosmina* and *Daphnia* increased dramatically and the total biomass increased to about 2,500 mg m^{-2}; the highest recorded to date. This increase was most likely the result of reduced predation pressure as the majority of smolts produced from the high escapement of 1989 left the lake, and the escapement in 1991 was 375,000. Unexpectedly, the total biomass decreased in 1993 to about the 1990 level. The major drop in production was *Cyclops*. Although the 1993 zooplankton biomass was similar to the 1990 level, there was a substantially higher number of cladocerans in 1993. The 1992 escapement of 345,000 that produced the age-0 fry rearing in 1993 was similar to that in 1991, yet the zooplankton biomass in 1993 was about 2.5 times lower. An explanation for the lower biomass in 1993 is that a high proportion of the fry produced from the 1991 escapement may have held over for an additional year of rearing. In 1994, the total zooplankton biomass declined further, with the lowest values observed since 1980. More ominously, the cladoceran population declined in 1994 to the values observed in 1990. In 1995 a substantial increase with the highest values of the seven year record were measured for both cladocerans and copepods. We are

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planning on seasonal evaluation of the zooplankton, phytoplankton, and nutrient trends for the final report in 1997. Hopefully we can observe some explanatory pattern relating primary productivity and predation to these major changes in annual biomass of the zooplankton community.

Akalura Lake did not show any trends in biomass or species composition related to the large 1989 sockeye salmon escapement (Table 7). The species composition of this system is also quite different from that observed in Red Lake. The zooplankton community of Red Lake is more comparable to that of Frazer Lake (Table 8). Frazer Lake was treated with nutrients to increase the forage base during 1988–1992. In 1993 when no nutrients were added to Frazer Lake, the zooplankton biomass decreased (compared to 1992) despite similar escapements the last three years. The 1995 data indicated a continued decrease in zooplankton biomass and do not suggest a coupling with the positive trend observed in Red Lake, contrary to our earlier observations (Schmidt and Tarbox 1996).

Limnological water quality parameters from the three Kodiak Island lakes in the oil spill studies were collected in 1995 (Tables 9–11). As in previous years, during 1995 no unusual values (outside the range for oligotrophic lakes in Alaska) for general water-quality parameters, nutrients, or chlorophyll a were detected. Specifically, no consistent trends in these parameters were apparent in Red and Akalura lakes that received high escapements in 1989 compared to nearby Upper Station and Frazer lakes that did not receive large escapements. Upper Station Lake was not sampled in 1995.

Preliminary data from sediment core analysis of Akalura Lake (Figure 24) suggests that the downturn in escapement reflects recent history. The core indicates approximately 700 years of marine nitrogen deposition. The deposition rate of marine nitrogen parallels changes observed in escapements in nearby Frazer and Karluk lakes (Personal Comm. Bruce Finney, Univ. of Alaska, Fairbanks, AK). Assuming this is also true in Akalura Lake, the poor escapements strongly suggest a fishery related cause in the decline of the $\delta^{15}N$ signal over the most recent decades. Climatic factors or other natural processes are unlikely to be the primary cause for the decrease. Consequently, remedial action in correcting the decline is warranted.

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Table 1. Kasilof River escapement and smolt production summary. Smolt numbers are given in thousands.

Brood Year	Spawner Escapement	Age-1 Smolt abundance	Age-1 Smolt Hatchery	Age-2 Smolt abundance	Age-2 Smolt Hatchery	Total Smolt Abundance
1981	256,625	6,817	40.7	2,869	20.6	9,686
1982	180,239	11,390	36.3	4,001	7.7	15,391
1983	210,270	12,580	27.8	2,223	11.1	14,803
1984	231,685	5,268	30.2	3,540	31.1	8,808
1985	505,049	1,074	59.2	2,549	17.0	3,623
1986	275,963	2,056	52.0	3,009	10.2	5,065
1987	249,246 [a]	3,109	30.3	3,521	3.0	6,630
1988	204,000	3,916	2.0	2,335	1.0	6,251
1989	158,206	2,400	7.0	2,012	1.3	4,412
1990	144,136	2,107	7.5	1,833	3.3	3,940
1991	238,269	7,189	6.3	1,763	1.1	8,952
1992	184,178	7,376	4.7	2,477	n/a	9853
1993	149,939	4,826	0			
1994	205,525					
1995	205,903					

[a] Because of sonar failure, escapement estimates were from stream surveys and spawning stream weir counts above Tustumena Lake. See Kyle (1992) for statistics of smolt abundance precision estimates.

Table 2. Kasilof River smolt age class composition
summary; n is the sample size.

| Smolt | | Composition (%) | |
Year	n	Age-1	Age-2
1983	1163	84	16
1984	1192	80	20
1985	1263	76	24
1986	1348	70	30
1987	1635	23	77
1988	1275	45	55
1989	1125	51	49
1990	1150	53	47
1991	1018	51	49
1992	1150	56	44
1993	942	80	20
1994	900	81	19
1995	421	72	28

Table 3. Mean and standard deviation (SD) estimates of fork length (in mm) of Kasilof River smolt; n is the sample size.

Year	Age-1			Age-2		
	n	Mean	SD	n	Mean	SD
1983	712	70	3.8	451	83	5.4
1984	1005	73	3.5	187	85	4.4
1985	981	70	2.8	282	84	5.4
1986	983	69	3.9	365	84	5.1
1987	412	64	6.1	1223	77	4.8
1988	623	68	4.0	652	78	4.5
1989	609	66	4.4	516	81	4.5
1990	683	69	4.4	467	82	4.2
1991	529	68	3.5	489	80	3.2
1992	594	74	3.8	556	87	4.7
1993	755	69	3.5	187	82	4.2
1994	737	72	3.6	163	86	4.0
1995	303	72	3.2	118	85	4.5

Table 4. Summary of mean fork length and wet weight of fall fry collected in Kenai Peninsula lakes. Missing values indicate no data available; n is the sample size and SD is the standard deviation.

Lake	Year	Age-0 Length n	m)	SD	Age-0 Weight n	(g)	SD	Age-1 Length n	mm)	SD	Age-1 Weight n	(g)	SD
Skilak	1986	15	57					8	74				
	1988	109	50	5.3	109	0.9	0.4						
	1989	136	50	3.3	136	1.2	0.3	126	64	6.0	126	2.8	0.7
	1990	928	49	4.3	290	1.3	0.3	34	73	3.3	20	4.0	0.4
	1991	863	51	4.9	286	1.5	0.5	55	74	3.8	14	4.7	0.5
	1992	883	54	6.0	883	1.8	0.6	10	89	3.0	10	7.0	0.8
	1993	2755	48	5.6	2755	1.2	0.5	124	76	4.4	124	4.5	0.8
	1994	687	50	3.9	687	1.4	0.4	110	68	3.9	110	3.6	0.6
	1995 [1]	760	53	5.8	760	1.7	0.6	47	79	5.0	47	5.7	0.9
Kenai	1986	227	52		227			2	77				
	1989	38	48	4.5	38	1.0	0.2	56	64	4.6	56	2.5	0.6
	1990	1484	52	4.6	1484	1.5	0.4	62	69	4.2	22	3.6	0.6
	1991	1364	54	6.5	1364	2.0	0.6	40	76	4.8	15	5.5	1.0
	1992	1492	56	7.3	1492	2.0	0.8	12	78	10.0	12	5.6	1.7
	1993	2969	45	4.0	2969	1.0	0.2	4	68	1.0	4	3.3	0.5
	1994	861	54	4.6	861	1.9	0.5	39	77	3.7	39	5.2	0.7
	1995 [1]	679	56	6.9	679	2.2	0.9	47	79	5.0	47	5.7	0.9
Tustumena	1980	222	59	6.1	222	2.3	0.7	20	80	3.5	20	5.7	0.7
	1981	197	55	5.1	197	1.6	0.4	21	73	4.6	21	3.8	0.7
	1982	194	54	5.1	194	1.8	0.5	17	74	3.9	17	4.0	0.9
	1983	562	60	6.1	562	2.5	0.7	55	80	5.0	55	5.8	1.1
	1984	388	61	4.6	388	2.5	0.6	186	79	3.7	186	5.3	0.8
	1985	173	56	5.6	173	2.1	0.6	52	78	5.0	52	5.6	1.2
	1986	156	50	6.4	156	1.3	0.5	92	73	4.5	92	4.1	0.7
	1987	143	53	5.9	143	1.8	0.6	50	71	3.8	50	4.2	0.6
	1988	303	55	5.3	303	1.8	0.5	89	75	3.6	89	4.5	0.6
	1989	47	52	5.7	47	1.9	0.6	18	74	4.6	18	5.1	0.9
	1990	200	57	5.5	200	1.5	0.4	50	75	2.9	50	3.4	0.5
	1991	202	57	5.4	202	2.0	0.5	47	78	6.5	47	5.1	1.2
	1992	323	59	4.4	323	2.0	0.4	21	79	4.1	21	4.5	0.7
	1993	417	63	6.7	417	2.9	0.8	46	81	3.0	46	6.2	0.7
	1994	318	64	5.0	318	2.6	0.6	76	83	3.0	76	5.5	0.5
	1995 [1]	270	64	5.9	270	2.8	0.7	49	78	3.3	49	5.2	0.7

[1] results are preliminary.

Table 5. Comparison of copepod biomass (seasonal means) and fall density estimates of sockeye salmon fry in Tustumena and Skilak lakes, 1986 to 1995. Also given is copepod biomass per fall fry for each lake.

| Rearing Year | Copepod Biomass (mg m^{-2}) | | | | | | Fall Fry Density[a] (no. m^{-2}) | | Cope. Biom. per Fry (mg fry^{-1}) | |
| | Skilak | | | Tustumena | | | | | | |
	Mean	SE	n	Mean	SE	n	Skilak	Tustumena	Skilak	Tustumena
1986	537	29.7	2	115	13.2	3	0.205	0.056	2,624	2,054
1987	613	18.4	2	100	22.9	3	0.091	0.045	6,717	2,238
1988	586	7.7	2	75	9.6	3	0.313	0.051	1,875	1,469
1989	687	136.0	2	90	18.1	3	0.221	0.056	3,111	1,597
1990	451	51.4	5	74	5.2	5	0.227	0.062	1,981	1,188
1991	570	40.3	10	165	15.4	5	0.068	0.052	8,414	3,180
1992	558	162.4	3	110	9.2	5	0.086	0.064	6,482	1,718
1993	745	172.1	3	204	28.3	5	0.334	0.048	2,230	4,240
1994	442	44.9	5	192	27.7	5	0.096	0.041	4,596	4,652
1995	443	40.7	5	125	17.2	5	0.079	0.035	5,589	3,577

[a] standard error of fall fry density estimates are < 25% of the mean in all cases.

Table 6. Multiple regression statistics for predicting abundance of fall fry in Kenai and Skilak lakes from mainstem spawner abundance and *Cyclops* biomass. The model is $\ln(R) = \alpha + \beta S + \delta SpC + \gamma SuC$, where R is recruited age-0 fall fry abundance from Skilak and Kenai lakes, S is mainstem spawner abundance[1], SpC is spring (May and June) mean Cyclops biomass, and SuC is summer (July and August) mean Cyclops biomass. Data was collected from 1986 to 1995 (lake rearing years).

Regression Statistics

Multiple R	0.97
R^2	0.94
Adjusted R^2	0.92
Standard Error	0.17
Observations	10

ANOVA

	df	SS	MS	F	P-Value
Regression	3.0000	3.0706	1.0235	34.3476	0.0004
Residual	6.0000	0.1788	0.0298		
Total	9.0000	3.2494			

Coefficient	Estimate	Std. Error	t-Stat	P-Value	Lower 95%	Upper 95%
Intercept α	7.5412	0.2235	33.74	0.0000	6.9943	8.0881
Variable S (β)	0.0011	0.0002	6.52	0.0006	0.0007	0.0016
Variable SpC (δ	0.0024	0.0003	8.03	0.0002	0.0017	0.0031
Variable SuC (γ	0.0010	0.0002	3.94	0.0077	0.0004	0.0015

[1]Sonar count less Hidden and Russian River escapements and sportfish harvest

Table 7. Red Lake zooplankton data summary from stations 1 & 2 (averaged). Data were not collected from 1987 to 1989.

YEAR	*Diaptomus* Density (no m^{-2})	Biomass (mg m^{-2})	*Cyclops* Density (no m^{-2})	Biomass (mg m^{-2})	*Bosmina* Density (no m^{-2})	Biomass (mg m^{-2})	*Daphnia* Density (no m^{-2})	Biomass (mg m^{-2})	*Epischura* Density (no m^{-2})	Biomass (mg m^{-2})	TOTAL Density (no m^{-2})	Biomass (mg m^{-2})
1986	70470	483	151979	628	140941	361	64528	244	0	0	427917	1715
1990	70674	222	303026	715	55573	54	11519	19	0	0	440791	1010
1991	23587	98	115139	198	57946	80	40364	59	646	1	237681	435
1992	85612	393	516432	1828	113279	202	57281	132	0	0	772603	2554
1993	74642	247	256878	558	92954	129	68471	117	0	0	492945	1050
1994	50779	197	189424	413	50270	67	12275	20	0	0	302748	697
1995	125753	412	597951	1878	245401	412	125443	267	0	0	1094547	2968
Mean	71645	293	304404	888	108052	186	54269	122	92	<1	538461	1490

Table 8. Akalura Lake zooplankton data summary for all sampling stations, 1986 to 1995. Blank cells indicate data unavailable.

Year	Sample Dates	Epischura Density (no m^{-2})	Biomass (mg m^{-2})	Size (mm)	Eurytemora Density (no m^{-2})	Biomass (mg m^{-2})	Size (mm)	Cyclops Density (no m^{-2})	Biomass (mg m^{-2})	Size (mm)	Bosmina Density (no m^{-2})	Biomass (mg m^{-2})	Size (mm)	Chydorinae Density (no m^{-2})	Biomass (mg m^{-2})	Size (mm)	TOTAL Density (no m^{-2})	Biomass (mg m^{-2})
1986	2	7528	43	1.07	73470	175	0.91	2505	3.0	0.64	48424	39	0.29	0	0.00		131927	261
1987	5	41242	198	0.99	108386	431	0.97	16242	18.0	0.57	122452	98	0.30	743	0.60		289065	746
1988	3	25035	97	0.95	45471	124	0.85	7741	10.0	0.63	59934	42	0.28	0	0.00		138181	273
1989	4	10152	18	0.71	49662	129	0.84	6403	7.0	0.56	80912	67	0.30	266	0.20		147395	221
1990	6	4282	33	1.23	51522	145	0.86	6847	7.5	0.56	79977	65	0.30	841	0.50	0.26	143468	251
1991	6	6675	33	0.97	18728	60	0.87	5664	6.5	0.62	41636	32	0.29	292	0.20		72994	131
1992	6	4472	13	0.82	10642	40	1.02	4370	6.5	0.65	8338	7	0.30	531	1.10	0.47	28353	67
1993	5	11720	40	0.82	33737	93	0.83	8658	10.0	0.61	38265	30	0.29	1451	0.80	0.24	93829	173
1994	5	16723	75	1.00	23298	119	0.92	6702	6.0	0.53	76037	57	0.29	0	0.00		122760	257
1995	6	15010	51	0.91	45023	201	0.85	4895	5.3	0.61	124546	92	0.29	0	0.00		189474	350
Mean	5	14203	61	0.95	46102	146	0.90	7237	8.3	0.60	61775	48	0.29	687	0.57	0.32	129775	264

Table 9. Frazer Lake zooplankton data summary from stations 1 and 3 (averaged).

YEAR	Diaptomus Density (no m⁻²)	Density (no m⁻³)	Biomass (mg m⁻²)	Size (mm)	Cyclops Density (no m⁻²)	Density (no m⁻³)	Biomass (mg m⁻²)	Size (mm)	Bosmina Density (no m⁻²)	Density (no m⁻³)	Biomass (mg m⁻²)	Size (mm)	Daphnia Density (no m⁻²)	Density (no m⁻³)	Biomass (mg m⁻²)	Size (mm)	TOTAL Density (no m⁻²)	Density (no m⁻³)	Biomass (mg m⁻²)
1985	40	1	0.0	0.70	1512	37	3	0.78	121746	3682	145	0.36	42255	1092	65	0.60	165552	4812	213
1986	38	1	0.0	0.00	3431	90	7	0.73	66766	2063	83	0.37	27516	777	42	0.60	97750	2931	132
1987	95	2	0.0	0.96	13175	378	23	0.70	47676	1453	67	0.39	18028	489	31	0.64	78973	2323	120
1988	0	0	0.0	0.00	5725	153	19	0.94	92281	3410	118	0.37	59256	1912	92	0.61	157261	5475	229
1989	0	0	0.0	0.00	15731	448	40	0.84	94708	3286	128	0.38	42142	1258	62	0.59	152581	4991	229
1990	74	3	0.0	0.82	50756	1498	106	0.77	58587	1461	82	0.39	2136	51	4	0.65	111552	3013	192
1991	228	10	0.0	0.64	55012	1341	112	0.76	111598	3720	114	0.34	2969	109	5	0.62	169806	5181	231
1992	8	0	0.0	1.24	133548	3416	395	0.91	117044	3756	169	0.39	28677	717	63	0.71	279277	7889	627
1993	213	4	1.0	0.95	120295	3035	242	0.76	161651	5079	164	0.33	12654	345	18	0.59	294812	8463	425
1994	93	4	0.5	1.04	49801	1183	94	0.73	114400	2954	156	0.38	28145	779	45	0.61	192439	4919	295
1995	0	0	0.0	0.00	59089	1267	85	0.65	39823	863	41	0.34	10404	217	16	0.60	109316	2347	141
Mean	72	2	0	0.58	46189	1168	102	0.78	93298	2884	115	0.37	24925	704	40	0.62	164483	4759	257

Table 10. Summary of general water chemistry parameters, nutrient concentrations, and algal pigments for Red Lake, 1994 to 1995.

Date	Station	Depth (m)	Sp. Cond. (umhos cm⁻¹)	pH (Units)	Alkalinity (mg L⁻¹)	Turbidity (NTU)	Color (Pt units)	Calcium (mg L⁻¹)	Magnesium (mg L⁻¹)	Iron (ug L⁻¹)	Total - P (ug L⁻¹)	Total filterable - P (ug L⁻¹)	Filterable reactive - P (ug L⁻¹)	Total Kjeldahl - N (ug L⁻¹)	Ammonia (ug L⁻¹)	Nitrate + nitrite - N (ug L⁻¹)	Reactive silicon (ug L⁻¹)	Carbon (ug L⁻¹)	Chlorophyll a (ug L⁻¹)	Phaeophytin (ug L⁻¹)
05/16/94	1	1	59	7.3	15.0	1.0	12	5.0	1.4	28	13.7	9.4	5.2	143	1.2	23.9	53	432	4.94	0.01
05/16/94	1	38	62	7.1	15.0	1.0	5	5.0	1.4	36	13.2	4.6	2.0	155	2.9	25.6	53	533	5.83	0.01
05/16/94	2	1	63	7.1	15.0	1.0	3	5.0	1.4	34	10.6	4.2	1.2	129	1.1	23.4	41	368	5.05	0.01
05/16/94	2	38	63	7.1	15.0	1.5	2	5.0	1.4	46	14.1	4.7	1.7	187	2.3	24.5	47	435	5.08	0.01
06/14/94	1	1	61	7.2	16.0	1.0	2	5.0	0.7	12	9.0	4.0	1.0	120	1.8	3.4	235	167	1.00	0.15
06/14/94	1	38	62	6.9	16.0	1.9	3	5.0	0.7	212	42.0	13.4	10.5	226	27.1	5.3	241	449	5.71	0.44
06/14/94	2	1	61	7.1	16.0	2.0	3	5.0	0.7	14	9.2	3.8	0.7	128	1.1	3.4	188	220	1.09	0.27
06/14/94	2	38	75	7.4	20.0	2.0	2	5.0	0.7	197	32.1	9.9	7.6	195	21.4	6.4	205	471	4.70	0.62
07/18/94	1	1	62	6.7	16.0	0.4	3	4.9	1.5	20	11.4	4.6	1.3	140	1.1	3.4	128	191	1.22	0.66
07/18/94	1	38	63	6.6	16.0	1.8	4	4.9	1.5	512	76.2	22.6	20.2	356	97.9	7.0	436	228	0.40	0.56
07/18/94	2	1	62	6.8	16.0	0.5	4	4.9	1.5	24	11.7	5.1	1.6	147	3.4	3.4	142	209	0.96	0.82
07/18/94	2	37	64	6.7	16.0	1.8	4	4.9	1.5	484	70.7	26.4	24.1	308	109.2	·6.4	436	230	0.34	0.84
08/18/94	1	1	64	6.7	16.0	0.5	4	5.8	1.2	3	20.6	6.3	2.5	246	5.7	3.4	299	399	5.84	0.69
08/18/94	1	38	65	6.2	15.0	2.7	9	4.8	2.4	873	125.3	63.1	60.0	330	131.7	112.7	800	233	0.19	0.69
08/18/94	2	1	63	6.7	16.0	0.5	3	5.8	1.2	3	10.5	6.9	2.2	213	3.4	3.4	299	282	4.37	0.37
08/18/94	2	37	70	6.3	16.0	3.4	5	4.8	2.4	1,288	130.4	45.8	44.7	334	154.2	88.9	764	441	0.27	1.19
09/22/94	1	1	65	6.8	15.0	0.8	4	5.9	1.2	22	17.2	9.5	4.6	201	10.2	8.7	129	231	3.52	1.22
09/22/94	1	37	65	6.4	15.0	1.8	5	4.9	1.9	529	111.2	40.0	38.1	122	7.4	182.7	762	183	0.52	0.66
09/22/94	2	1	63	6.9	15.0	0.8	4	4.9	1.2	34	17.9	10.7	5.5	168	10.2	13.2	117	242	3.86	1.30
09/22/94	2	37	65	6.3	14.5	2.0	4	5.9	1.2	648	147.9	44.8	44.8	176	19.2	189.5	886	318	0.60	1.03
10/22/94	1	1	62	6.9	12.0	1.1	5	5.0	0.7	74	34.8	16.8	13.8	154	16.4	49.9	62	258	4.04	0.44
10/22/94	1	37	61	6.3	17.0	1.0	6	6.0	1.4	91	33.6	23.4	15.6	157	14.5	50.7	74	288	na	na
10/22/94	2	1	62	6.4	17.0	1.1	6	6.0	1.4	77	34.2	18.1	14.6	159	18.2	53.1	68	280	8.33	0.86
10/22/94	2	37	62	6.4	19.0	1.5	5	6.0	1.4	144	39.4	17.7	14.9	171	16.4	51.5	56	293	8.75	0.84
Mean			64		15.8	1.4	4.5	5.2	1.33	225	43.2	17.3	14.1	194	28.3	39.3	272	308	3.33	0.60
05/16/95	1	1	62	6.9	15.7	0.8	5	4.8	1.3	20	10.1	3.9	0.8	106	3.4	1.4	70	239	3.46	0.97
05/16/95	1	37	63	6.8	15.2	1.5	11	4.8	1.3	32	14.7	7.8	3.8	112	16.0	6.0	76	270	2.78	0.95
05/16/95	2	1	62	6.9	15.4	0.9	12	4.8	1.3	20	9.8	4.2	1.0	125	6.5	3.0	70	206	2.82	0.80
05/16/95	2	37	63	6.8	15.2	0.9	9	4.8	1.3	31	12.7	7.1	3.2	124	11.8	0.6	64	248	2.99	0.92
06/22/95	1	1	69	7.4	19.7	0.8	2	8.0	1.2	44	10.8	6.3	2.4	136	-5.7	1.4	62	292	2.25	0.68
06/22/95	1	37	70	7.0	20.1	1.0	4	6.0	1.2	190	27.2	16.7	12.8	227	111.3	7.4	246	224	0.95	1.04
06/22/95	2	1	62	7.1	16.2	1.5	10	5.0	1.2	66	10.1	6.6	2.0	116	-6.2	1.4	62	278	2.21	0.56
06/22/95	2	39	63	6.7	17.2	1.0	4	5.0	1.2	152	25.2	15.8	12.9	219	105.5	7.4	240	204	1.18	1.22
07/27/95	1	1	61	7.0	15.9	1.4	3	4.4	1.6	42	9.4	4.2	0.8	174	-0.5	5.9	418	259	1.91	0.54
07/27/95	1	37	63	6.4	16.0	1.5	2	4.4	2.4	392	65.5	29.5	23.2	265	147.7	100.7	708	281	0.37	1.23
07/27/95	2	1	61	7.1	16.0	0.8	3	4.4	2.4	18	8.1	3.4	0.5	128	7.8	1.4	329	200	1.62	0.60
07/27/95	2	37	63	6.3	15.7	1.9	4	5.3	2.4	492	104.6	33.0	29.7	358	185.6	112.7	774	287	0.40	1.31
08/13/95	2	1	na	na	na	na	2	na	na	335	49.0	8.7	3.5	378	22.4	81.1	362	na	na	na
08/13/95	2	38	63	6.6	16.0	2.7	2	4.4	0.6	126	34.9	18.2	15.0	120	4.7	91.7	389	176	1.67	0.90
09/13/95	1	1	61	7.0	16.2	0.6	3	4.7	1.3	5	8.2	4.7	1.1	132	-2.5	1.4	159	228	4.48	1.01
09/13/95	1	37	62	6.2	15.3	1.7	4	4.7	1.3	526	160.6	75.5	70.9	126	27.6	219.6	1120	337	0.35	1.34
09/13/95	2	1	60	7.0	16.2	0.5	3	4.7	1.3	7	6.5	4.0	1.8	123	-1.0	2.9	39	322	4.56	1.14
09/13/95	2	37	62	6.2	15.7	3.0	3	4.7	2.3	1,250	334.0	122.0	115.1	185	73.4	180.5	1294	282	0.35	1.88
10/03/95	1	1	43	6.9	16.5	0.5	5	4.7	1.3	36	15.5	9.3	6.7	151	-2.0	29.9	354	231	5.51	1.23
10/03/95	1	38	62	6.2	15.1	2.6	3	4.7	1.9	846	266.7	82.5	77.0	128	20.3	218.1	1440	224	0.28	1.24
10/03/95	2	1	61	6.9	16.1	0.9	2	5.7	0.7	23	14.0	9.8	6.3	147	1.6	39.0	366	220	5.30	1.21
10/03/95	2	36	62	6.3	15.3	2.5	4	4.7	1.9	778	207.0	88.0	80.8	161	13.6	224.1	1318	184	0.29	1.22
Mean			62	6.7	16.2	1.4	4.5	5.0	1.5	247	63.8	25.5	21.4	170	33.7	60.8	453	247	2.18	1.05

na indicates not available.

Table 11. Summary of general water chemistry parameters, nutrient concentrations, and algal pigments for Akalura Lake, 1994 to 1995.

Date	Station	Depth (m)	Sp. Cond. (umhos cm⁻¹)	pH (Units)	Alkalinity (mg L⁻¹)	Turbidity (NTU)	Color (Pt units)	Calcium (mg L⁻¹)	Magnesium (mg L⁻¹)	Iron (ug L⁻¹)	Total - P (ug L⁻¹)	Total filterable - P (ug L⁻¹)	Filterable reactive - P (ug L⁻¹)	Total Kjeldahl - N (ug L⁻¹)	Ammonia (ug L⁻¹)	Nitrate + nitrite - N (ug L⁻¹)	Reactive silicon (ug L⁻¹)	Carbon (ug L⁻¹)	Chlorophyll a (ug L⁻¹)	Phaeophytin (ug L⁻¹)
05/16/94	1	1	58	6.9	13.0	2.1	9	5.0	1.4	56	12.5	6.3	3.9	205	1.8	23.4	752	487	5.75	0.12
05/16/94	1	17	58	7.2	14.0	3.0	8	5.0	1.4	128	16.7	3.1	2.0	242	6.2	34.2	776	565	7.23	1.69
05/16/94	2	1	58	7.0	13.5	2.4	4	4.0	1.4	56	12.7	3.4	2.2	194	3.4	27.9	724	490	5.73	0.36
05/16/94	2	14	58	7.1	14.0	3.0	5	5.0	1.4	64	11.7	3.4	2.5	193	3.4	27.9	724	524	6.16	0.63
06/14/94	1	1	58	6.8	14.0	2.3	6	5.0	0.7	40	9.5	2.8	1.7	172	3.4	0.8	705	348	2.58	0.60
06/14/94	1	16	59	6.6	14.0	3.0	5	5.0	0.7	218	12.1	2.6	1.7	133	50.7	8.2	922	224	2.36	0.87
06/14/94	2	1	58	6.8	14.0	3.0	4	5.0	0.7	58	10.1	3.0	1.7	133	3.4	7.0	664	280	2.25	0.52
06/14/94	2	14	58	6.6	13.0	3.0	8	5.0	0.7	283	16.9	3.8	2.5	224	59.6	7.6	940	318	2.78	1.63
07/18/94	1	1	58	6.9	14.0	3.2	4	4.9	1.5	41	9.6	2.7	2.2	241	6.8	0.8	596	509	5.45	0.77
07/18/94	1	16	61	6.6	15.0	2.0	10	4.9	1.5	644	18.6	7.5	4.9	318	149.7	18.9	1,358	239	0.73	0.81
07/18/94	2	1	58	7.0	14.0	3.3	4	4.9	1.5	36	10.4	3.2	2.7	241	7.9	4.0	609	609	5.29	0.93
07/18/94	2	13	58	6.6	15.0	2.4	5	4.9	1.5	156	11.7	3.1	2.7	272	45.1	5.9	797	427	4.09	0.44
08/18/94	1	1	57	6.7	14.0	7.5	6	5.0	1.7	22	19.8	3.5	3.0	461	1.7	4.0	935	1,227	14.67	0.01
08/18/94	1	17	63	6.4	16.0	2.1	12	5.0	1.7	1,140	50.9	13.6	8.6	433	176.7	78.8	1,717	524	0.39	0.87
08/18/94	2	1	59	7.2	15.0	13.0	9	5.0	1.7	184	10.6	14.1	8.9	379	1.7	0.8	959	1,038	13.70	0.15
08/18/94	2	14	61	6.3	15.0	1.7	9	5.0	1.7	390	19.9	6.5	4.8	218	75.4	125.1	1,546	138	0.65	0.73
09/26/94	1	1	64	7.0	15.0	0.8	6	4.9	1.3	98	22.9	6.7	4.8	302	91.2	47.1	1,408	319	2.10	1.06
09/26/94	1	16	64	7.0	15.0	1.1	3	4.9	1.3	112	22.5	5.6	4.0	303	92.3	46.0	1,396	399	3.01	0.51
09/26/94	2	1	64	7.0	15.0	1.0	4	4.9	1.3	107	18.5	6.4	4.7	280	90.1	44.9	1,420	312	1.93	0.59
09/26/94	2	14	63	7.0	15.0	1.0	6	4.9	1.3	129	20.1	6.8	4.8	285	93.4	47.1	1,420	269	1.77	0.98
Mean			60		14.4	3.0	6.4	4.9	1.3	198	16.9	5.4	3.7	261	48	28	1018	462	4.43	0.71
05/16/95	1	1	60	7.2	15.0	2.0	6	4.8	1.3	162	14.8	4.5	2.3	188	1.7	78.1	513	484	7.83	1.58
05/16/95	1	16	63	7.2	15.8	2.0	5	4.8	1.3	196	18.3	3.7	2.2	163	6.8	81.1	667	446	9.81	2.55
05/16/95	2	1	59	7.1	14.1	1.9	5	4.8	1.3	94	11.7	3.9	1.5	172	1.7	69.1	506	495	6.17	1.38
05/16/95	2	16	60	6.9	13.9	2.0	5	4.8	1.3	152	11.0	3.1	1.2	165	1.7	87.1	550	450	8.89	1.63
06/28/95	1	1	60	6.8	14.4	0.9	3	4.5	1.3	78	12.1	3.0	0.8	153	1.7	1.4	91	240	2.59	1.02
06/28/95	1	15	60	6.6	14.4	1.0	5	4.5	1.3	262	9.1	3.8	1.6	163	31.8	17.9	265	185	2.20	1.15
06/28/95	2	1	60	6.9	14.4	1.0	3	4.5	1.3	74	8.6	4.0	1.6	184	1.7	5.9	79	271	2.07	0.84
06/28/95	2	14	60	6.8	14.5	1.0	4	4.5	1.3	114	8.0	5.5	3.1	138	1.7	11.9	104	225	2.39	1.02
07/27/95	1	1	59	7.0	15.0	1.5	3	4.4	2.4	66	7.8	4.5	1.4	154	1.7	1.4	262	235	2.21	0.92
07/27/95	1	16	58	7.0	14.9	0.9	5	4.4	2.4	40	9.1	6.1	2.3	163	1.7	1.4	262	235	2.21	0.92
07/27/95	2	1	62	6.3	16.0	2.3	10	4.4	2.4	874	14.2	4.6	2.7	330	157.1	20.9	897	409	1.45	1.24
07/27/95	2	15	61	6.4	16.0	1.7	9	4.4	1.6	605	10.8	4.0	1.8	223	102.0	23.9	774	202	1.83	1.24
08/13/95	1	1	59	6.5	16.0	2.4	4	5.3	0.6	116	10.5	4.0	1.1	155	3.2	5.9	470	269	3.82	1.58
08/13/95	1	16	60	6.6	16.5	2.2	5	4.4	0.6	126	9.7	3.6	1.1	148	3.7	5.9	457	260	4.00	1.52
08/13/95	2	1	60	6.7	14.7	2.6	4	4.4	0.6	140	12.2	3.4	0.9	162	4.2	5.9	457	303	3.59	1.40
08/13/95	2	15	61	6.5	15.1	3.4	8	4.4	0.6	428	11.2	6.4	2.7	173	52.0	17.9	702	206	3.31	1.13
09/13/95	1	1	59	6.8	15.8	0.9	5	4.7	1.3	117	9.9	4.1	1.4	158	19.3	11.9	795	212	4.88	0.87
09/13/95	1	16	60	6.5	15.8	1.2	14	3.8	1.3	334	11.8	7.2	4.6	215	113.9	23.9	1,216	191	1.61	1.67
09/13/95	2	1	59	6.8	16.2	0.8	6	4.7	1.3	123	8.0	4.5	1.5	136	21.4	10.4	789	242	4.87	1.60
09/13/95	2	15	59	6.7	15.8	1.3	8	4.7	1.3	236	10.9	4.0	1.8	194	56.8	14.9	970	254	2.37	1.67
10/03/95	1	1	59	6.9	15.2	2.0	5	4.7	1.3	139	16.4	4.2	1.5	185	17.8	58.6	1,006	419	9.84	2.60
10/03/95	1	15	59	7.0	16.0	1.6	5	4.7	1.3	156	23.0	4.0	1.6	204	30.7	60.1	1,049	371	8.59	2.76
10/03/95	2	1	59	7.0	14.7	2.2	8	4.7	1.3	136	21.0	5.0	1.9	224	21.9	60.1	1,000	344	10.35	2.98
10/03/95	2	15	60	7.1	15.7	1.4	3	4.7	1.3	131	16.6	4.1	2.1	187	26.1	57.0	1,025	309	8.91	2.09
Mean			60		15.2	1.7	5.8	4.6	1.3	204	12.4	4.4	1.9	181	28.4	30.5	622	303	4.81	1.55

Table 12. Summary of general water chemistry parameters, nutrient concentrations, and algal pigments for Frazer Lake, 1994 to 1995.

| Date	Station	Depth (m)	Sp. Cond. (umhos cm⁻¹)	pH (Units)	Alkalinity (mg L⁻¹)	Turbidity (NTU)	Color (Pt units)	Calcium (mg L⁻¹)	Magnesium (mg L⁻¹)	Iron (ug L⁻¹)	Total - P (ug L⁻¹)	Total filterable - P (ug L⁻¹)	Filterable reactive - P (ug L⁻¹)	Total Kjeldahl - N (ug L⁻¹)	Ammonia (ug L⁻¹)	Nitrate + nitrite - N (ug L⁻¹)	Reactive silicon (ug L⁻¹)	Carbon (ug L⁻¹)	Chlorophyll a (ug L⁻¹)	Phaeophytin (ug L⁻¹)
06/02/94	1	1	55	7.3	15.0	1.3	6	4.8	1.1	9	6.9	2.0	1.7	100	2.2	75.0	1,841	149	0.58	0.13
06/02/94	1	23	56	7.2	14.0	0.5	8	4.8	0.2	8	3.7	2.6	1.9	92	4.4	85.0	1,900	124	0.96	0.08
06/02/94	3	1	55	7.1	14.0	0.8	8	4.8	1.1	12	11.0	3.5	2.4	139	4.4	79.2	1,876	190	0.66	0.20
06/02/94	3	50	54	7.0	13.0	0.5	4	4.8	1.1	3	3.2	2.1	1.6	87	9.8	90.7	1,923	116	0.75	0.17
07/19/94	1	1	56	6.5	13.0	0.4	5	4.9	1.3	13	9.8	1.8	1.5	103	8.8	53.6	1,901	165	0.52	0.16
07/19/94	1	23	55	6.6	14.0	0.5	5	4.9	1.3	14	3.3	1.9	1.3	90	5.5	56.4	1,913	171	0.52	0.21
07/19/94	3	1	55	6.6	13.0	0.9	4	4.9	1.3	36	3.9	1.8	1.2	95	3.3	47.9	1,931	124	0.61	0.17
07/19/94	3	50	54	6.5	13.0	0.4	4	4.9	1.3	10	5.2	2.2	1.8	97	16.4	75.0	2,004	80	0.36	0.24
08/25/94	1	1	54	7.3	15.0	0.4	6	4.7	1.4	3	3.6	1.7	1.2	91	7.7	42.1	1,924	127	0.79	0.17
08/25/94	1	24	52	7.0	14.0	0.3	4	4.7	1.4	3	3.6	1.7	1.2	101	22.9	67.8	2,015	138	0.42	0.14
08/30/94	3	1	54	6.8	13.0	0.4	6	4.8	1.3	3	5.8	2.5	1.9	112	5.5	30.7	1,963	132	0.76	0.17
08/30/94	3	50	54	6.5	12.5	0.4	4	4.8	1.3	6	3.4	1.2	1.0	101	33.8	80.7	2,143	36	0.18	0.09
10/11/94	1	1	57	6.7	13.0	0.3	4	5.0	1.3	10	4.8	1.6	1.0	86	1.1	73.5	1,932	102	0.71	0.08
10/11/94	1	23	56	6.6	12.0	0.4	3	5.0	1.3	11	4.7	1.8	1.2	84	1.1	76.4	2,014	134	0.62	0.10
10/11/94	3	1	56	6.7	12.5	0.4	4	5.0	1.3	11	4.9	1.6	1.0	89	1.1	70.7	2,059	102	0.78	0.13
10/11/94	3	43	55	6.6	12.0	0.4	3	5.0	1.3	12	13.5	1.5	1.0	106	4.4	70.7	1,983	70	0.56	0.13
Mean			55		13.3	0.5	4.9	4.9	1.2	10	5.7	2.0	1.4	98	8.3	67.2	1958	123	0.61	0.15
05/18/95	1	1	51	6.6	12.9	2.0	10	4.8	1.3	53	5.3	2.5	1.6	103	1.3	99.1	2,174	135	1.25	0.48
05/18/95	1	44	na	na	na	na	10	na	na	na	4.0	2.4	2.0	88	2.4	103.8	na	119	2.01	0.57
05/18/95	3	1	52	6.6	12.7	1.0	9	4.8	1.3	31	4.5	2.6	1.8	103	1.8	101.5	2,235	119	0.88	0.36
05/18/95	3	50	52	6.6	12.7	0.7	9	4.8	1.3	22	4.8	2.1	1.5	82	2.3	104.6	2,241	69	1.50	0.54
07/05/95	1	1	49	6.6	11.8	0.5	8	4.5	0.7	13	5.5	1.8	1.2	110	1.3	72.7	2,206	196	1.59	0.41
07/05/95	1	43	52	6.5	11.2	0.5	6	4.5	0.7	13	4.2	1.3	1.2	82	8.6	95.5	2,246	88	1.14	0.46
07/05/95	3	1	52	6.2	12.9	0.9	4	4.5	0.7	12	5.5	1.5	1.1	109	2.8	60.6	2,217	135	1.01	0.33
07/05/95	3	50	52	6.3	12.8	0.5	4	4.5	0.7	9	5.4	1.8	1.1	97	10.7	103.1	2,258	40	1.03	0.38
08/08/95	1	1	53	6.9	12.8	1.9	5	4.4	0.6	8	4.3	2.0	1.6	78	1.8	56.0	2,276	183	2.16	0.77
08/08/95	1	44	54	6.6	14.0	2.2	6	4.4	0.6	12	4.2	2.0	1.5	84	14.4	97.0	2,439	80	1.56	0.48
08/08/95	3	1	53	6.8	15.0	1.9	8	4.4	0.6	12	4.6	2.0	1.4	87	1.8	62.9	2,330	283	2.60	0.69
08/08/95	3	50	53	6.6	10.6	1.9	5	5.3	0.2	14	3.6	2.0	1.4	67	15.4	97.8	2,439	77	0.84	0.43
09/27/95	1	1	47	6.9	14.1	0.7	8	4.3	1.2	18	5.7	2.0	1.4	87	5.0	53.8	2,111	135	2.93	0.71
09/27/95	1	45	46	6.7	14.0	0.7	3	4.3	1.2	37	3.4	1.8	1.4	68	16.0	84.1	2,275	69	1.47	0.46
09/27/95	3	1	46	6.9	14.4	0.7	6	4.3	1.2	32	6.2	1.9	1.4	85	6.5	60.6	2,172	117	2.93	0.65
09/27/95	3	57	46	6.7	13.6	0.7	10	4.3	1.2	31	4.8	2.1	1.8	73	16.0	113.7	2,385	37	0.67	0.36
Mean			51	6.6	13.0	1.1	6.9	4.5	0.9	21.1	4.8	2.0	1.5	88	6.8	85.4	2267	118	1.60	0.51

na indicates not available.
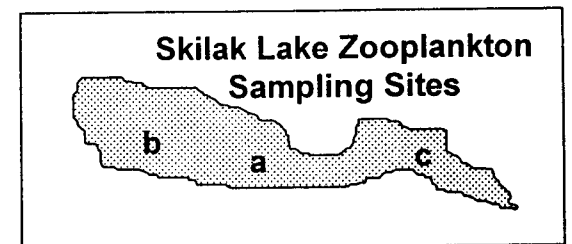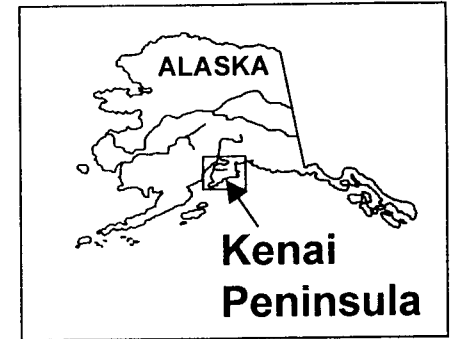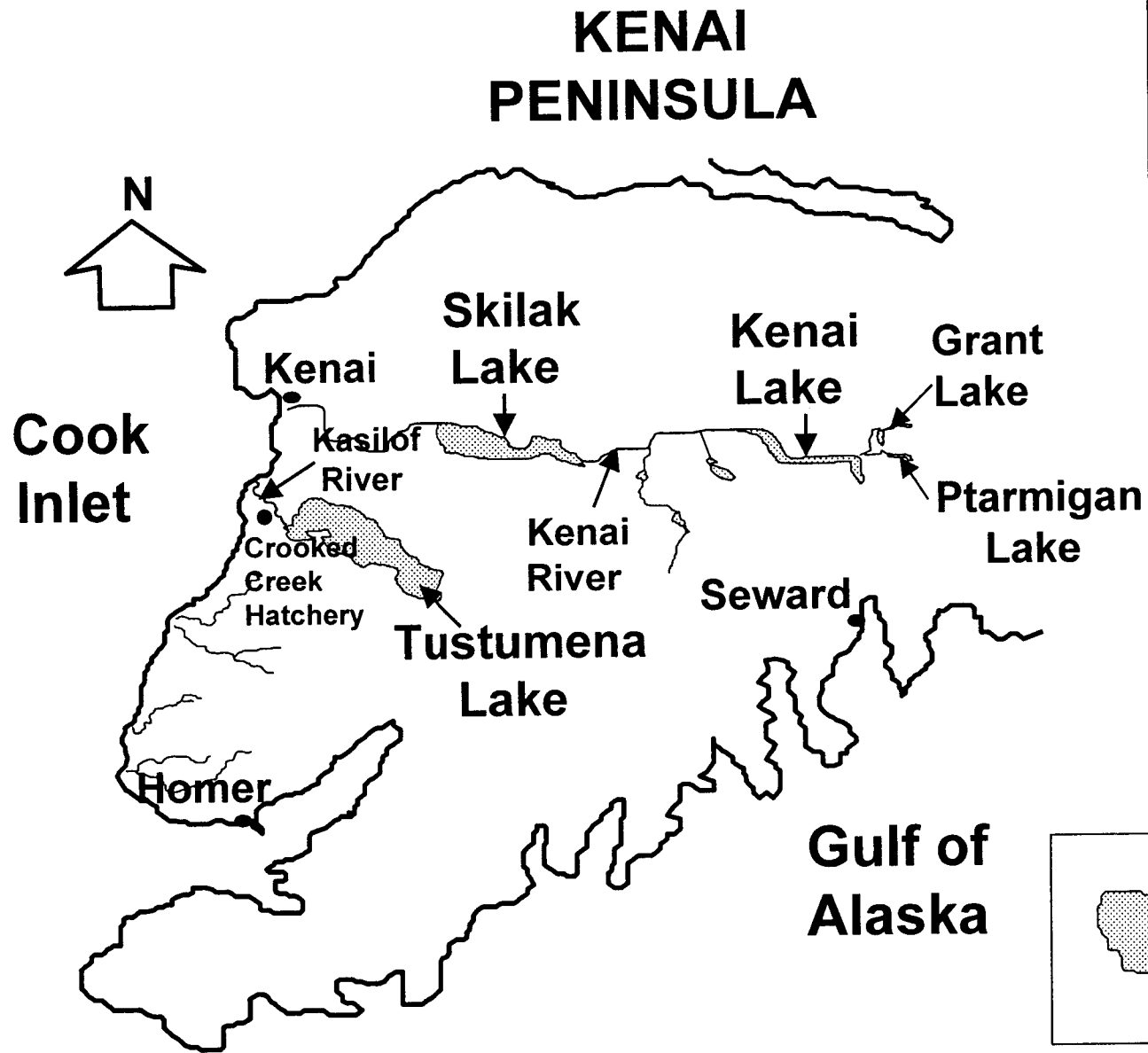
Figure 1. Location of study lakes within the Kenai River drainage, Kenai Peninsula, Alaska.
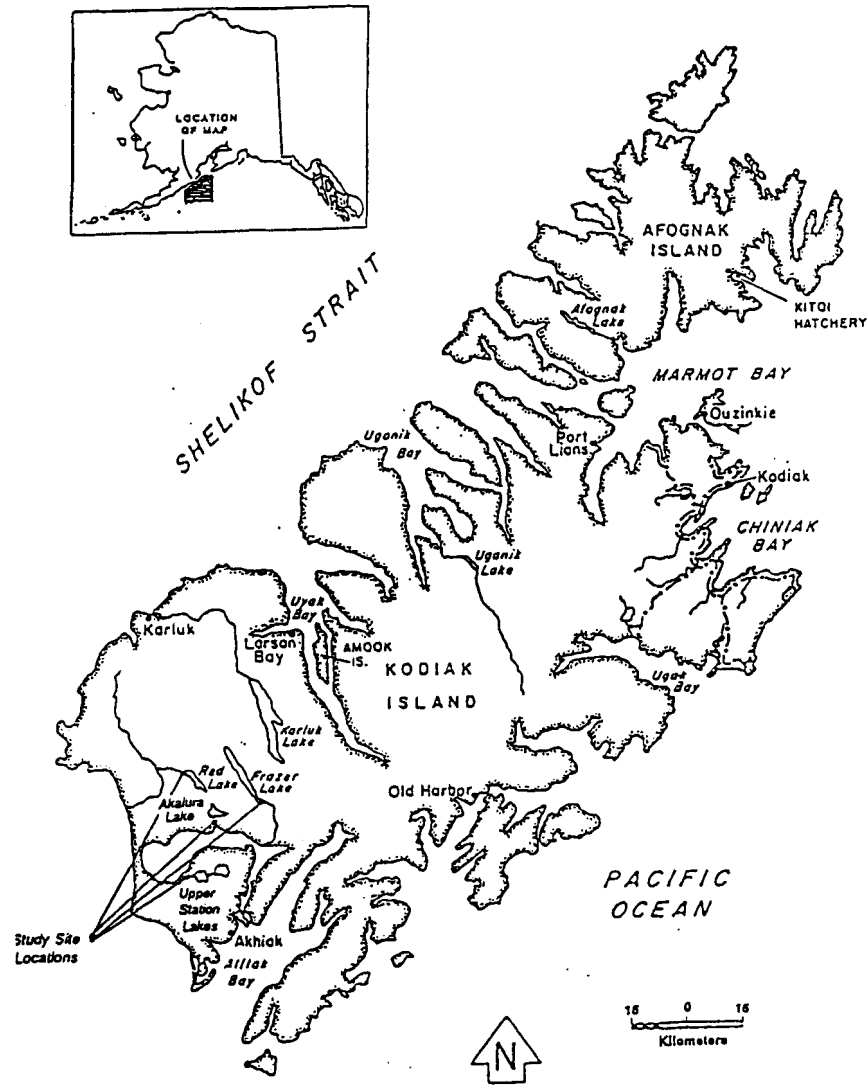
Figure 2. Location of Red, Akalura, and Upper Station lakes on the southern end of Kodiak Island, Alaska.
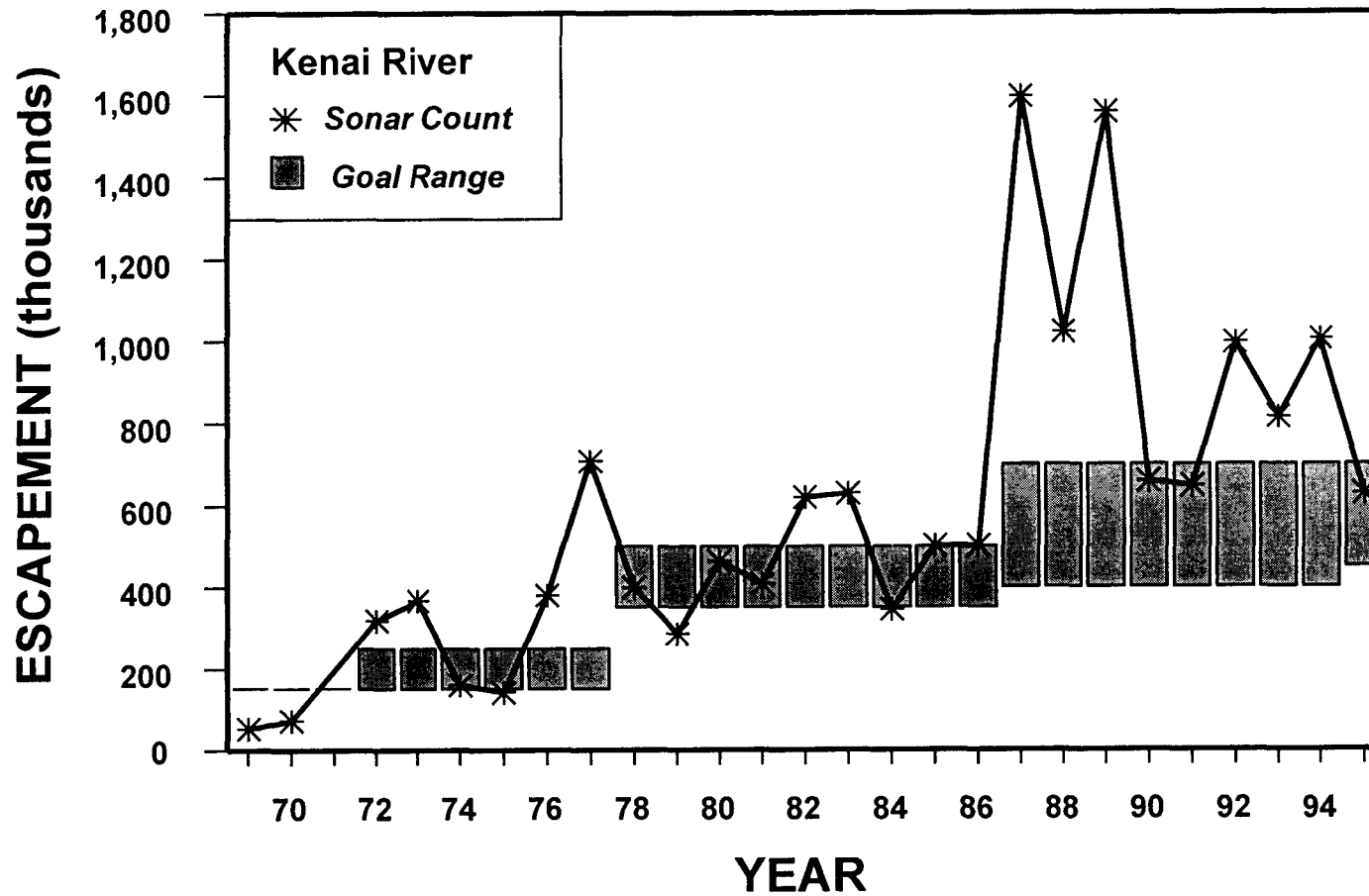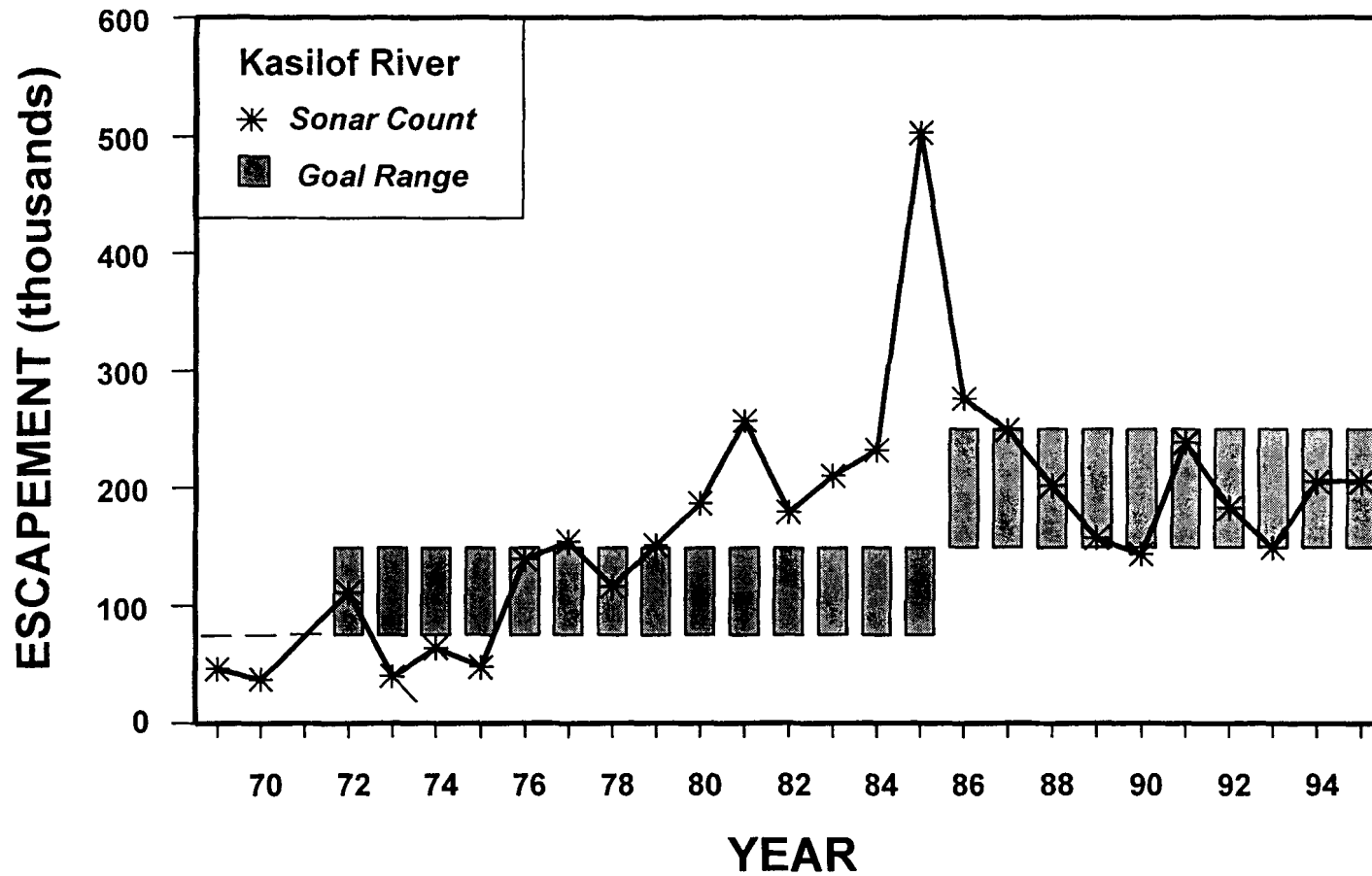
Figure 3. Summary of sockeye salmon escapements and historical escapement goal ranges for the Kenai River. Data represent total cumulative daily apportioned sonar counts at mile 19 of the Kenai River. Top of bars represents the maximum escapement goal and the bottom of bars represents the minimum escapement goal.

Figure 4. Summary of sockeye salmon escapements and historical escapement goal ranges for the Kasilof River. Escapement data represent total cumulative daily apportioned sonar counts at mile 11 of the Kasilof River. Top of bars represents the maximum escapement goal and the bottom of bars represents the minimum escapement goal.
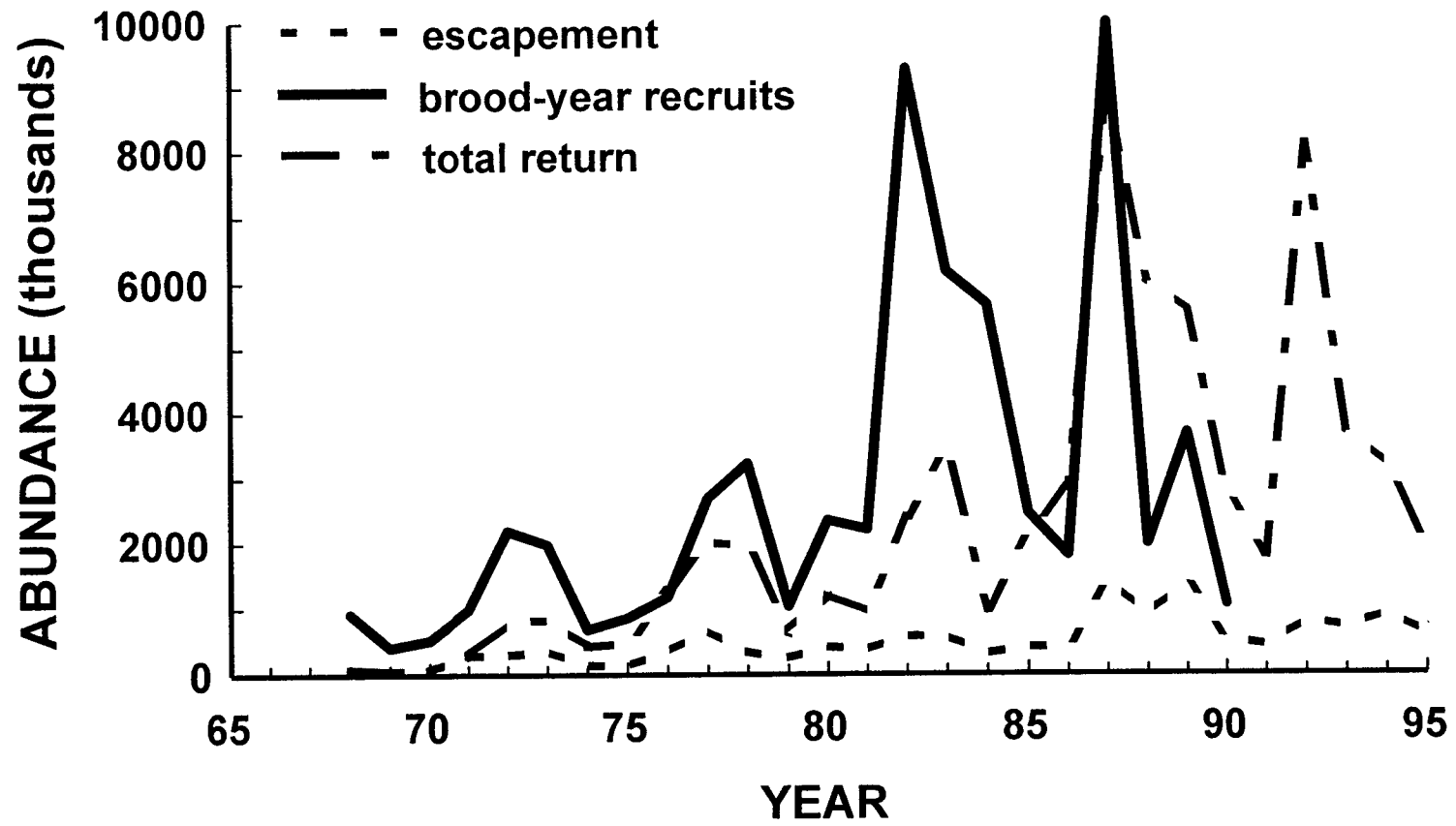
Figure 5. Historical pattern of escapements, total adult return, and brood-year recruitment of sockeye salmon into the Kenai River system.

Kenai System
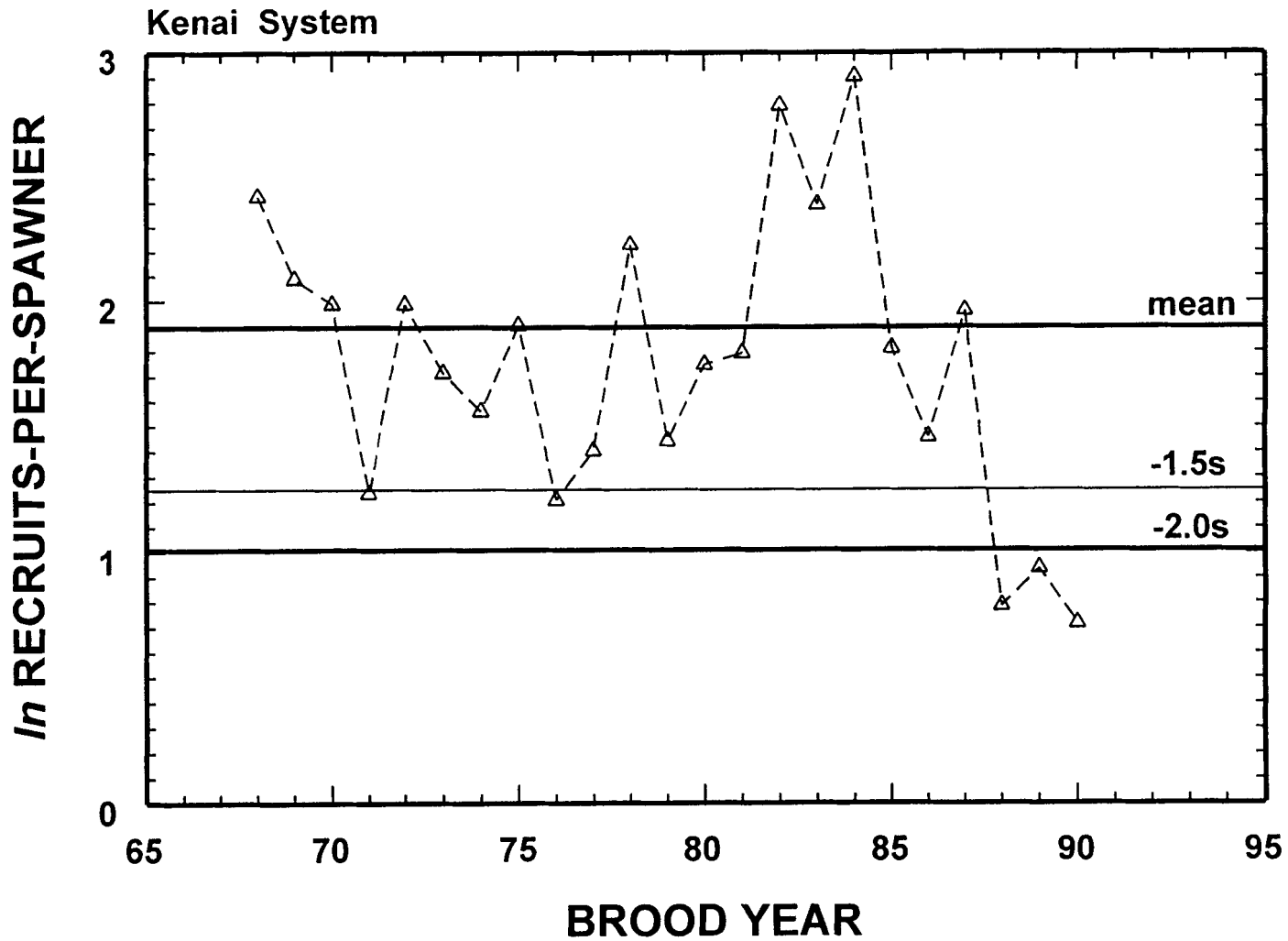
Figure 6. Inter-annual pattern in *In* recruits-per-spawner of sockeye salmon in the Kenai River. Statistical process control methods were used to analyze the data. The mean, lower warning limit (-1.5s), and lower control limit (-2.0s) were established using pre-1987 data as the reference series.
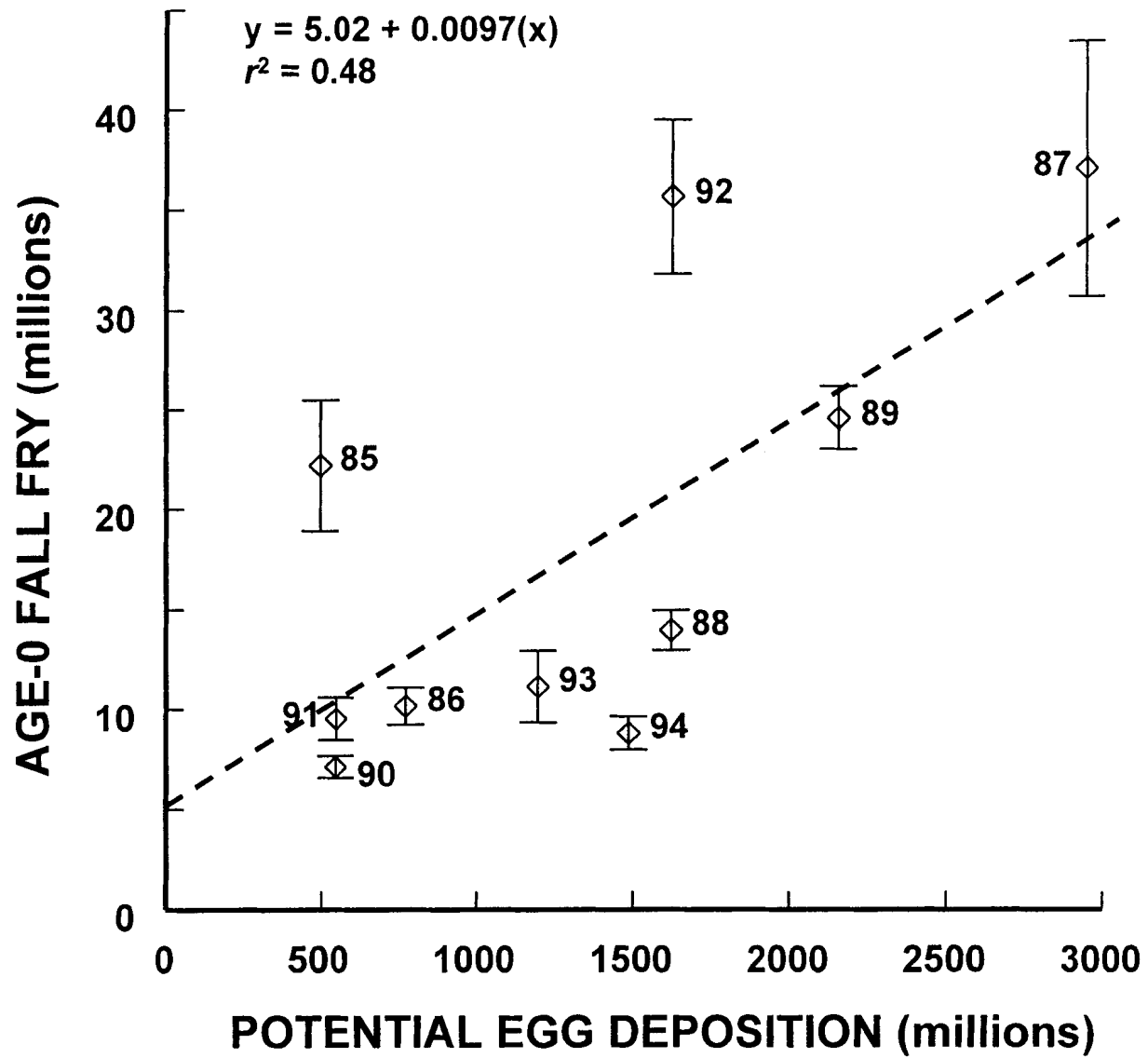
Figure 7. Relationship between the number of sockeye salmon fall fry in Kenai and Skilak lakes and mainstem potential egg deposition. Vertical bars are standard errors of estimated fry abundance.
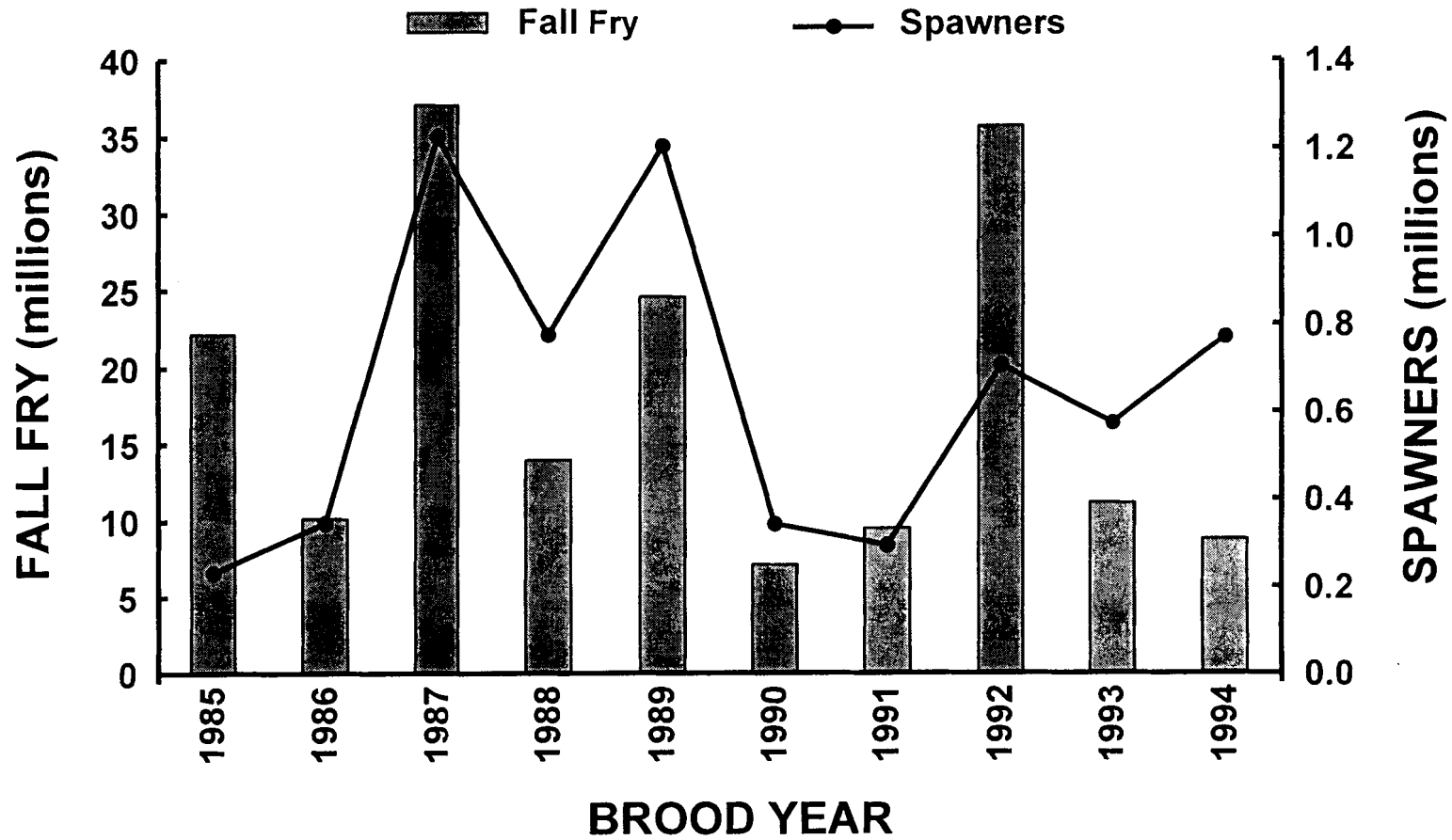
Figure 8. Interannual variation of mainstem Kenai River sockeye salmon spawners and fall fry estimates from Kenai and Skilak lakes combined. Mainstem spawner abundance is estimated annually from apportioned sonar counts minus sport fish harvests and escapement estimates for Russian River and Hidden Lake. Fall fry estimates are from September sonar surveys of Kenai and Skilak lakes.
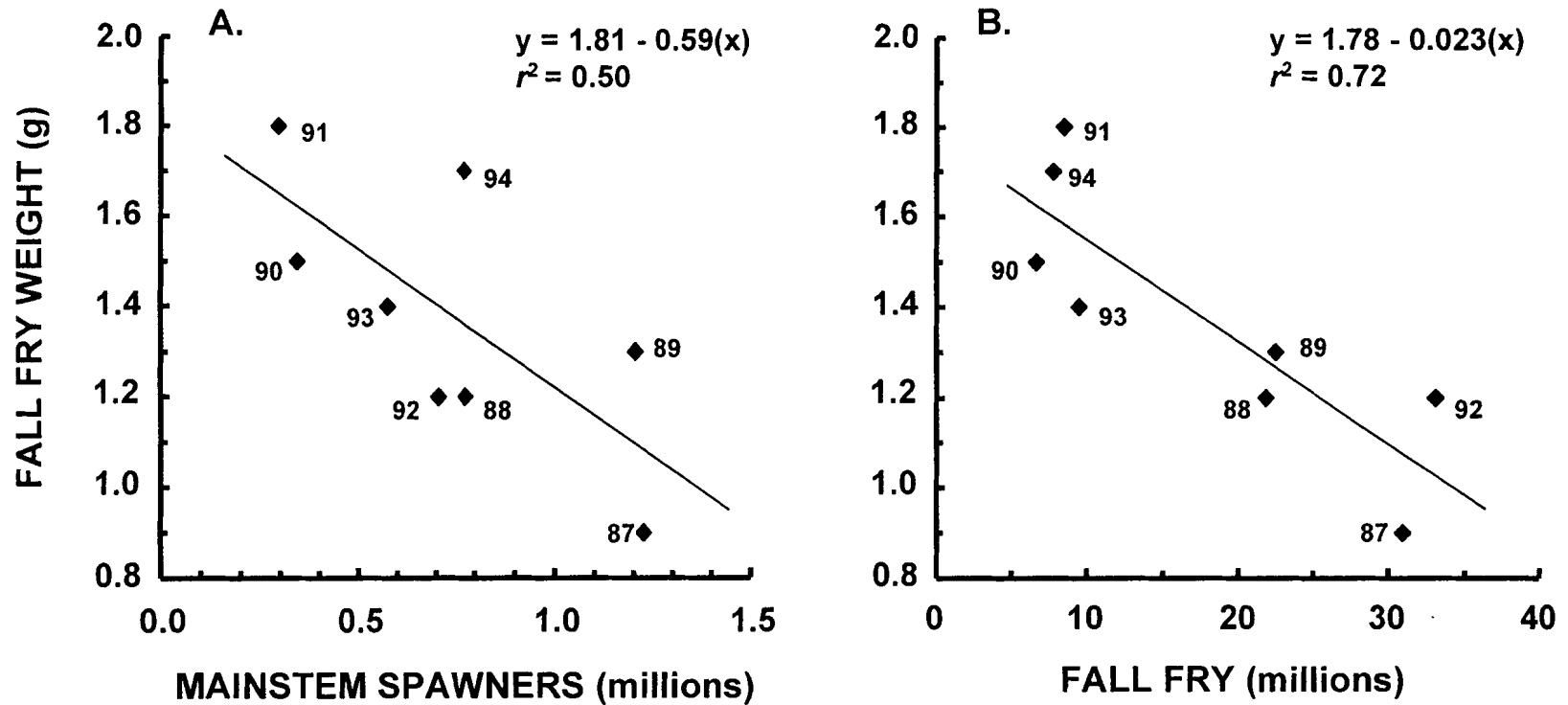
Figure 9. Relationship between the average weight of age-0 fall fry in Skilak Lake and (A) abundance of Kenai River sockeye salmon mainstem spawners and (B) Skilak Lake fall fry abundance. Data points are labeled by brood year (e.g., 1993 indicates weight of fall fry in 1994).
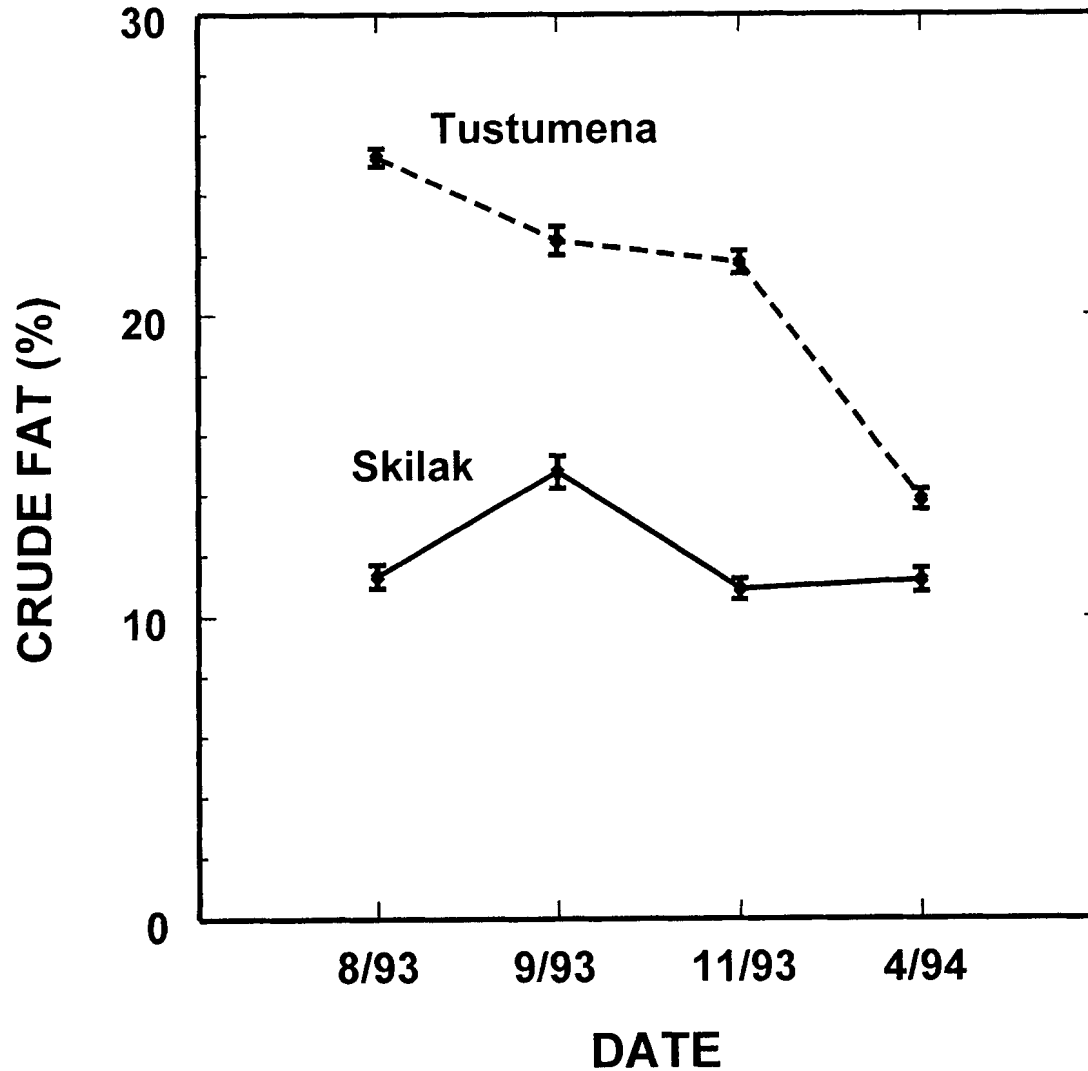
Figure 10. Comparison of the temporal pattern of percent crude fat in sockeye salmon fry between Skilak and Tustumena lakes. Analysis of the data using two-way ANOVA indicated a significant ($P < 0.001$) interaction between lake and date and that Skilak Lake fry consistently contained less fat that Tustumena Lake fry. Vertical bars are standard errors of the least squares means.
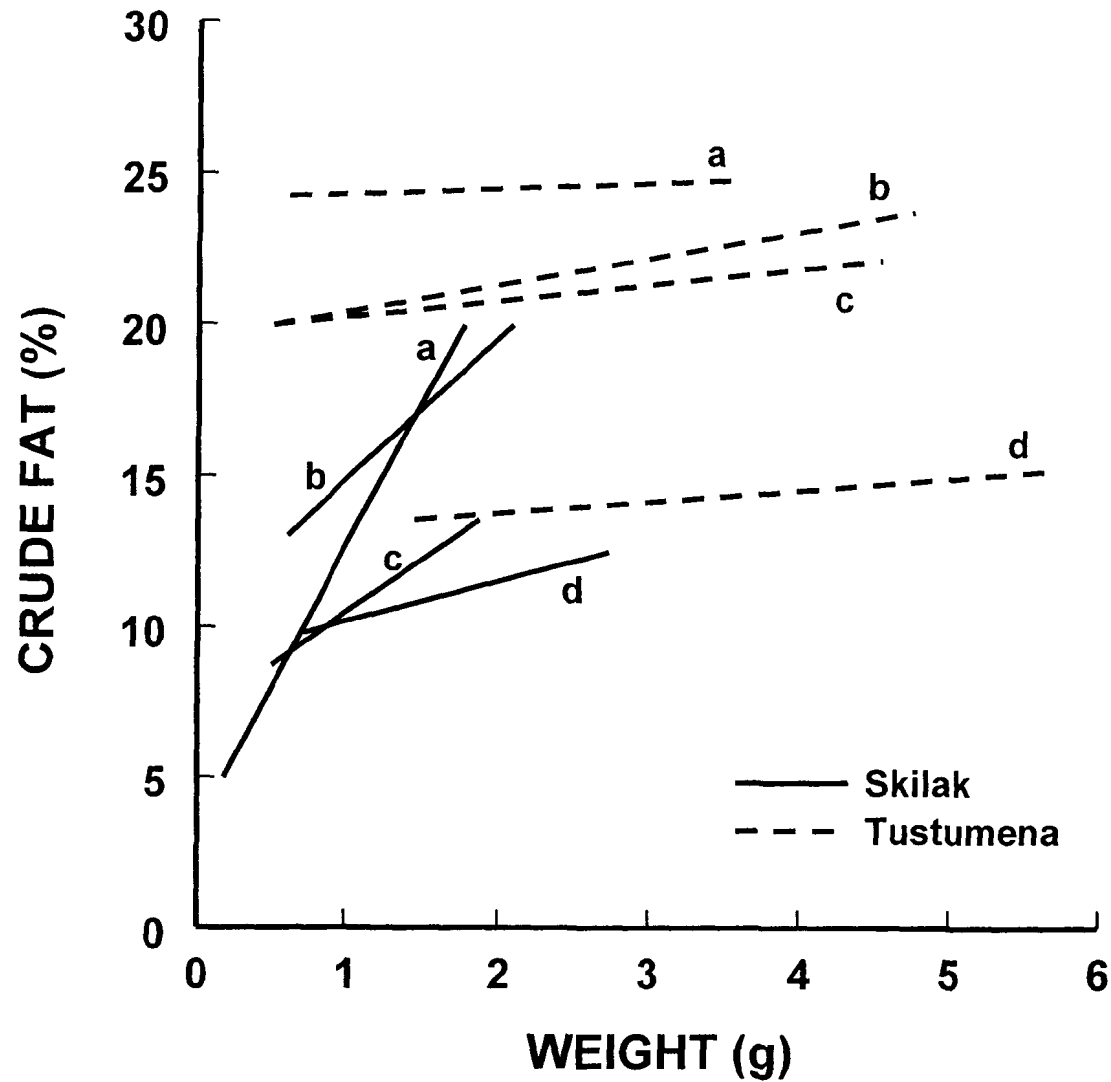
Figure 11. Comparison of slopes from the relationship between wet weight and percent crude fat in sockeye salmon fry collected from Skilak and Tustumena lakes; 'a' indicates August 1993, 'b' is September 1993, 'c' is November 1993, and 'd' is April 1994. Data for each lake were analyzed using analysis of covariance. The relationship was not significant ($P > 0.05$) for Tustumena Lake fry. However, Skilak lake fry exhibited a significant temporal change in the slope ($P < 0.001$).
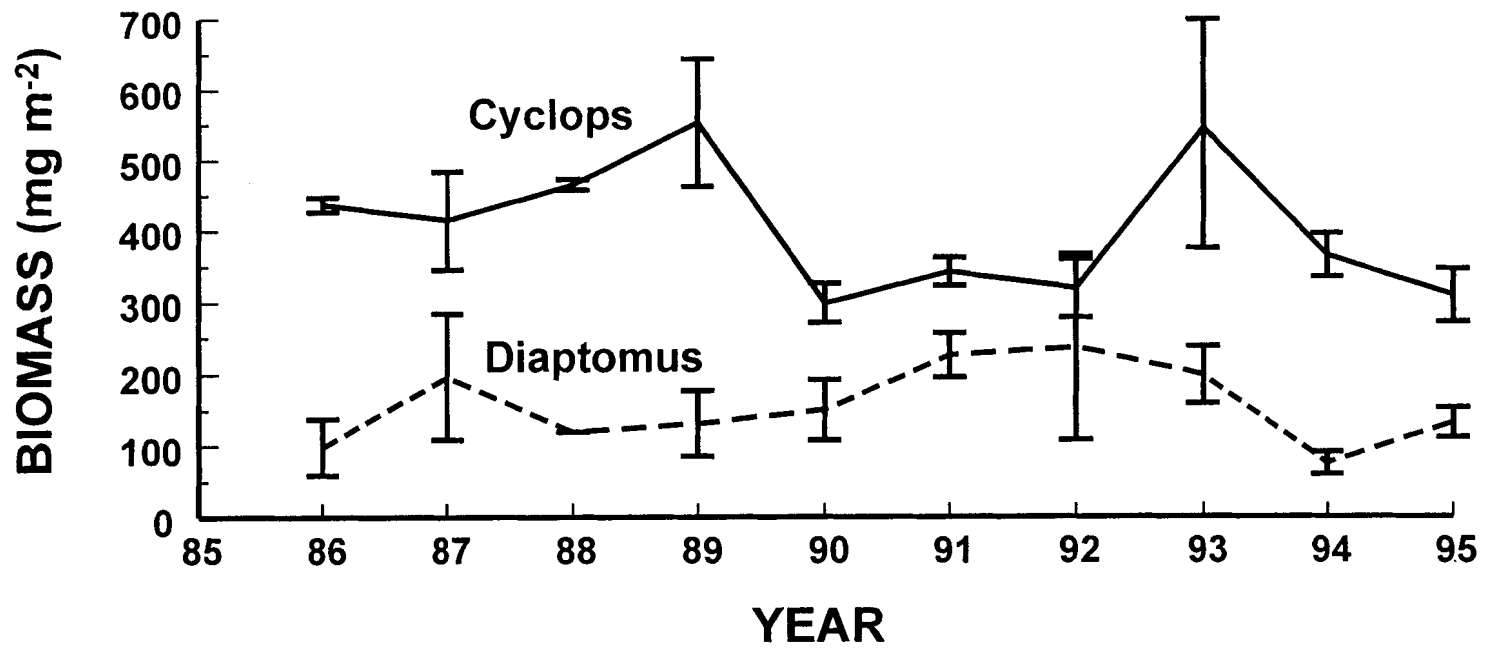
Figure 12. Inter-annual variation of macrozooplankton seasonal mean biomass (mg m⁻²) in Skilak Lake. Vertical bars indicate one standard error among sampling stations for each taxa.
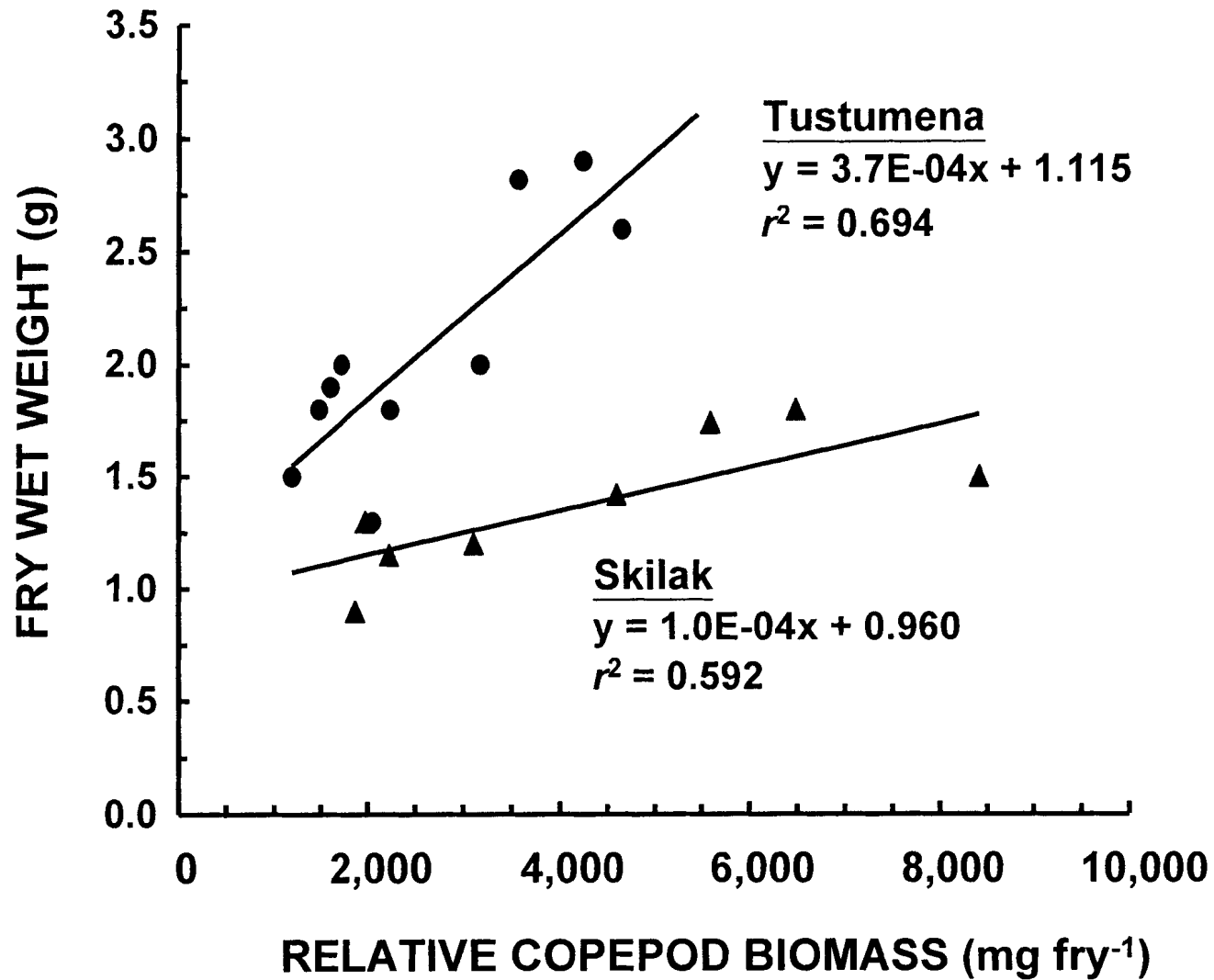
Figure 13. Comparison of the relationship of relative copepod biomass (mg fry^{-1}) and fall fry wet weight (g) between Skilak and Tustumena lakes. Analysis of covariance indicated a significant ($P = 0.008$) difference between the slopes
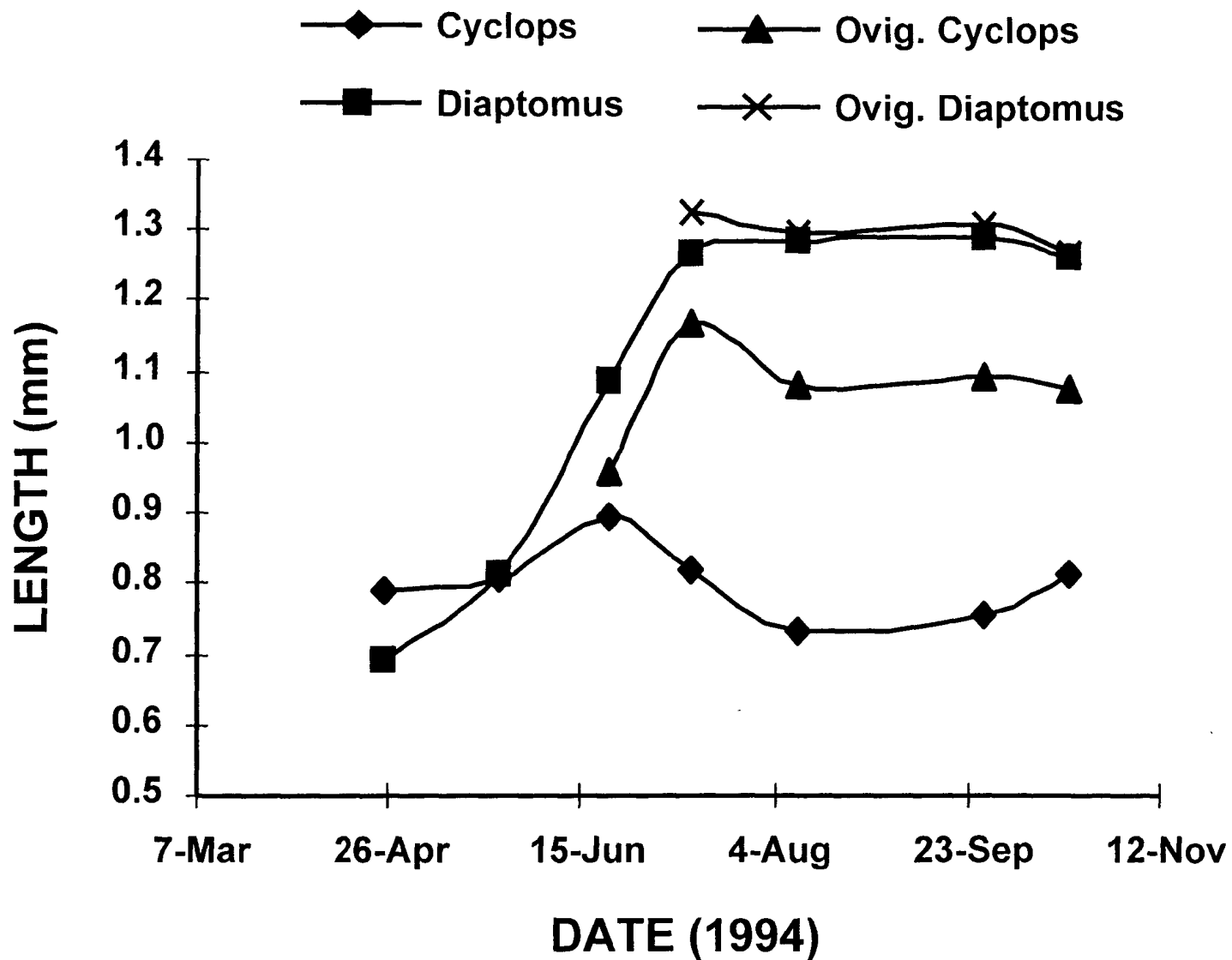
Figure 14. Plot of seasonal changes in mean length of *Cyclops* spp. and *Diaptomus* spp., including ovigerous individuals. The data were collected in 1994.
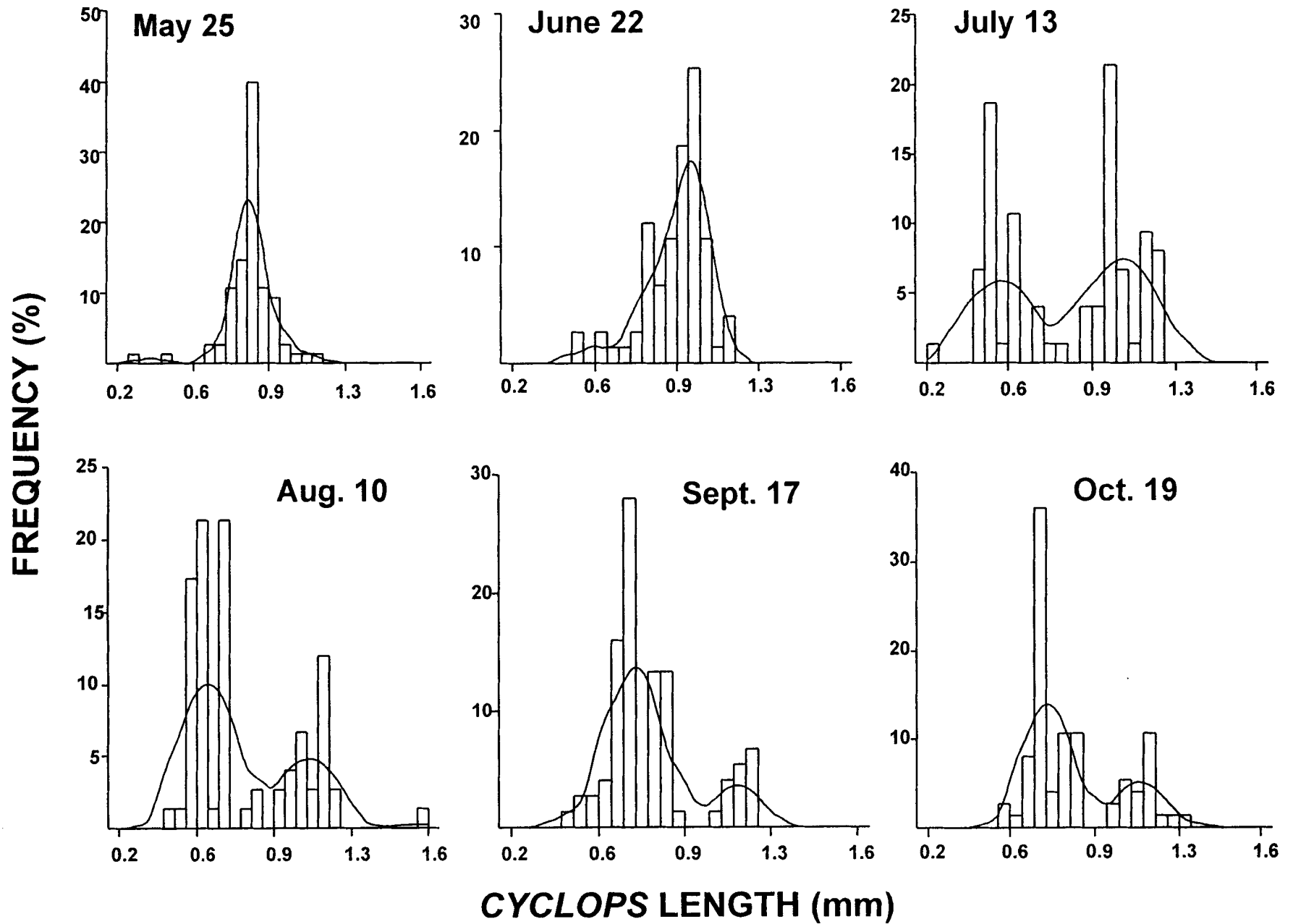
Figure 15. Comparison of monthly length frequency distributions of *Cyclops* spp. collected in 1994. Bimodality in the distributions becomes apparent in July, indicating separate age-class cohorts.
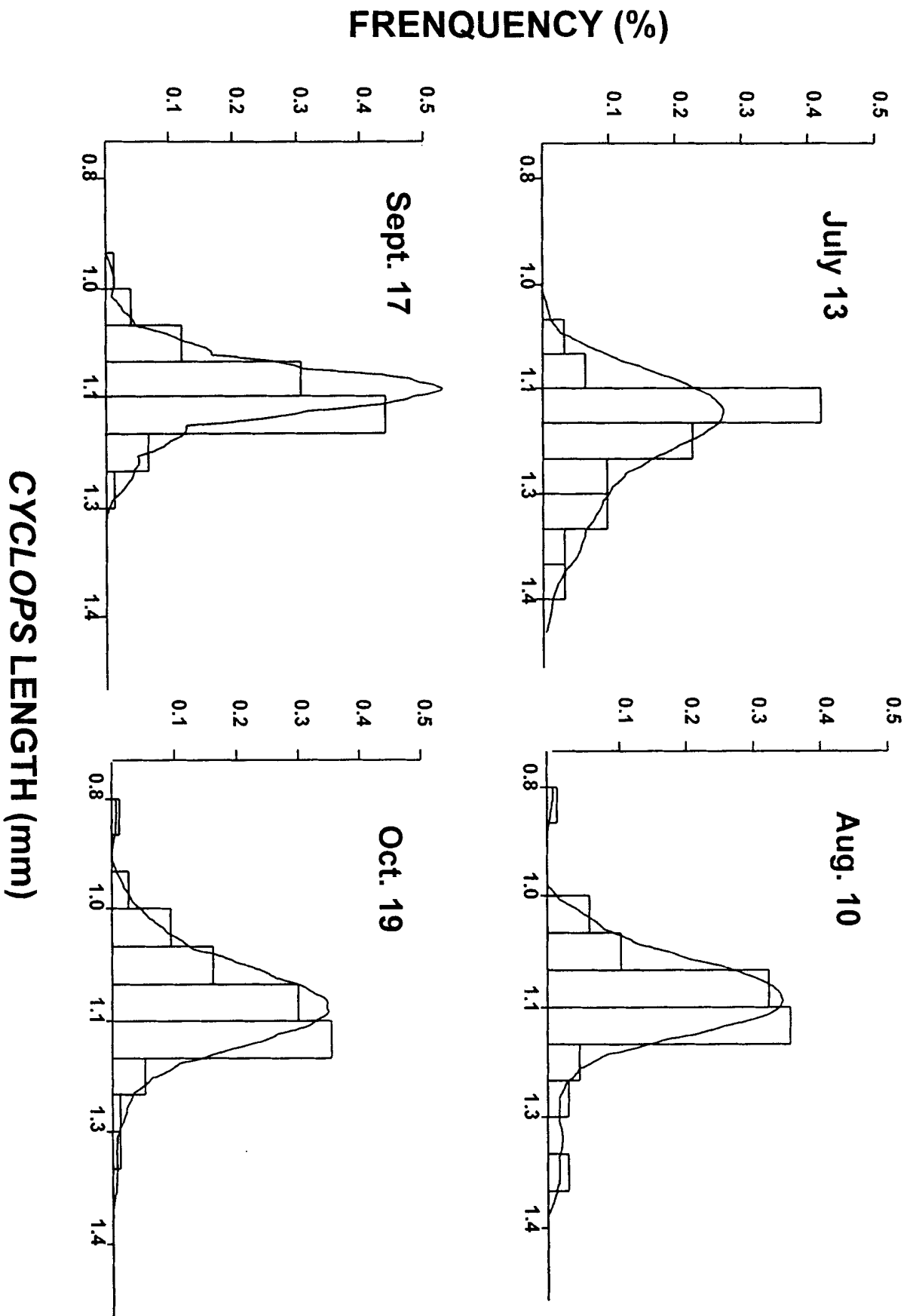
Figure 16. Comparison of monthly length frequency distributions of ovigerous *Cyclops* spp. collected in 1994. Distributions parallel the age-1 cohort from Figure 15.
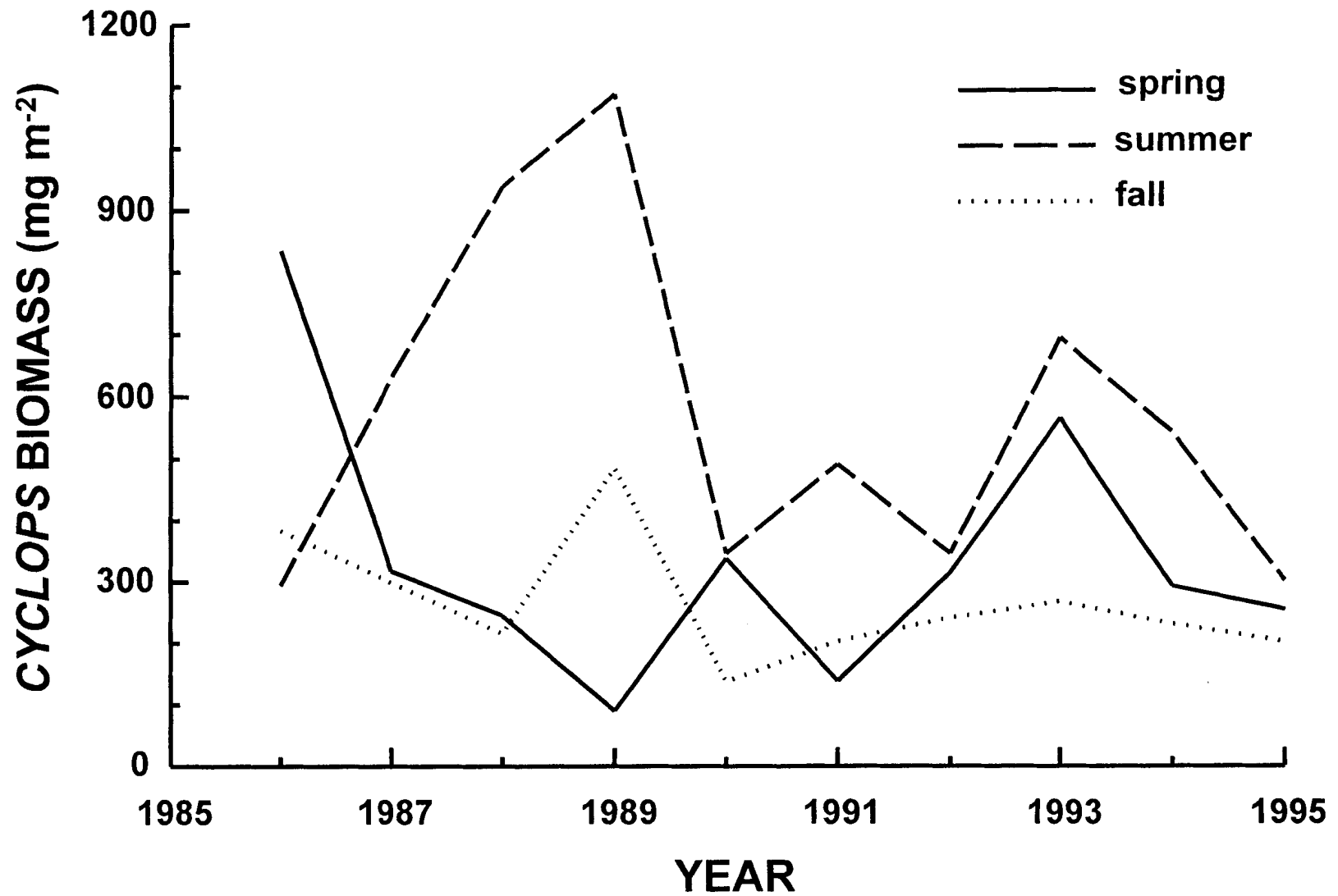
Figure 17. Inter-annual variation in *Cyclops* spp. biomass (mg m⁻²) for spring (May to June), summer (July to August), and fall (September to November) sampling periods in Skilak Lake, 1986 to 1994. Analysis of the data using a split-block design indicated a significant ($P < 0.05$) interaction between season and year.
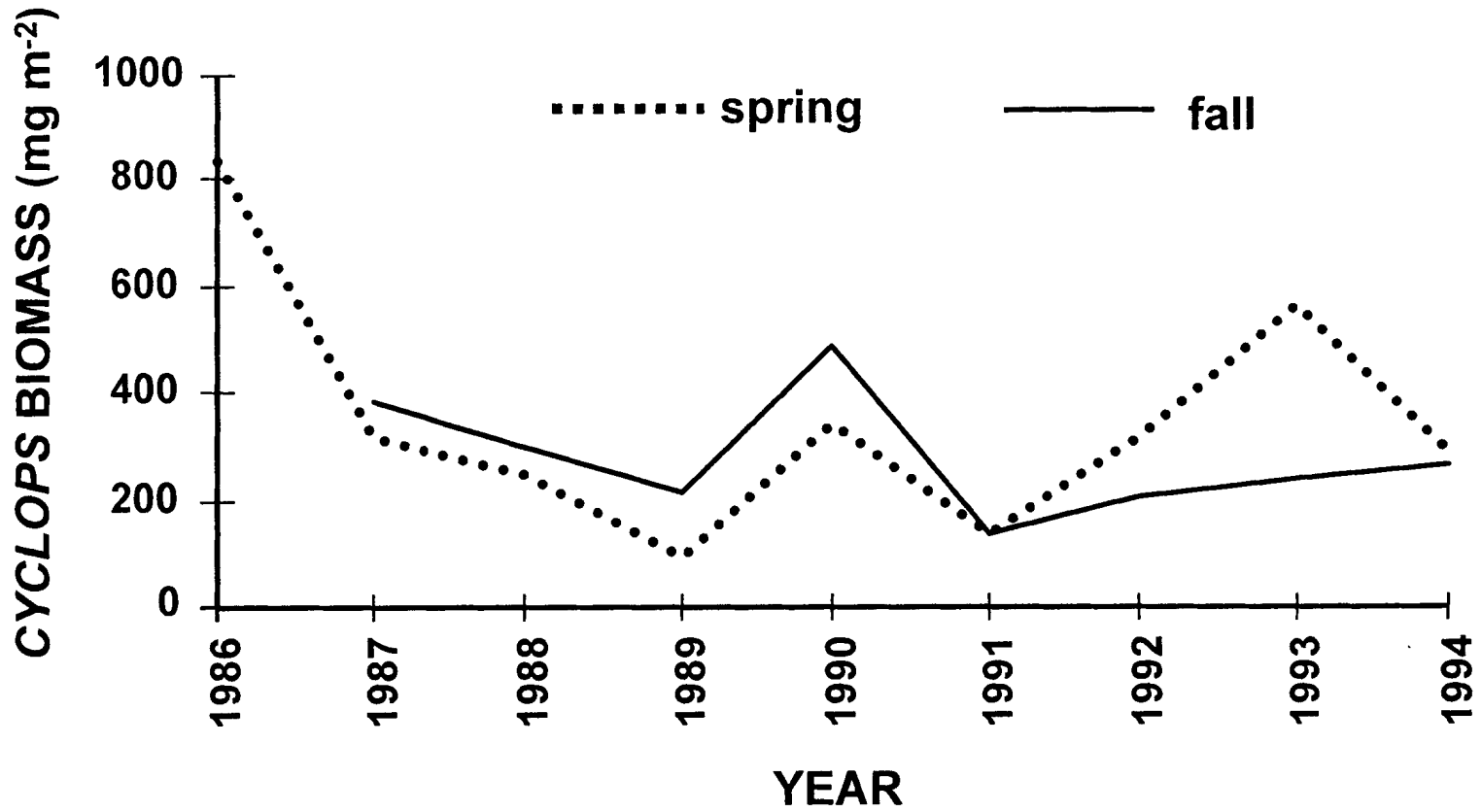
Figure 18. Comparison of fall (September to October) and subsequent spring (May to June) biomass of *Cyclops* spp.
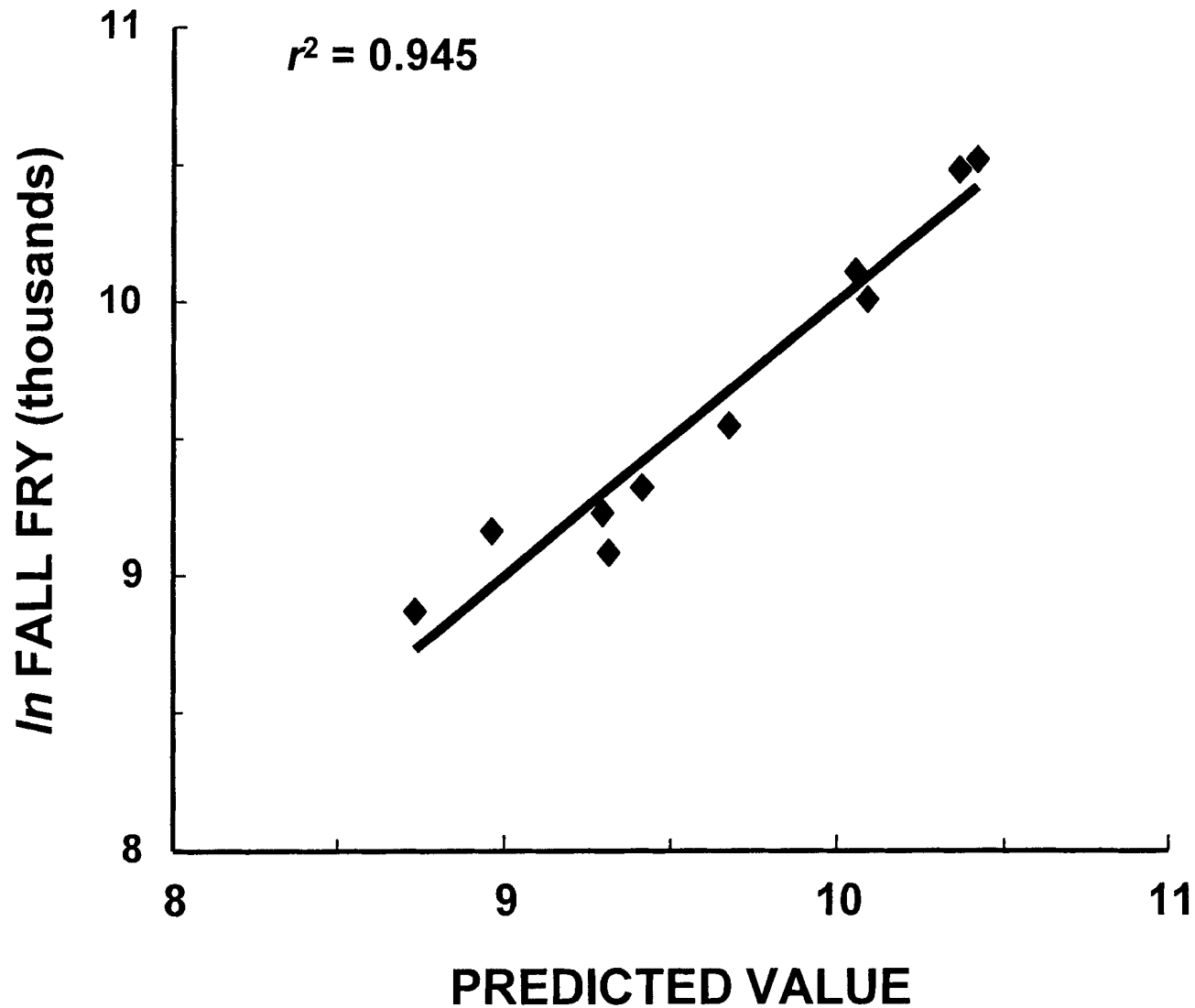
Figure 19. Predicted versus observed values from a multiple regression analysis of the model
In fall fry = α + β(mainstem spawners) + δ(spring *Cyclops* biomass) + γ (summer *Cyclops* biomass).
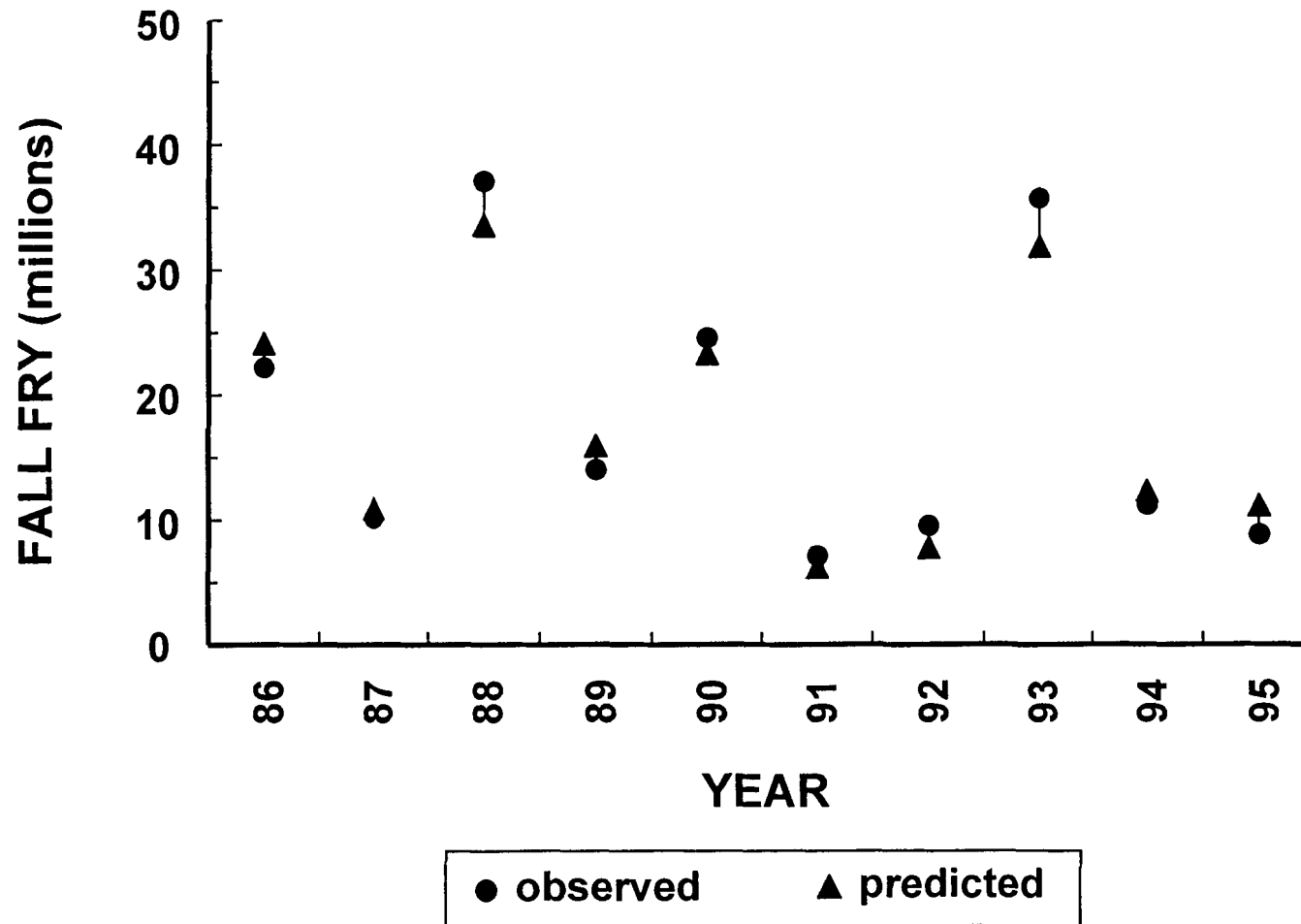Details of the analysis are given in Table 6

Figure 20. Temporal pattern in predicted and observed abundance of fall fry from a multiple regression analysis of the model *ln* fall fry = α + β(mainstem spawners) + δ(spring *Cyclops* biomass) + γ (summer *Cyclops* biomass). Details of the analysis are given in Table 6.
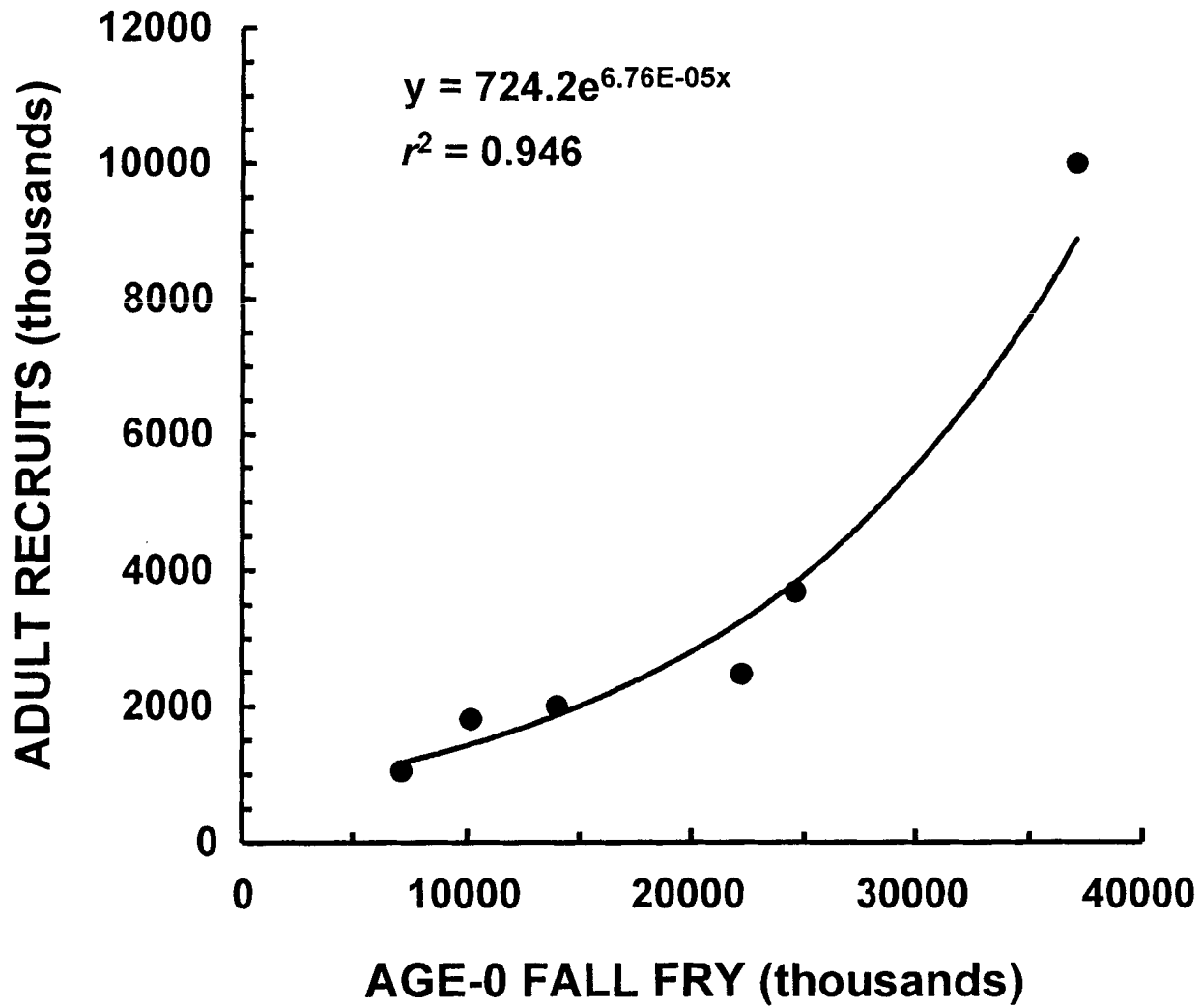
$$y = 724.2e^{6.76E-05x}$$

$$r^2 = 0.946$$

Figure 21. Relationship between fall fry and year-class adult recruitment for the Kenai/Skilak lakes system.
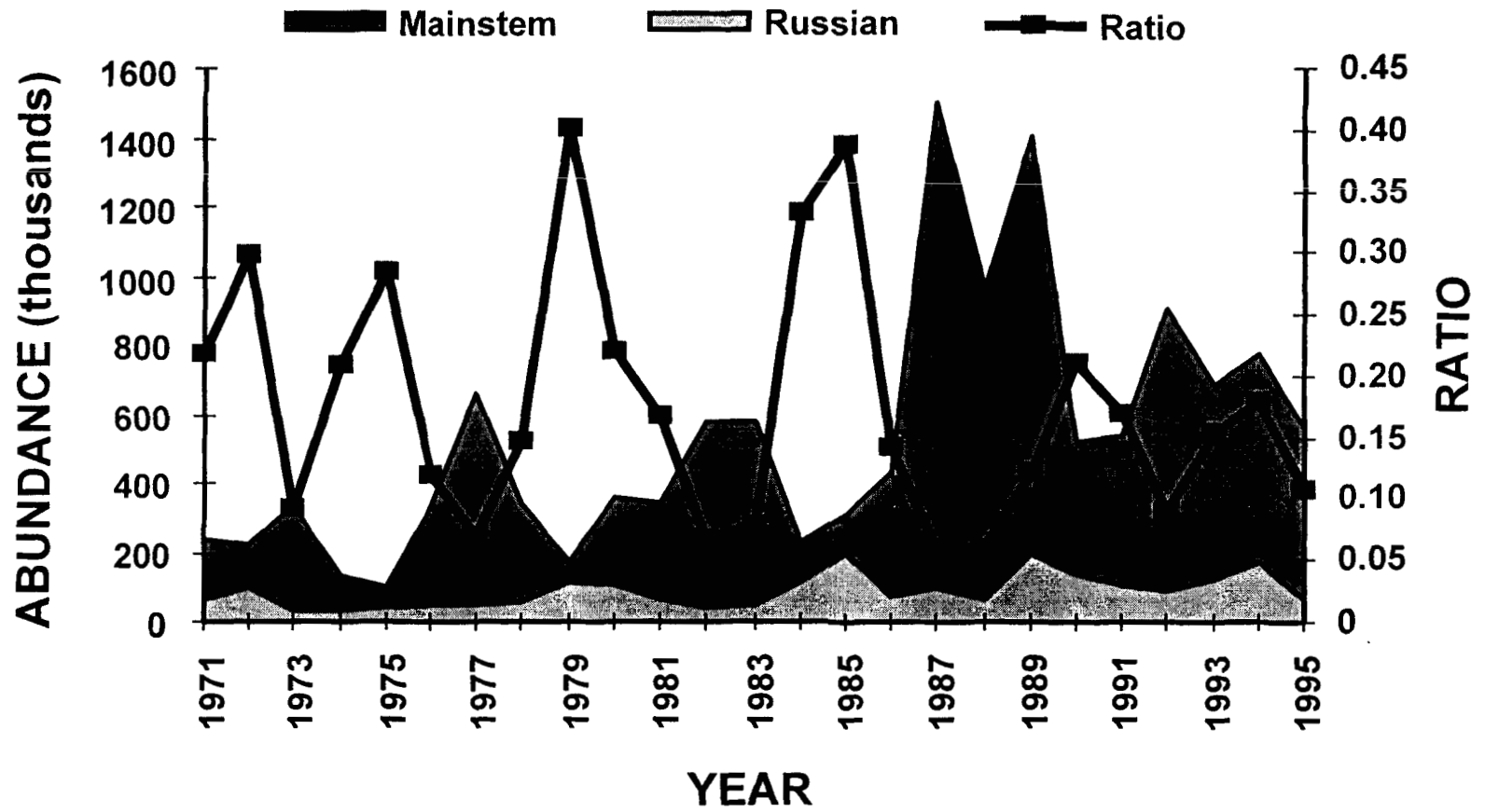
Figure 22. Temporal pattern of Kenai River Mainstem and Russian River spawner abundance. The ratio of Russian River to Mainstem spawners indicates a five year cyclic dominance pattern of mainstem run strength.
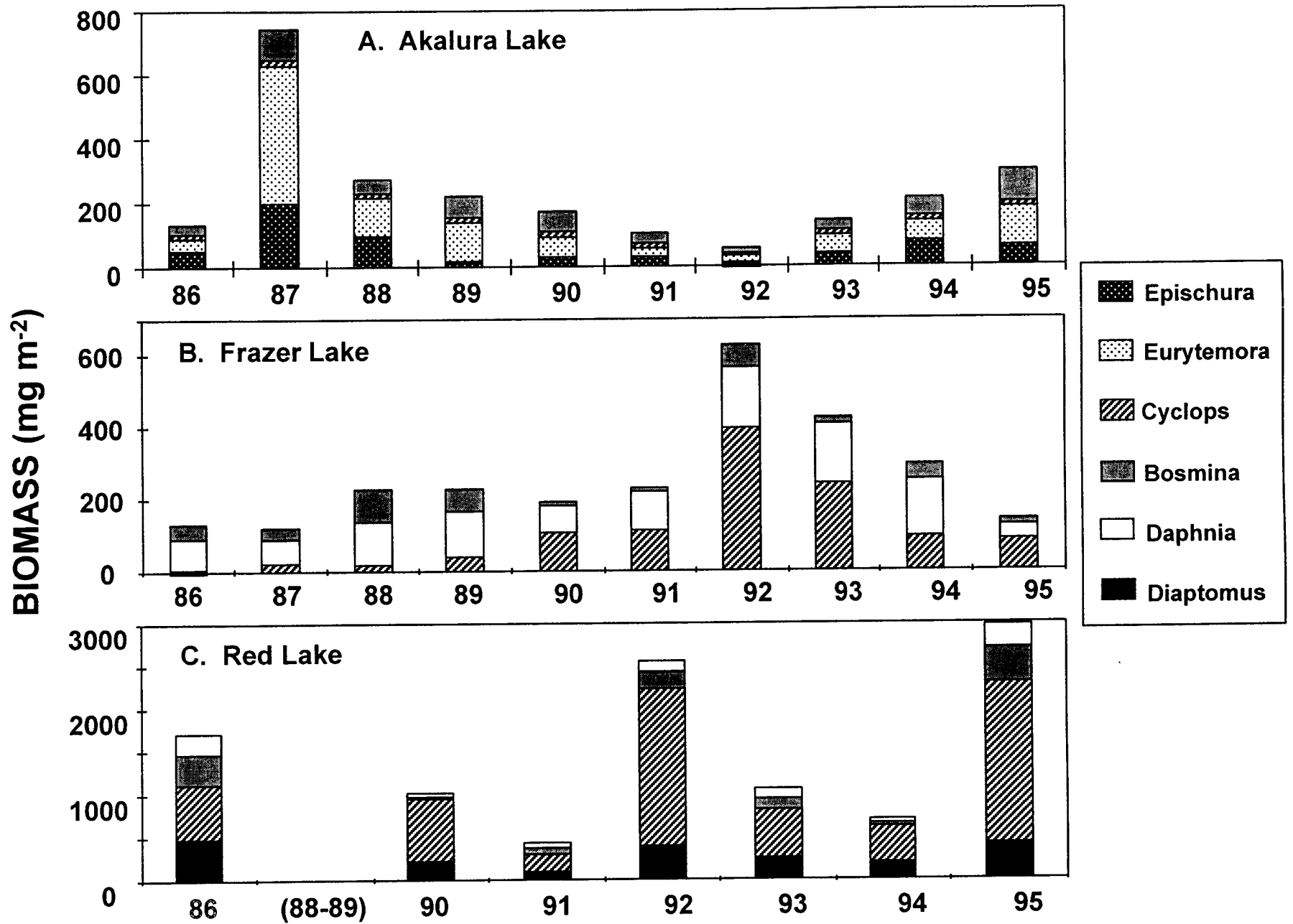
Figure 23. Inter-annual variation in zooplankton biomass from Kodiak Island study area lakes.
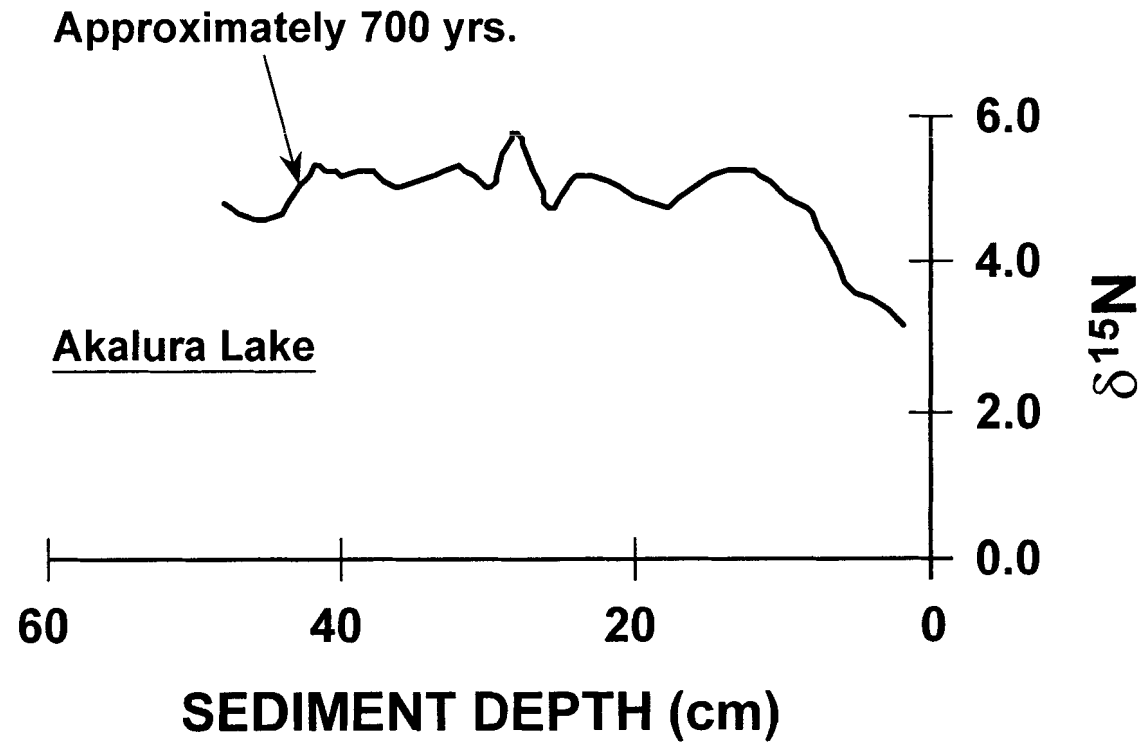
Figure 24. 700 year history of sediment marine nitrogen concentrations in Akalura Lake. The recent decline reflects the history of commercial fishing and decreased escapements.

APPENDIX A:

Sockeye Smolt Population Estimates, Outmigration Timing,
and Size at Age Characteristics for
Red, Akalura, and Frazer Lakes, 1995

by

Charles O. Swanton, Patricia A. Nelson, and Lewis G. Coggins Jr.