Exxon Valdez Oil Spill
Restoration Project Final Report

Sockeye Salmon Overescapement
(Kenai River Component)

Restoration Project 96258A-1
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K. E. Tarbox

Alaska Department of Fish and Game
Division of Commercial Fisheries
333 Raspberry Road
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Study History: Following the 1989 *Exxon Valdez* oil spill off Bligh Reef in Prince William Sound, the Kenai River system was selected for a damage assessment and restoration program to determine the effects of large sockeye (*Oncorhynchus nerka*) salmon escapements on the production of sockeye salmon. Restoration Project 96258A-1 is a continuation of the oil spill damage assessment program (Fish/Shellfish Study 27) initiated in 1990 by Alaska Department of Fish and Game (ADF&G) (Schmidt et al. 1993), which was subsequently modified in 1993 (Restoration Project 93002) and 1994 (Restoration Project 94258) based on the study results (Schmidt et al. 1995), and last reported on in 1997 (Restoration Project 95258) (Schmidt et al. 1997). Early investigations suggested that high densities of sockeye fry, produced from large escapements, induced cyclopoid copepods (pelagic zooplankton), the major prey for rearing sockeye juveniles, to undergo exaggerated diel vertical migration (DVM) in the major nursery lakes (Skilak and Kenai). Such behavioral changes (DVM) in zooplankton were thought to contribute to a substantial decline in the production of sockeye salmon in the Skilak-Kenai lake system through a vertical mismatch between fry and ovigerous cyclopoids (Schmidt et al. 1994), which led to decreased overwinter survival of age-0 sockeye (Schmidt et al. 1996). Further studies indicated that grazing by juvenile sockeye on a cohort of *Cyclops columbianus*, the dominant copepod in Skilak and Kenai lakes, affected recruitment of fry from the subsequent year class and impacted future production of *C. columbianus* (Schmidt et al. 1997). Taken together, these factors were hypothesized as an important biological mechanism underlying the patterns in sockeye salmon returns for the Kenai River system and provided a plausible explanation for the apparent compensatory responses to the high 1987-1989 (post oil spill) escapements (Schmidt et al. 1997).

Originally, Restoration Project 96258A-1 was considered part of Restoration Project 96258 (Sockeye Salmon Overescapement), which in addition to the Kenai River studies, included a monitoring and restoration program for select lake systems (Red, Akalura, and Frazer lakes) on Kodiak Island. In October 1997, the ADF&G Principal Investigator (ADF&G Statewide Limnology) for Restoration Project 96258 retired, following termination of the Statewide Limnology Program, and the Kenai River studies were severed from the Kodiak component and given the current project number 96258A-1. Responsibility for completing Restoration Project 96258A-1 fell to the original ADF&G Co-Principal Investigator (ADF&G Upper Cook Inlet Research). Prior to completing the project final report, however, the Co-Principal Investigator also retired (May 2001). In August 2001, ADF&G Central Region Limnology (Edmundson and Todd 2001) assumed lead responsibility for preparing the final report for project 96258A-1. The report herein on Restoration Project 96258A-1 describes the final research findings on the production of sockeye salmon from the Kenai River system impacted by the 1989 *Exxon Valdez* oil spill. The Kodiak portion of the original study (Restoration Project 96258A-2) has been finalized by others and submitted for review.

Abstract: The 1989 *Exxon Valdez* oil spill in Prince William Sound resulted in many commercial fishery closures, which led to significantly higher than normal escapements in some sockeye salmon systems. For the Kenai River (south-central Alaska), the number of sockeye salmon returning to spawn that year was twice the recommended escapement goal. A weak positive relationship existed between spawner abundance and the number of sockeye fry rearing in the fall in glacially turbid Skilak and Kenai lakes during the fall. The variability of total copepod biomass in the spring (May-June), coupled with abundance of adult spawners, provided a much higher degree of predictability of fall fry production. In addition, grazing by juvenile sockeye on cyclopoid copepods in the spring strongly influenced recruitment of the next generation of juvenile sockeye salmon. The adjacent year interaction of juvenile sockeye salmon competing for copepods in the spring was consistent with a brood interaction model that best described the spawner recruit relationship for this stock. In addition, total copepod biomass was also reduced when the depth of the euphotic zone decreased. In Skilak Lake, euphotic zone depths declined throughout much of the 1990s from increased glacier melting and its attendant silt loading and inorganic turbidity. Thus, changing climatic conditions may further modulate the interaction of copepods with recruitment of juvenile sockeye salmon in this large glacial system.

Key Words: Brood interaction, copepods, escapement, euphotic zone depth, fry, glacial lakes, Kenai River, *Oncorhynchus nerka*, planktivory, recruitment, sockeye salmon, turbidity, zooplankton.

Project Data: *Description and format of data* – Data used in this study are stored electronically by Alaska Department of Fish and Game (ADF&G), Central Region Limnology, Soldotna. Data are formatted as follows: map drawings (Photo-Paint version 7), physical data and zooplankton information (Microsoft Excel), water chemistry, nutrient and chlorophyll concentrations (Microsoft Excel), and fisheries (adult return and fry abundance) data (SPSS Systat and Microsoft Excel). *Custodian* - Custodian of the data used in this project is J. A. Edmundson, ADF&G, Division of Commercial Fisheries, 43961 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669, telephone: (907) 260-2917, facsimile: (907) 262-4709, electronic mail: jim_edmundson@fishgame.state.ak.us. *Availability* – ADF&G holds proprietary research rights to the data. Requested data will be made available under the discretion of the data custodian.

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EXECUTIVE SUMMARY

In March 1989, the tanker vessel *Exxon Valdez* grounded on Bligh Reef in Prince William Sound spilling nearly 11 million gallons of oil that spread slowly into the waters of Prince William Sound, Upper and Lower Cook Inlet, and the Kodiak archipelago. As a result of fishery closures that summer due to potential spill effects, many lake systems in these areas that produce sockeye salmon (*Oncorhynchus nerka*) received large spawning escapements. For the Kenai River system in Upper Cook Inlet, the 1989 escapement of approximately 1.3 million sockeye was more than twice the recommended escapement goal (550,000). Beginning in 1990, studies were initiated to examine the effects of the large escapements on the production of juvenile sockeye salmon from the Skilak and Kenai lakes the most important nurseries in the Kenai River system. In particular, this project focused on the immediate and longer term ecological consequences of large escapements.

Our research demonstrated that large numbers of spawners (escapement) produced larger fry populations; however, there was a significant negative relationship between fry abundance in the fall and fry weight indicating density dependent growth occurred in the system. After correcting for the effect of fish density, both fry weight and fall fry abundance were strongly related to the biomass of copepod (*Cyclops* + *Diaptomus*) zooplankton in the spring. Our assessment of length frequency distributions of *Cyclops columbianus*, the dominant copepod species, indicated that this species exhibits a two-year life cycle. We hypothesized that grazing by juvenile sockeye salmon on a cohort of *C. columbianus* is an important factor affecting the survival of juvenile sockeye salmon from the subsequent year class. That is, the biomass of survivors from the age-0 cohort of *C. columbianus* in the spring, strongly influenced survival of emergent sockeye salmon fry. Simply put, predation on copepods (mainly *Cyclops*) by fry in a given year affects copepod biomass the following spring, which has a compensatory effect on fry survival and subsequent adult returns. Recently, Carlson et al. (1999) specified a brood interaction spawner-recruit model for the Kenai River sockeye stock, which contained a statistical interaction term (cross product) of the current and prior years' spawner abundance. Our spawner-recruit analysis supported the hypothesis that large sockeye salmon escapements into the Kenai River watershed cause reduced returns from current and future spawner populations.

Total copepod biomass was also reduced when the depth of the euphotic zone decreased. In Skilak Lake, euphotic zone depths have declined over the past decade due to increased glacier melting and its attendant silt loading and inorganic turbidity, thereby reducing the productive (photosynthetic) capacity of this system. Persistent levels of higher turbidity may affect (lessen) vertical migration behavior of copepods or possibly reduce predation by visually attuned sockeye fry. Thus, regional-scale changes in climatic conditions may further modulate the interaction of copepods with juvenile sockeye salmon affecting salmon production. This is the final report on sockeye salmon overescapement, Restoration Project 96258A-1.

INTRODUCTION

The Kenai River watershed in south-central Alaska contains two large glacially turbid lakes, Skilak and Kenai that produce most of the sockeye salmon in upper Cook Inlet (Fox and Shields 2000). The number of sockeye salmon returning to spawn in the Kenai River watershed has increased from a few hundred thousand in the 1970s to more than a million in the late 1980s. However, the annual number of sockeye spawners in the system in recent years (1990s) averaged around 600,000. This trend of increasing escapement (spawner abundance) resulted from several factors including changes in management objectives (i.e., higher escapement goals), larger than expected salmon runs, and fishery closures as a result of the effects of oil spills from the tanker vessel (TV) *Glacier Bay* in 1987 and TV *Exxon Valdez* in 1989 (Schmidt et al. 1994). The *Exxon Valdez* spilled nearly 11 million gallons of oil that spread slowly into the waters of Prince William Sound, Upper and Lower Cook Inlet, and the Kodiak archipelago. From 1987-1989, sockeye escapements into the Kenai River system were approximately twice (1.3 million) that of previous years and double the Alaska Department of Fish and Game (ADF&G) management goal (550,000). Our study has focused on the ecological consequences of these large escapements.

Variation in the supply of zooplankton has been linked to growth and production of juvenile sockeye salmon (Goodlad et al. 1974; Hyatt and Stockner 1985; Koenings and Burkett 1987; Hume et al. 1996; Edmundson and Mazumder 2001). Assuming food is limited, greater food supply (zooplankton) should lead to higher growth rates and larger juvenile sockeye biomasses. On the other hand, negative responses of pelagic zooplankton to predation by rearing sockeye juveniles and subsequent effects on sockeye production have been observed in some lake ecosystems. For example, consecutive years of large numbers of spawners can severely depress macrozooplankton populations leading to a collapse of subsequent broods of sockeye (Kyle et al. 1988; Koenings and Kyle 1997; Edmundson et al. 1997). Kyle et al. (1988) found that large sockeye escapements into clear water Frazer Lake on Kodiak Island (Alaska) resulted in subsequent reductions in the size of sockeye juveniles (smolts) and fewer adult recruits produced per spawner that were correlated with lower zooplankton densities.

However, the effect of planktivory on macrozooplankton community composition may be more pronounced than the effect on total zooplankton biomass. It is also well known that, in lakes, planktivorous fish selectively consume large-bodied zooplankton and can shift zooplankton communities toward dominance by smaller species (Carpenter et al. 1985; Northcote 1988; Mazumder 1994; Brett and Goldman 1997; Ives et al. 1999). Intense planktivory by juvenile sockeye salmon has been related to a reduced abundance of large-bodied zooplankton with a corresponding decrease in growth of sockeye in freshwater (Goodlad et al. 1974; Kyle et al. 1988; Hume et al. 1996). Recently, Mazumder and Edmundson (2002) demonstrated that the abundance of large-sized *Daphnia*, rather than the total biomass of the macrozooplankton community, was the major determinant of size and production of juvenile sockeye in Packers Lake (Alaska).

Predation by planktivorous fish can also trigger behavioral responses in zooplankton (Bollens and Frost 1989). Under the predator-avoidance hypothesis (Iwasa 1982; Lampert 1989) zooplankton are assumed to migrate to avoid size-selective, visually-attuned predators. Diel vertical migration (DVM) is a common behavioral tactic in both marine and freshwater ecosystems where animals lessen the risk of predation by coming to the surface at night to feed and migrating to deeper depths during the day. Schmidt et al. (1994) hypothesized that high fry densities (from large escapements) in turbid Skilak Lake (Alaska) induced cyclopoid copepods to undergo exaggerated DVM, migrating to depths of greater than 50 m during the day and ascending to the surface layers at night presumably to avoid predators (fry). Furthermore, Schmidt et al. (1996) hypothesized that behavioral changes (DVM) in zooplankton contributed to a substantial decline in the production of sockeye salmon in the Skilak-Kenai lake system through a vertical mismatch between fry and ovigerous cyclopoids.

Within pelagic lake environments, crustacean zooplankton and planktivore vertical distribution patterns are often tightly coupled (Narver 1970; Levy 1990a). However, in some British Columbia lakes where juvenile sockeye underwent DVM, Levy (1990a) found that zooplankton assemblages were non-migratory, remaining near the surface. In other lakes where sockeye fry migrated to the surface during the day and descended at night (i.e., reverse DVM), Levy (1990a) discovered that zooplankton underwent normal DVM patterns. Hume et al. (1996) found *Daphnia* biomass was much higher in the refugia of the near surface waters of Shuswap Lake (British Columbia) where warmer temperatures precluded the presence of foraging sockeye fry. Vertical migration probably represents a complex interaction of predation pressure, food resource availability, environmental (physical) cues, and bioenergetic constraints (Eggers 1978; Beauchamp et al. 1989; Levy 1990ab; Bevelhimer and Adams 1993; Stockwell and Johnson 1999).

There is a widespread consensus that marine plankton and fish populations respond to climatic events and that major changes have taken place in ocean-climate conditions in the past few decades (Francis and Hare 1994; Roemmich and McGowan 1995; Mantua et al. 1997; Hare et al. 1999). The role of climate in regulating zooplankton prey abundance, fish recruitment, and food web structure in lakes has received much less attention (Beamish 1995). It has been suggested that climate warming or large-scale climate oscillations may alter seasonal dynamics of limnetic zooplankton (George 2000; Gerten and Adrian 2000; Scheffer 2001). Substantial changes in aquatic environments from increasing CO_2 levels and other greenhouse gases in the atmosphere have led to both increases and decreases in the production of freshwater fishes (Lehtonen and Lappalainen 1995; Minns and Moore 1995; Stefan et al. 1995). However, evidence of climatic forcing of long-term changes in aquatic communities may be masked because of variable ecological processes and lake typology effects (Schindler et al. 1996; Fee et al. 1996; Gerten and Adrian 2000, 2001; Edmundson and Mazumder 2001, 2002).

Future climatic changes are also assumed to have a profound influence on the variability and magnitude of glacial meltwater and its effects on flow regimes in glacier-fed systems (Brittain and Milner 2001). In North America, glaciers have, for the most part, retreated over the past 50 years, presumably as a result of an enhanced greenhouse effect (Melack et al. 1997). Therefore, in glacially influenced lakes that support populations of juvenile sockeye, significant increases in glacier meltwater intrusion would likely increase the magnitude of silt loading and turbidity. Studies of sockeye nursery lakes in Alaska have shown that increases in water turbidity produced from glacial silt not only reduce light penetration (Koenings and Edmundson 1991), but also tend to decrease phytoplankton and zooplankton abundance and lower fish yield (Koenings et al. 1990; Edmundson and Carlson 1998; Edmundson and Mazumder 2001). Thus, we hypothesize the interaction between long-term (decadal) changes in environmental conditions, brought about by regional climatic effects, and variable grazing pressure by rearing sockeye juveniles imposed on zooplankton, may regulate fry recruitment and population dynamics of sockeye salmon in the glacier-fed Kenai River system.

Hypotheses

In this final report, we evaluate the hypotheses that (1) large escapements of adult sockeye salmon into the Kenai River watershed cause reduced returns from current and future spawner population, (2) intense grazing by large fry populations in Skilak Lake reduces spring copepod densities the following spring causing reduced survival of emergent fry and elevated overwinter mortality of fry the following winter, and (3) increased water turbidity from glacial run-off reduces the EZD in Skilak Lake and the biomass of copepods, the primary food resource for rearing sockeye juveniles. We examine a 17-year data set on copepod zooplankton (*Cyclops* and *Diaptomus*) abundance and their size distribution, fry abundance and size, water turbidity, and light penetration in conjunction with historical (1971-2001) adult sockeye return information. We investigate relationships between zooplankton, climate, and sockeye fry recruitment and develop an overall hypothesis describing the freshwater processes that may regulate adult sockeye returns to the Kenai River watershed, Alaska.

Description of study site

The Kenai River is located on the Kenai Peninsula in south-central Alaska (Figure 1). Within the Kenai River watershed, Skilak and Kenai lakes are the major nursery areas for sockeye salmon fry. The glacial waters of the Snow River feed into Kenai Lake, the outlet of which is the beginning of the Kenai River. Downstream from this lake, the Kenai River flows into Skilak Lake. The river channel below Skilak Lake, the larger of the two lakes, has a relatively low gradient and flows westerly into Upper Cook Inlet. Of the two largest glacial lakes in the system, Skilak Lake is the most studied because it accounts for more than 90% of the total (Skilak + Kenai) fry production (DeCino 2002). Skilak Lake has a surface area of 99 km^2, mean depth of 73 m, and maximum depth of 160 m (Figure 2); Kenai Lake has a surface area of 55.9 km^2, mean depth of 91 m, and maximum depth of 165 m (Figure 2). During 1986-2001, the average ($\pm$1 standard deviation) turbidity of Skilak Lake in the 1-m stratum was 10 $\pm$8 nephelometric turbidity units (NTU). For Kenai Lake, limnological data were available for seven years (1990-1996) and the mean turbidity was 9.0 $\pm$6.0 NTU. In both lakes, the copepods *Cyclops columbianus* and *Diaptomus pribilofensis* compose nearly all of the limnetic zooplankton in terms of both density and biomass (Schmidt et al. 1997). Table 1 summarizes general

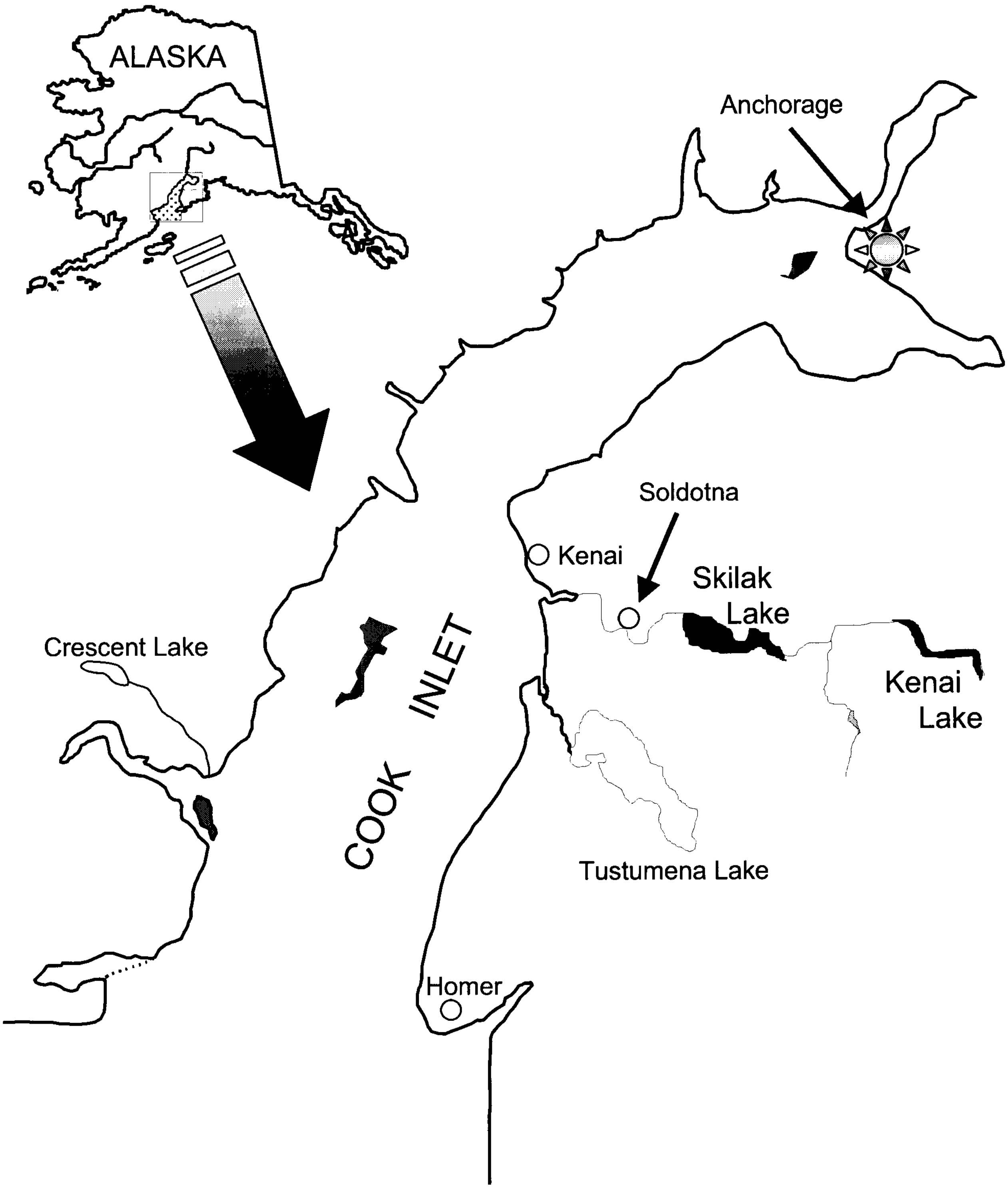

Figure 1. Geographic location of Skilak Lake in relation to the Kenai River system and Cook Inlet, Alaska.

Table 1. Summary of water chemistry, nutrients, and chlorophyll *a* for Skilak (1990-2001) and Kenai (1990-1994) lakes. Data were derived from the 1-m stratum.

		Skilak Lake				Kenai Lake			
Parameter	Units	n	Min	Mean	Max	n	Min	Mean	Max
Conductivity	μmhos cm^{-1}	230	54	63	73	143	55	69	78
pH	units	230	6.4	7.2	7.8	143	6.3	7.2	7.7
Alkalinity	mg L^{-1}	230	12	23	28	143	17	23	27
Turbidity	NTU	230	0.8	8.9	47.9	143	1.7	9.0	29.9
Color	Pt units	230	2	4	14	143	2	5	18
Calcium	mg L^{-1}	230	1.0	9.8	15	143	9.2	11.1	15.2
Magnesium	mg L^{-1}	230	0.2	0.6	3.4	143	0.1	0.6	2.7
Iron	μg L^{-1}	230	15	384	2,508	143	21	395	1,440
Total phosphorus	μg L^{-1}	230	2.1	11.0	40.4	142	3.4	12.6	47.5
Total filterable phosphorus	μg L^{-1}	230	0.2	2.3	13.2	143	0.6	2.1	11.8
Filterable reactive phosphorus	μg L^{-1}	230	0.6	2.1	9.0	143	0.2	2.0	11.1
Kjeldahl nitrogen	μg L^{-1}	230	11	40	98	142	5	30	55
Ammonia	μg L^{-1}	230	0.2	4.7	24.0	143	1.0	2.6	10.2
Nitrate+nitrite	μg L^{-1}	230	110	181	295	143	127	205	288
Silica	μg L^{-1}	228	1,228	1,440	1,712	143	1,240	1,544	1,848
Particulate organic carbon	μg L^{-1}	229	7	77	715	143	7	67	294
Chlorophyll *a*	μg L^{-1}	228	0.0	0.3	2.8	142	1.0	0.3	3.4

water chemistry, nutrient concentration, and algal biomass levels for these two sockeye nursery lakes.

METHODS

Sockeye salmon data

Alaska Department of Fish and Game (ADF&G) estimated sockeye escapement in the Kenai River system by fixed sonar counters and fish wheels for collecting samples of the escapement for species apportionment (King and Tarbox 1991). Total number of spawners in the Kenai River was estimated from sonar counts minus the enhanced component of the Hidden Lake escapement and the estimated sport fishing harvests above the counting sites (Tobias and Willette 2001). To obtain the number of mainstem spawners for the Kenai River, spawner estimates were further adjusted by removing escapement estimates from both Russian River and Hidden Lake (weir counts), which are two other important sockeye producers within the Kenai River watershed. Therefore, adjusted sonar counts are considered equal to the number of mainstem Kenai River sockeye spawners. Abundance, size, and freshwater age of juveniles (fry) rearing in Skilak and Kenai lakes were estimated using hydroacoustic (sonar) surveys and tow net sampling for species apportionment (DeCino 2002). The surveys consisted of multiple (12-16) orthogonal transects and the hydroacoustic data were analyzed by a combination of echo integration and echo counting techniques. Fry were collected from surface trawls using a 2 m × 2 m closing net system designed by Biosonics, Incorporated (DeCino 2002). Size (length and weight) of juvenile sockeye fry was measured on preserved (10% formalin) specimens and age was determined from scale pattern analysis using direct visual analysis of scales. During 1993-1994, we also examined seasonal changes in lipid content of juvenile sockeye. The University of Alaska, Palmer Agricultural Laboratory analyzed total lipid content in 403 fishes using the Randall ether extraction process (Randall 1974).

Limnological data

During 1986-2001, two stations (A and B) in Skilak Lake (Figure 2) were sampled consistently to profile light penetration and water temperatures, and to collect representative zooplankton and water samples. In 1990, station C located approximately mid-way between stations A and B was added to our surveys. These limnological surveys were conducted throughout the ice-free period at about three week intervals usually from early May through October. Underwater irradiance (light penetration) was measured with an International Light or Li-Cor submarine photometer equipped with a cosine corrected sensor. We calculated euphotic zone depth (EZD), the depth equivalent to 1% of the subsurface light, after Kirk (1994). Samples for water turbidity, as reported herein, were collected from the 1-m stratum. Turbidity (NTU) was measured in the laboratory using a formazine calibrated HF Scientific Instruments model DRT 100 or 00B nephelometer.

To collect zooplankton, vertical hauls were made from a depth of 50 m using a 153-µm Nitex mesh net with a 0.5-m diameter stainless steel ring at the mouth and a 200-ml

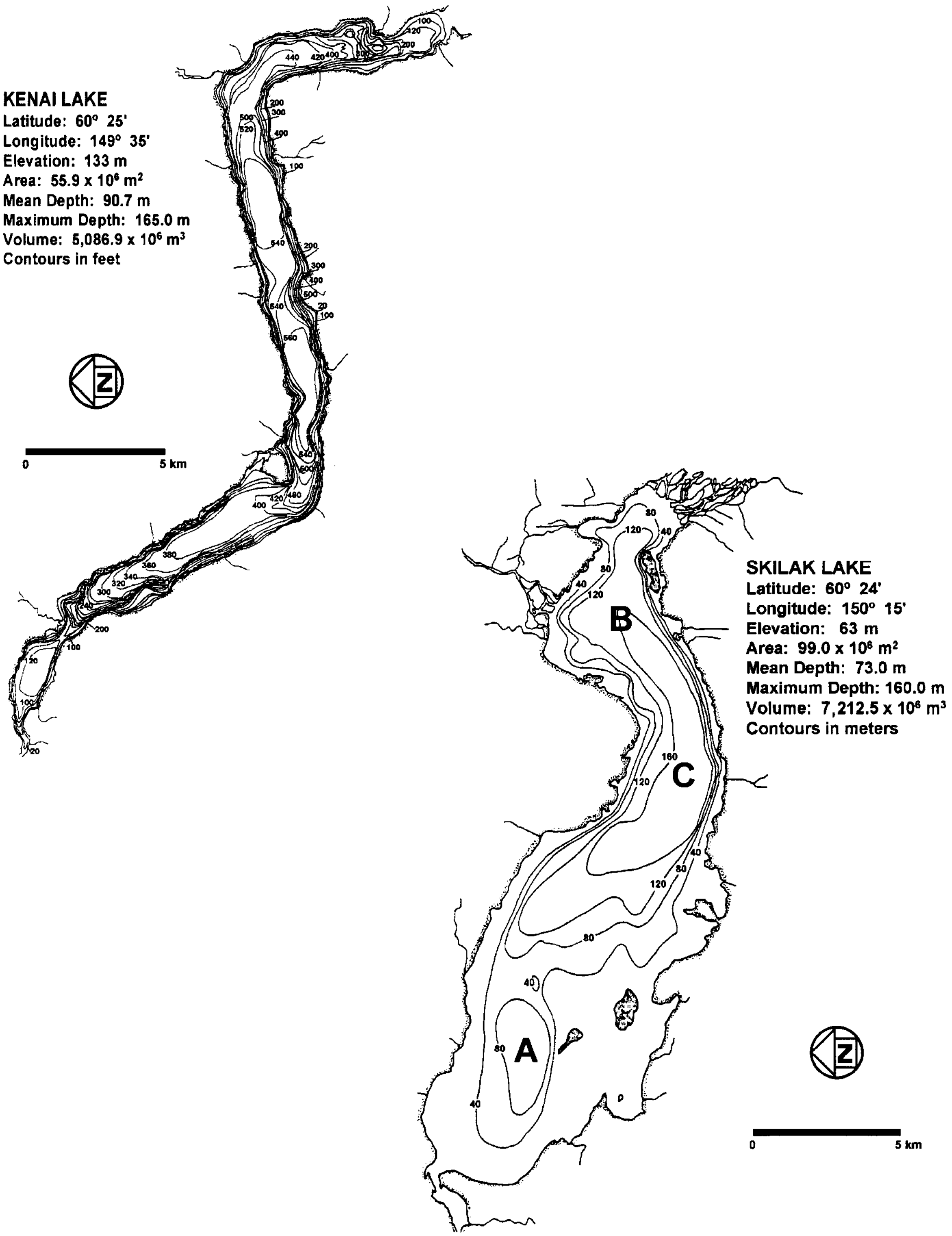

Figure 2. Bathymetric maps of Kenai and Skilak lakes with morphometric data. Letters (A-C) denote the location of the limnology sampling sites.

collection bucket. The net was hoisted to the surface at a rate of about 0.5 m s^{-1}. The net contents were poured into a 125-ml polybottle and brought to a final solution of 10% buffered formalin. In the laboratory, macrozooplankters were enumerated from triplicate 1-ml subsamples, and sized to the nearest 0.02 mm using a 70× power dissecting scope. Counts were converted to areal density (number m^{-2}) estimates. Individual dry weight was estimated by means of mass-length regression equations for zooplankton, as reported by Koenings et al. (1987). To compute species biomass, average dry weight was multiplied by areal density. For each year, the instantaneous biomass measurements (for each species) were averaged over both sampling stations and then across all survey dates to obtain mean annual biomass. For seasonal mean biomass, we computed average biomass of each species for three periods: spring (May-June), summer (July-August) and fall (September-October). We expressed annual and seasonal mean biomass on the basis of per-unit lake area (mg m^{-2}) rather than on a volumetric basis because the latter implies a uniform distribution. Use of area estimates of crustacean abundance and biomass in regression analyses of fish production, biomass, or yield is commonly reported in the literature. All samples were processed by ADF&G limnology laboratory located in Soldotna and followed standardized procedures and quality assurance methods (Koenings et al. 1987).

Glacier mass balance and climatological data

Source data for glacier mass balances for Wolverine Glacier in the Kenai Mountains were available from U.S. Geological Survey (USGS) as part of their long-term ice and snow-monitoring program (http://ak.water.usgs.gov/glaciology/index.html). Although water runoff from Wolverine Glacier does not enter Skilak Lake directly, Wolverine Glacier makes up part of the large Harding ice field that includes Skilak Glacier, which feeds into the eastern basin of Skilak Lake and is its major source of glacial meltwater intrusion (turbidity). Hence, we considered the summer mass balance of the Wolverine Glacier as a reasonable index of summer mass balance for Skilak Glacier. The summer ice balance (SIB) is the loss of snow and ice mass calculated from the extrapolation of point measurements on the glacier surface (Fountain et al. 1997). SIB is expressed in water equivalents (meters); where smaller (more negative) SIB values equate to greater mass loss and more glacier runoff (meltwater).

Data for computing annual and summer air temperature anomalies were obtained from the Alaska Climate Research Center (http://climate.gi.alaska.edu/). We used the 52-year data set (1950-2001) of temperatures measured at the City of Kenai, Federal Aviation Administration airport (Station 504546). For each year, we subtracted the individual mean annual temperature from the 52-year average temperature to obtain the annual air temperature anomaly. In a similar fashion, the summer air temperature anomaly was computed as the difference between the summer (June-August) mean for a specific year and the average June-August temperature calculated over the 52-year time series.

Statistical analysis

Spawner-recruitment models

We evaluated five models to explain the relationship between number of spawners and recruitment of Kenai River sockeye salmon. We first fit a general Ricker model that provides for depensation at low stock size and compensation at high stock size (Reish et al. 1985; Hilborn and Walters 1992; Quinn and Deriso 1999), i.e.

$$R_t = S_t^{\gamma} \exp(\alpha - \beta S_t + \varepsilon_t), \qquad (1)$$

where R_t is recruits, S_t is spawners, α is a density-independent parameter, γ and β are density-dependent parameters, and t indicates the brood year. In all of the models, density-independent survival is given by ε_t, which is assumed to be a random variable with a mean of zero and a constant variance σ^2. When $\gamma>0$, the spawner-recruit curve is dome shaped like the Ricker model (Quinn and Deriso 1999). Depensation is indicated if γ is significantly greater than 1.0. Hilborn and Walters (1992) suggest that γ should be 2.0 or larger for strong depensatory effects. The classic Ricker model (Ricker 1954, 1975) is a special case when $\beta>0$ and $\gamma=1$, i.e.

$$R_t = S_t \exp(\alpha - \beta S_t + \varepsilon_t). \qquad (2)$$

The Cushing model (Cushing 1971, 1973) is a special case when $\beta=0$ and $\gamma>0$, i.e.

$$R_t = \alpha S_t^{\gamma} + \varepsilon_t. \qquad (3)$$

However, the Cushing model is not used much in practice, because it predicts infinite recruitment for infinite spawning stock (Quinn and Deriso 1999). The case when $\gamma\leq 0$ does not correspond to a valid spawner-recruit model, because it does not go through the origin (Quinn and Deriso 1999).

Several authors have examined density-dependent models that include interactions terms between brood-year spawners and prior year spawner with lags from 1-3 years (Ward and Larkin 1964; Larkin 1971; Collie and Walters 1987; and Welch and Noakes 1990). However, Myers et al. (1997) examined data from 34 sockeye stocks and found no evidence for brood interactions at lags exceeding one year. We fit the Kenai River sockeye salmon data to a modified Ricker model used by many of these investigators with only a 1-year lag, i.e.

$$R_t = S_t \exp(\alpha - \beta_1 S_t - \beta_2 S_{t-1} + \varepsilon_t) \qquad (4)$$

where S_{t-1} is spawners from the previous year. We then developed a general Ricker model with brood-interaction that also included a statistical interaction term between brood-year spawners and spawners from the previous year, i.e.

$$R_t = S_t^{\gamma} \exp[\alpha - \beta_1 S_t - \beta_2 S_{t-1} - \beta S_t S_{t-1} + \varepsilon_t]. \qquad (5)$$

A stepwise multiple regression procedure was then applied to develop the most parsimonious brood-interaction model. The F and t statistics were used to select variables for inclusion in the model. A variable was retained in the model if $P\leq 0.10$, considered significant if $P\leq 0.05$, and marginally significant if $0.05<P\leq 0.10$. To provide for

comparisons of fit among models, the coefficient of determination was calculated by regressing observed on predicted recruits (natural logarthim transformed).

Ecological data

Least squares regression analysis was used to test the functional relationship between pairs of variables with a significance level of $\alpha = 0.05$. For variables that were considered functionally dependent on more than one other variable, we used backward elimination, a stepwise regression technique. The significance for retaining variables was also $\alpha = 0.10$. In our regression analyses, we used mean (May-October) annual zooplankton biomasses in Skilak Lake as individual data points. Because station C was not sampled prior to 1990, we excluded it from the statistical analyses. We used one-way analysis of covariance (ANCOVA) to test for differences in slopes and intercepts of the relationship between percent lipid content, following square root arcsine transformation, and wet weight of fry among different (monthly) sample periods. A significant effect of month indicates different y-intercepts and a significant interaction term (month × weight) indicates different slopes. One-way analysis of variance (ANOVA) was used to assess the difference in lipid content of fry collected in different time periods. The locally weighted scatter-plot smoothing (LOWESS) procedure was used to assess the underlying relationship between two variables and possible trends in time-series data. To evaluate the shape of zooplankton and sockeye juvenile size frequency histograms, we imposed a non-parametric kernel density estimator on the distribution (SPSS 1998). All statistical tests were conducted using SYSTAT (SPSS 1998).

RESULTS

Sockeye escapement and adult returns

Over the past 30 years, there has been a general trend of increasing escapements of sockeye salmon into the Kenai River system as evidenced by LOWESS fits to the time series of data (Figure 3A). During the 1970s, sockeye escapements were generally less than 400,000; the exception was 1977 when nearly 700,000 spawners entered the river. In 1987 and 1989, approximately 1.3 million spawners migrated up river largely as a result of commercial fishery closures associated with the July 1987 TV *Glacier Bay* oil spill in Upper Cook Inlet and March 1989 grounding of the tanker vessel *Exxon Valdez* on Bligh Reef in upper Prince William Sound. The number of sockeye spawners entering the Kenai River in each of these oil spill years was more than twice the recommended escapement goal (550,000). Since then, periodic changes in salmon management objectives have led to incremental increases in the escapement goal. Consequently, from 1990 to 2002 the number of spawners into the Kenai River averaged 638,000, about 60% more than in the 1970s and early 1980s.

Total adult recruits by brood year for the Kenai River system were available from 1971 through 1995. When fitted to LOWESS, the number of recruits produced by brood year showed an increasing trend through the 1970s (mean 1.7 million) and then a leveling off in the 1980s (mean 4.5 million). Since 1989 sockeye production by brood year seemingly declined (mean 1.7 million) (Figure 3B). The highest returns of approximately

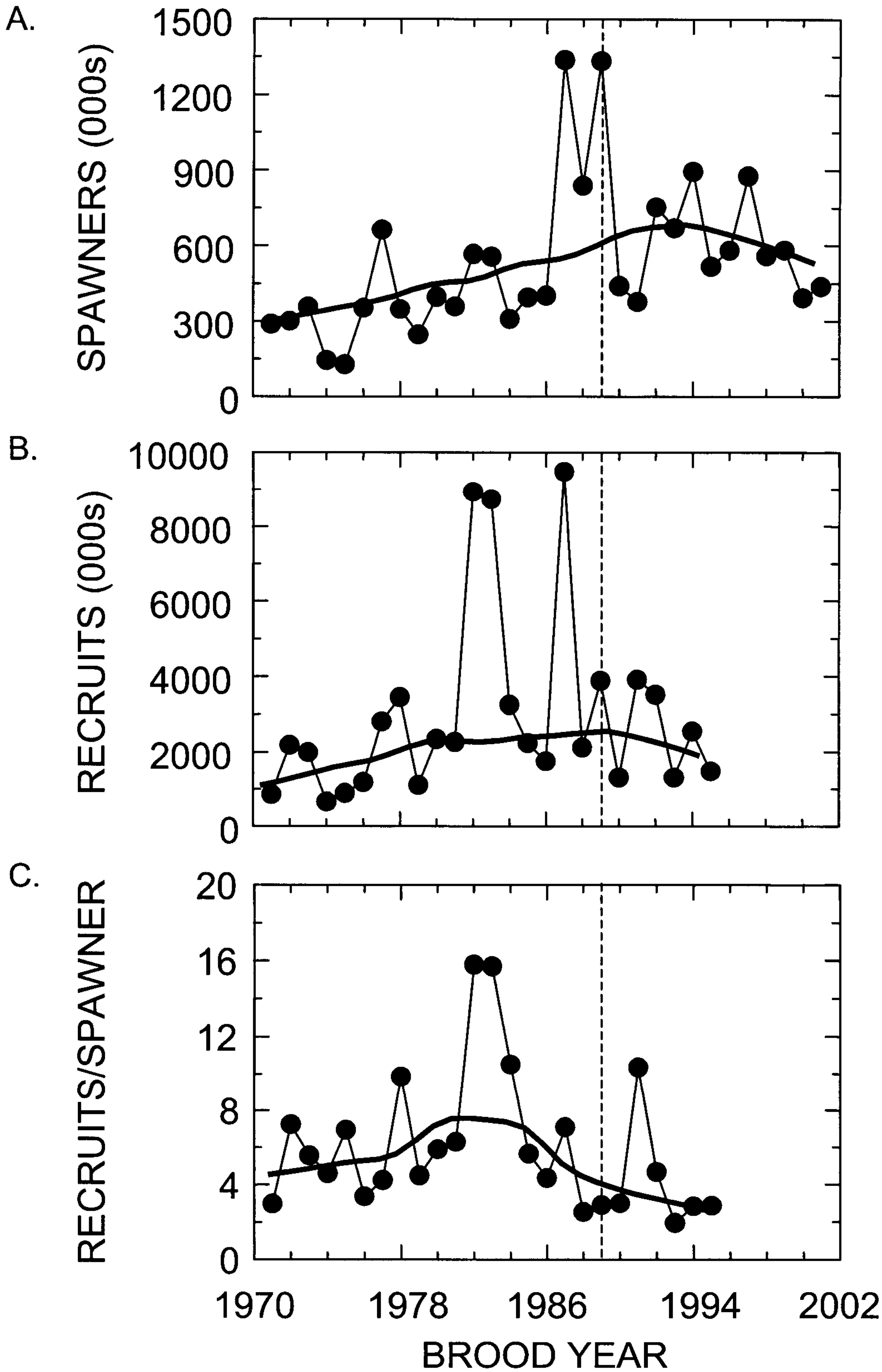

Figure 3. Temporal pattern in (A) number of sockeye spawners, (B) adult recruits, and (C) recruits-per-spawner by brood year for the Kenai River system, 1971-2001 (excluding enhanced component of Hidden Lake). Returns are incomplete for brood years 1996-2002. Smoothed lines are LOWESS fits to the data and vertical dashed line marks the 1989 oil spill.

9 million sockeye were produced from the 1982-1983 and 1987 brood years. In addition, there is some evidence of a 4-5 year cycle in Kenai River sockeye returns. The 1977, 1982, 1987, and 1991-1992 brood years had particularly strong recruitment. The time series of recruit-per-spawner (RPS) values revealed a marked increase in stock productivity beginning with the 1978 brood year and continuing through the 1983 brood year, after which RPS values generally declined (Figure 3C). We also observed reduced RPS values after the large escapements in 1987-1989. Prior to the 1989 *Exxon Valdez* oil spill event, RPS values averaged 6.8 ±3.7 (n=18) compared to 4.1 ±2.9 (n=7) after the oil spill.

Spawner-recruitment models

The Ricker and Cushing models did not adequately describe the spawner-recruit relationship for Kenai sockeye salmon. The density-dependent parameter in the general Ricker model (β) was not significantly different from 0, although γ was significantly different from 0 (P=0.008) but not different from 1.0 (Table 2). In the classic Ricker model, β was also not significantly different from 0. The density-dependent parameter (γ) in the Cushing model was significantly different from 0 (P<0.001) but not different from 1.0 (Table 2). Although, γ was different from 0, the general Ricker and Cushing models cannot be considered valid, because spawner-recruit models must exhibit some level of density dependence at high stock size. To provide density dependence, γ must be greater than 1.0 (Quinn and Deriso 1999). Finally, the density-dependent parameters in the classic Ricker model with a single brood-interaction term were not statistically significant, so this also cannot be considered a valid spawner-recruit model (Table 2).

A stepwise regression procedure revealed a brood-interaction model that described the spawner-recruit relationship for Kenai River sockeye salmon. All of the independent variables in a 3-parameter model were significantly different from 0, but γ was not different from 1.0 (Table 2). A simplified 2-parameter brood interaction model best described ($R^2 = 0.62$) the spawner-recruit relationship for this stock (Table 2; Figure 4A). Examination of the observed versus predicted values indicated that the model was diagnostically well behaved in that there were no gross outliers (Figure 4B). However, a declining trend in model residuals since the early 1980's (Figure 5A) suggested some additional process was affecting stock productivity. Further examination revealed a significant relationship between the residuals from this spawner-recruit model and euphotic zone depth in Skilak Lake (Figure 5B). This positive relationship suggested that the productivity of the Kenai River sockeye salmon might be limited in part by light penetration.

Fry recruitment and density-dependent growth

For salmon brood years (i.e., year of spawning) 1985-2000, a significant ($r^2 = 0.27$; P=0.039) positive relationship existed between the number of Kenai River main stem (MS) spawners (excluding escapement estimates from Hidden and Russian lakes) and the numbers of age-0 sockeye salmon fry (FN, in millions) rearing in Skilak and Kenai lakes in the fall of the next year (1986-2001) (Figure 6A). The regression equation was $FN = 7.86\times10^6 + 16.70MS$. In this model, fall fry counts were based on combined estimates from Skilak and Kenai lakes. However, the linear relationship accounted for only 27% of

Table 2. Summary of models evaluated to explain the stock-recruitment relationship for Kenai River sockeye salmon. Statistics indicated for γ are tests for whether the parameter is different from 1.

Model	Method of Estimation	Results
General Ricker model	Mulitple Regression $\ln R = \hat{\alpha} + \hat{\gamma} \ln S - \hat{\beta} S + \varepsilon$	R^2=0.558, P<0.001 $\hat{\alpha} = 2.58, P = 0.095$ $\hat{\beta} = 0.000225, P = 0.753$ $\hat{\gamma} = 0.863$, P=0.650
Classic Ricker model	Linear Regression $\ln\left(R/S\right) = \hat{\alpha} - \hat{\beta} S + \varepsilon$	R^2=0.556, P=0.125 $\hat{\alpha} = 1.90, P < 0.001$ $\hat{\beta} = 0.000511, P = 0.125$
Cushing model	Linear Regression $\ln R = \hat{\alpha} + \hat{\gamma} \ln S + \varepsilon$	R^2=0.556, P<0.001 $\hat{\alpha} = 2.97, P = 0.001$ $\hat{\gamma} = 0.78, P < 0.001$
Classic Ricker model with brood interaction	Multiple Regression $\ln\left(R/S\right) = \hat{\alpha} - \hat{\beta}_1 S_t - \hat{\beta}_2 S_{t-1} + \varepsilon$	R^2=0.596, P=0.093 $\hat{\alpha} = 2.03, P < 0.001$ $\hat{\beta}_1 = 0.000241, P = 0.505$ $\hat{\beta}_2 = 0.000557, P = 0.121$
General Ricker model with brood interaction (3-parameter model)	Multiple Regression $\ln R = \hat{\alpha} + \hat{\gamma} \ln S_t - \hat{\beta}(S_t S_{t-1}) + \varepsilon$	R^2=0.615, P<0.001 $\hat{\alpha} = 1.73, P = 0.098$ $\hat{\beta} = 0.0000009, P = 0.061$ $\hat{\gamma} = 1.03$, P=0.871
Simple brood interaction model (2-parameter model)	Mulitple Regression $\ln R = \hat{\alpha} - \hat{\beta}(S_t S_{t-1}) + \varepsilon$	R^2=0.615, P=0.014 $\hat{\alpha} = 1.89$, P<0.001 $\hat{\beta} = 0.00000085, P = 0.014$

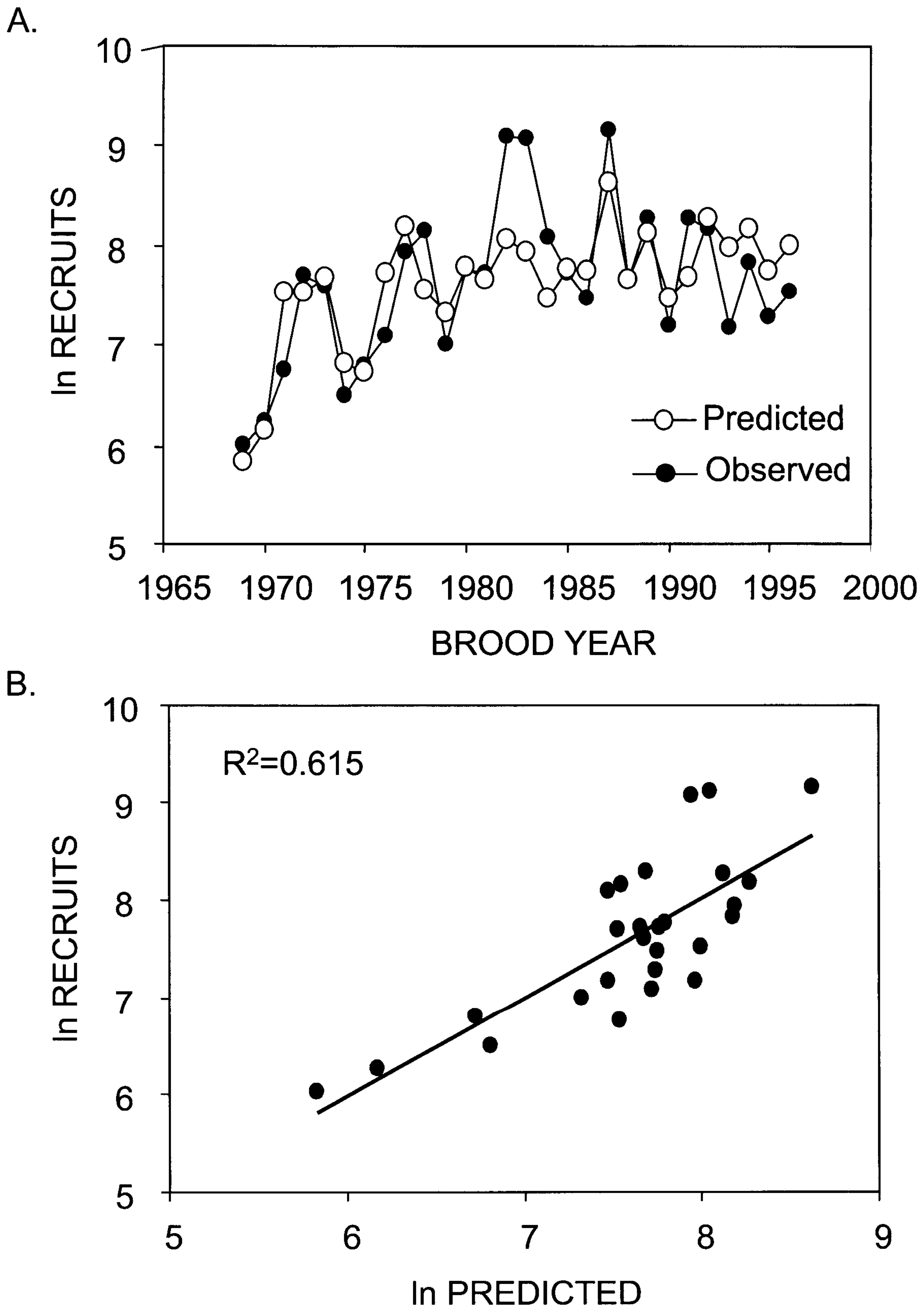

Figure 4. Plot of (A) residuals from the brood-year interaction model used to explain the spawner-recruit relationship for Kenai River sockeye salmon and (B) plot of observed versus predicted values.

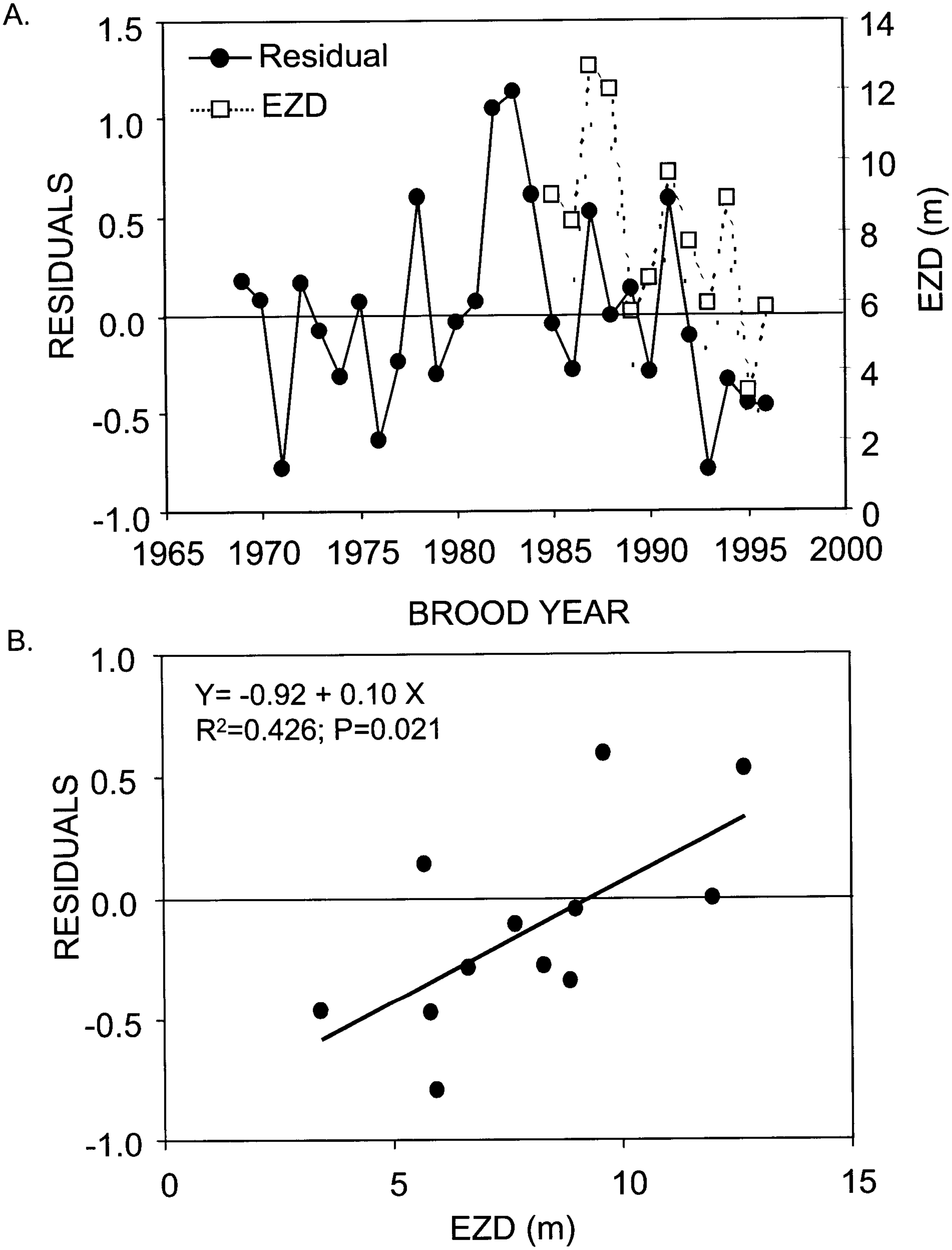

Figure 5. Plot of (A) residuals from the brood-year interaction model used to explain the spawner-recruit relationship for Kenai River sockeye salmon and euphotic zone depth (*EZD*) on the subsequent rearing year and (B) linear regression of the residuals against EZD.

the variation in age-0 fry, suggesting that fall fry production is not principally a function of escapement. We found a weaker (r^2 = 0.18), but marginally significant (P=0.110) negative relationship between the mean age-0 fry weight from Skilak Lake (FW) and the estimated number of mainstem spawners for the Kenai River system (Figure 6B). The regression equation was $FW = 1.567 - 4.52\times10^{-7}MS$. The 1987 and 1996-1997 brood-year escapements, which ranged from an estimated 580,000 to 1.3 million (i.e., main stem spawners), produced the smallest sized (less than 1.0 g) fry. In comparison, the 1991 brood year escapement of 278,000 produced the largest sized fall fry (1.8 g). In addition, we also found that within the range of 5 to 35 million fry (age-0), a reasonably strong (r^2=0.34; P=0.022) negative relationship existed between the number of age-0 fry and the mean weight of fry (Figure 6C), suggesting that density-dependent growth occurred in this system. The regression equation was $FW = 1.63 - 2.18\times10^{-7}FN$. For the years when fry abundance was greater than 20 million, the average size of age-0 fry was approximately 1.0 g compared to 1.5 g when the number of fall fry was less than 20 million.

Variation in lipid content of fry and over-winter mortality

For 403 salmon fry collected in August 1993 (n=143), September 1993 (n=58), November 1993 (n=98) and April 1994 (n=104), lipid content averaged (±1 standard deviation) 11.7 ±4.3%. Very few fry (n=27) contained less than 6% lipids suggesting this level as a survival threshold in terms of body fat content. Results of one-way ANOVA, with month as the categorical variable, suggested significant differences (F=12.7; P<0.001) in percent lipid content (after arcsine square root transformation) over the course of the season. A comparison of average percent lipid content from August 1993 to April 1994, showed an increase from mid-summer (August, 11.3%) to early fall (September, 14.8%) followed by a sharp decline in early winter (November, 10.9%), but pairwise (Tukey's) comparisons suggested there was little difference (P>0.05) in the percent lipid content between summer, winter, and the following spring (Figure 7A). In addition, there was a significant positive (P<0.001), but weak relationship (r^2=0.11) between percent lipid content, following acrsine square root transformation, and the wet weight of fry. However, results of ANCOVA with lipid content as a response variable, month as a category variable, and the independent variable wet weight as a covariate indicated different slopes (F=15.4; P<0.001) (Figure 7B). In Skilak Lake, the slope of the positive relationship between lipid content and wet weight decreased over time. In winter (November) and spring (April), there was little change in the percent of lipids as a function of fry weight, which suggests either heavy fall to winter or overwinter mortality.

Further examination of the temporal pattern in size (wet weight) distribution of juvenile sockeye (n = 406) used in the above lipid analysis helped confirm when most mortality occurred and what size-classes suffered the greatest mortality (Figure 8A-D). The change in frequency distribution in fry weight between August and September 1993 suggested growth. That is, most fry were below the 0.6-0.8 g size-class interval in summer (August) and none were represented in size class intervals greater than 2.0 g, whereas in the fall (September), most fry were greater than the 0.8-1.0 g size-class intervals, including a substantial number of fry above 2.0 g. In early winter (November), the peak of the size distribution shifted right, to the 1.0-1.2 g size interval, which may indicate

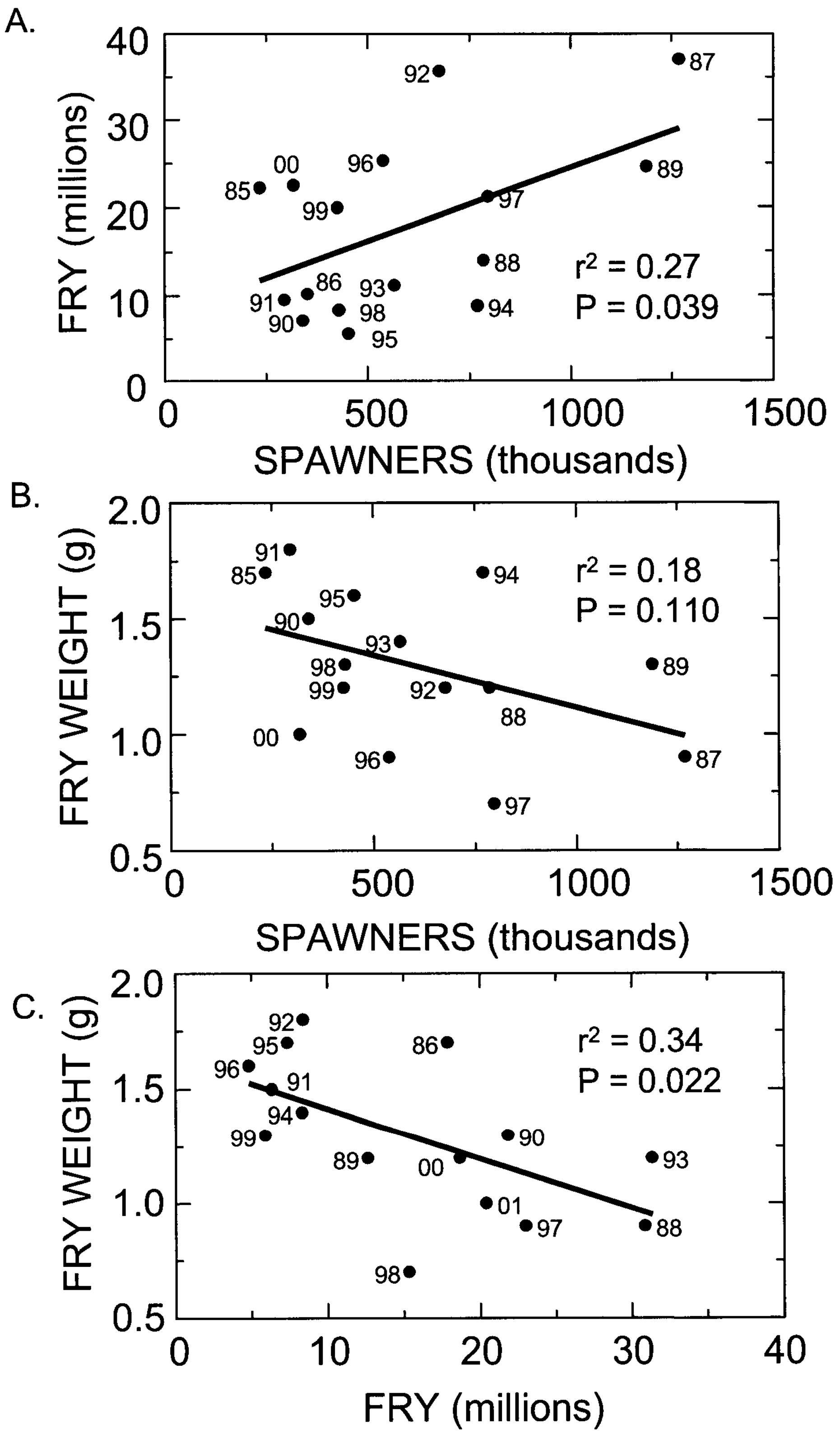

Figure 6. Relationship between (A) number of Kenai River mainstem spawners (*MS*) and age-0 (Skilak + Kenai) fall fry abundance; (B) relationship between age-0 fry weight from Skilak Lake and MS; and (C) age-0 fry weight as a function of fry abundance in Skilak Lake. Data points are labeled by brood year (A-B) and rearing year (C).

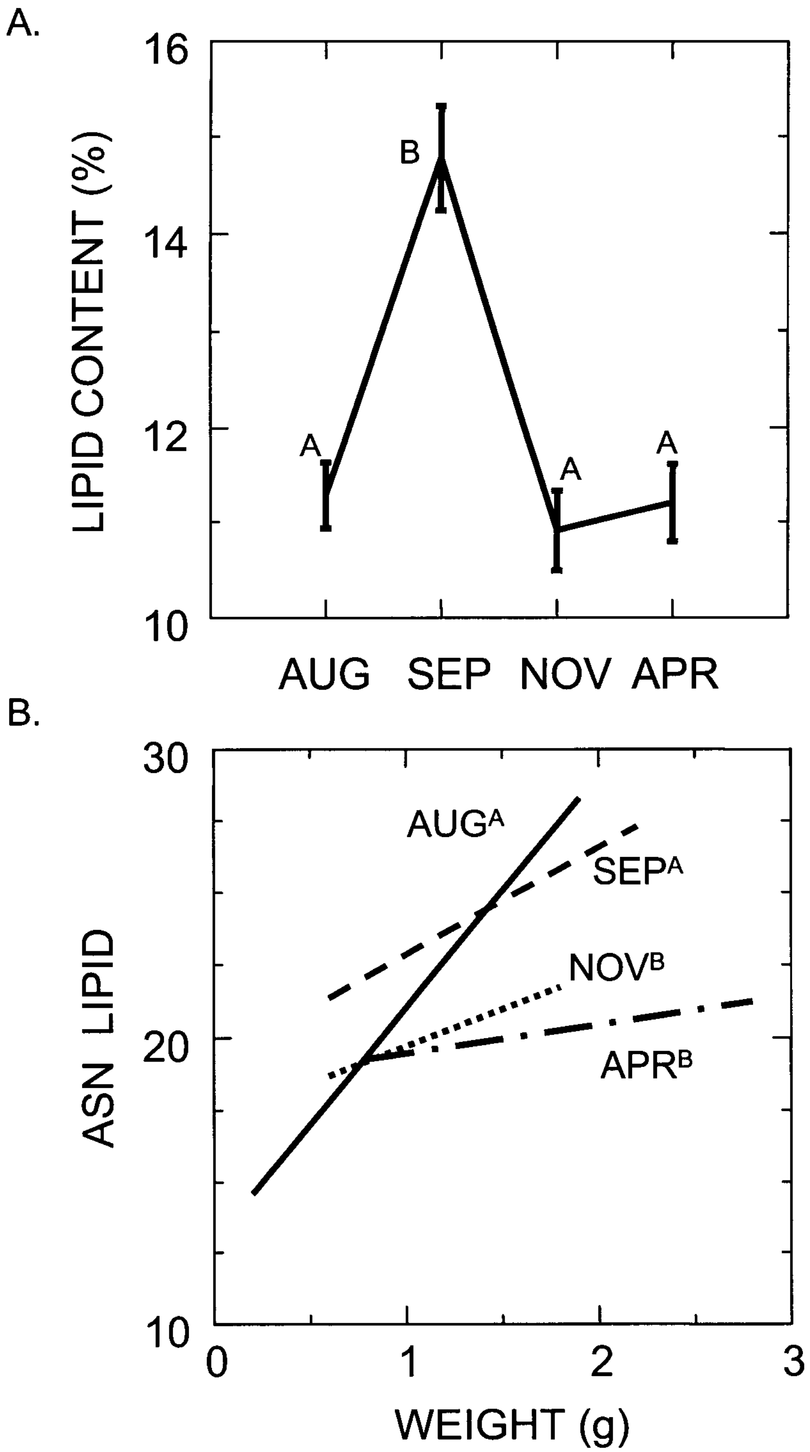

Figure 7. Comparison of (A) the temporal pattern in average (+1 standard error) lipid content (as percent dry weight) in sockeye salmon fry collected from August 1993 to April 1994. Values that share the same letter are not significantly (*P*>0.05) different (ANOVA); (B) slopes of the liner regression between lipid content, after arcsine square root transformation (ASN), and wet weight of fry in Skilak Lake. Slopes that share the same letter are not significantly (*P*>0.05) different (ANCOVA).

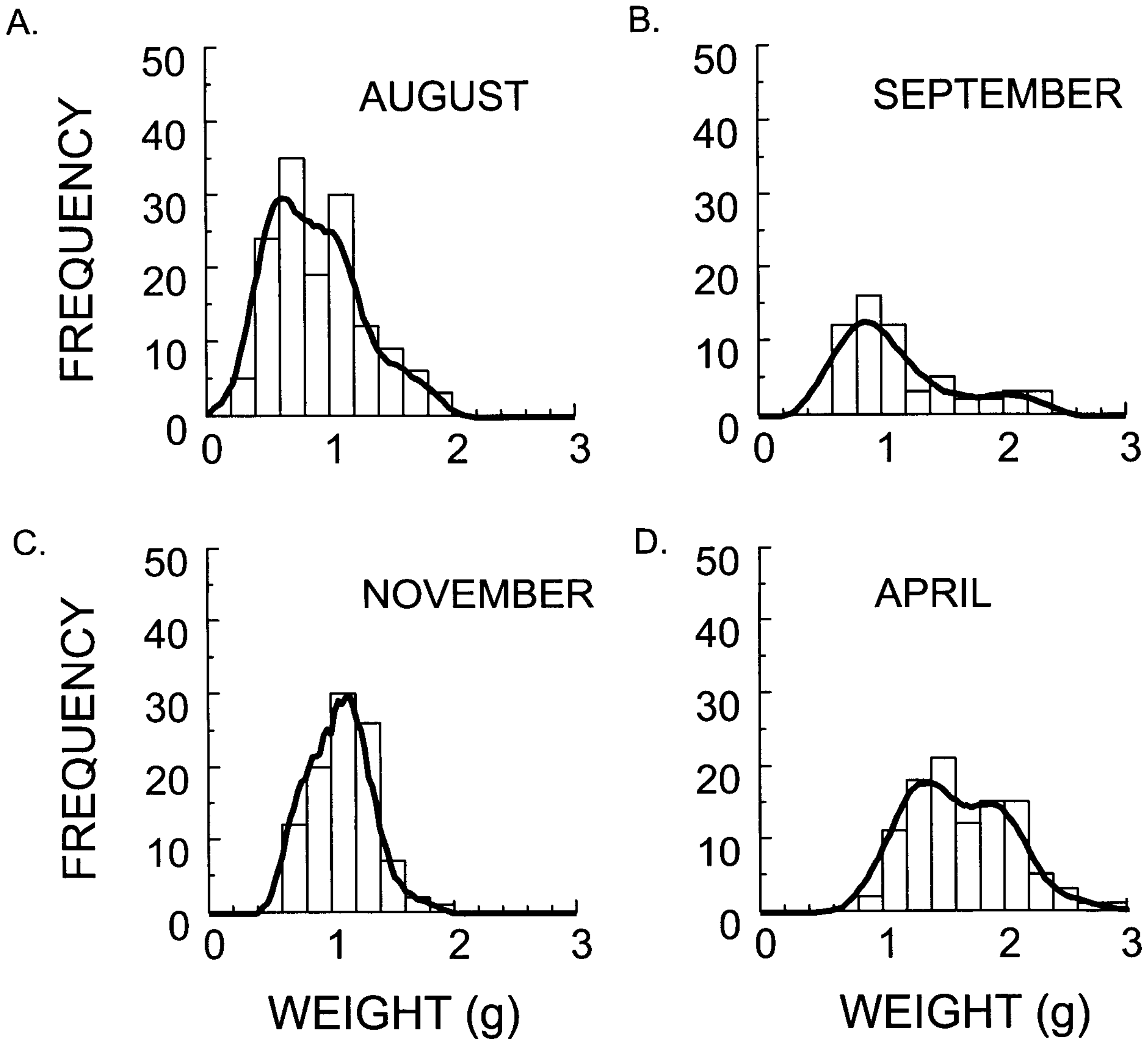

Figure 8. Histogram of wet weight of sockeye juveniles collected from (A) August 1993, (B) September 1993, (C) November 1993, and (D) April 1994 in Skilak Lake Curved lines are the non-parametric density estimators.

further growth between the fall and winter periods; however, by the following spring (April) the peak of the density estimator (kernel curve) increased to 1.4 g and there were no fry below the 0.8-1.0 g size interval. This shift toward a larger size distribution of sockeye juveniles between early winter and spring suggested most of the mortality occurred during this period. That is, none of the size-class intervals less than about 0.6-0.8 g that were present at the onset of winter (November) were represented in the sample the following spring (April). However, it is difficult to use size-frequency histograms to detect mortality schedules with large confidence. Thus, the April histogram could also be interpreted to mean bi-modal growth, instead of overwinter mortality.

Fall fry and adult recruitment

In contrast with growth responses and seasonal changes (decreases) in lipid content of fry, there were no obvious density-dependent effects fry to adult survival for the Kenai River system. There were positive relationships between fall fry abundance (FN) and both subsequent total adult (R) returns and age 1.3 year-class (R_{13}) returns (Figure 9). For the dominant age 1.3-year class, fry to adult survival ranged from 5.2 to 26.5% and averaged 10.9%. The regression equations were $R = 478.9 + 152.2FN$ (r^2=0.54; P=0.010) and $R_{13} = -66.4 + 112.1FN$ (r^2=0.54; P=0.006). In addition to being statistically significant, the density independent (linear) models were reasonably strong with the number of fry accounting for more than ½ of the variance in both total year-class and age 1.3 adult returns.

Zooplankton biomass and size distribution

Figure 10A-C illustrates the interannual variation and trend in average biomass of *Cyclops columbianus* and *Diaptomus pribilofensis* and total (*Cyclops* + *Diaptomus*) copepods in Skilak Lake from 1986 to 2002. Over that time period, *Cyclops* composed from 53% to 88% of the average total copepod biomasses. The maximum biomass of *Cyclops* (574 mg m^{-2}) occurred in 1989 and another large peak (534 mg m^{-2}) occurred in 1993. In the interval between, *Cyclops* biomass was only about ½ that amount and averaged 290 mg m^{-2}. Following the 1993 peak, the biomass again declined noticeably and in 1997 biomass levels fell below 200 mg m^{-2}. Since then (1998-2002), *Cyclops* biomass increased modestly by about 70 mg m^{-2} per year. The mean biomass of *Diaptomus* fluctuated between 31 and 281 mg m^{-2}, but unlike *Cyclops* there was no obvious long-term pattern in the time series. Mean total copepod (COPB) and *Cyclops* biomass (CYCB) were strongly correlated ($r^2 = 0.83$; $P<0.001$). The regression equation was $COPB = 103.3 + 1.05\ CYCB$. In addition, results from linear regression indicated that COPB declined significantly ($r^2 = 0.25$; P=0.039) by about 14 mg m^{-2} per year: $COPB = 1{,}800 - 14.1YEAR$. In summary, both *Cyclops* and total copepod biomass appeared to decline substantially over the 17-year sampling period, as evidenced by LOWESS fits to the data, but *Diaptomus* did not.

Representative seasonal changes in mean length of *Cyclops* and *Diaptomus* in Skilak Lake during 1997-2000 are presented in Figure 11A-D. The difference in the size of ovigerous (egg-bearing) *Cyclops* compared to that of the non-ovigerous population suggested the presence of at least two cohorts, whereas for *Diaptomus* evidence for multiple cohorts was lacking. The mean size of non-ovigerous *Cyclops* ranged from 0.7

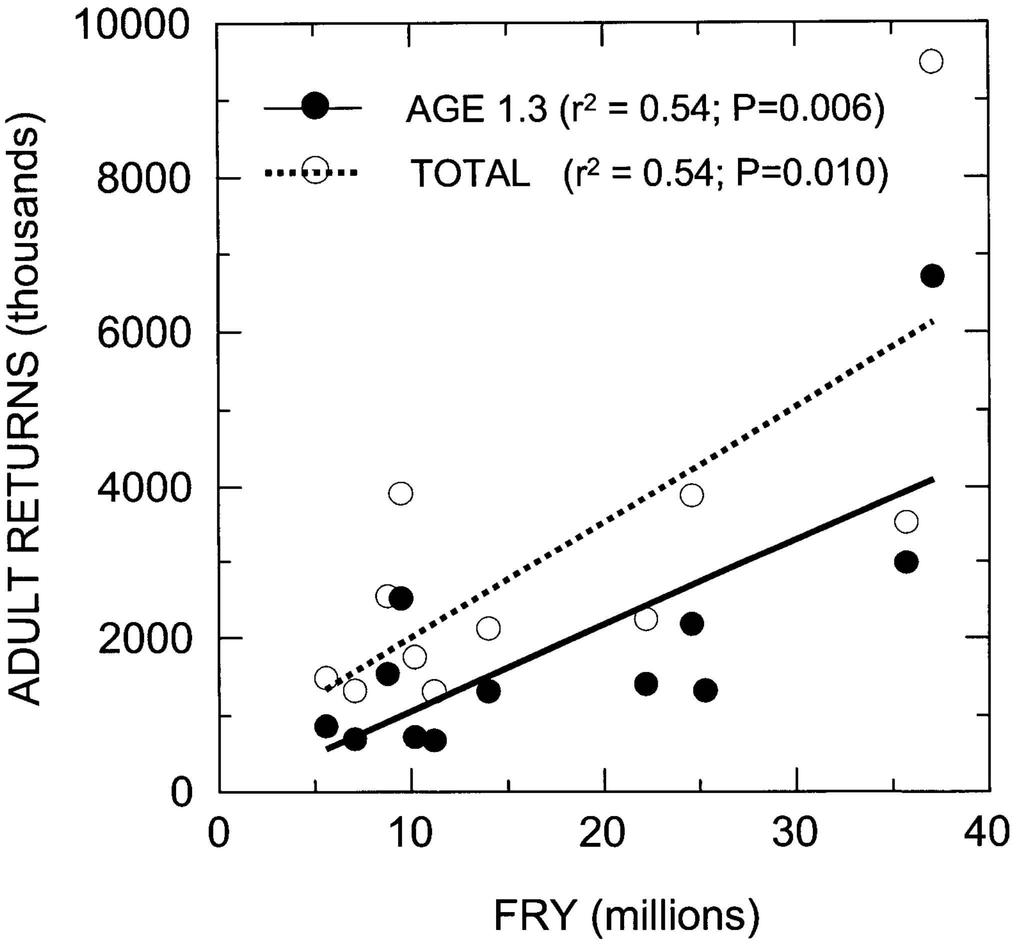

Figure 9. Relationship between sockeye fry abundance and subsequent age 1.3 year-class (n = 12) and total adult (n = 11) recruits for the Kenai River system.

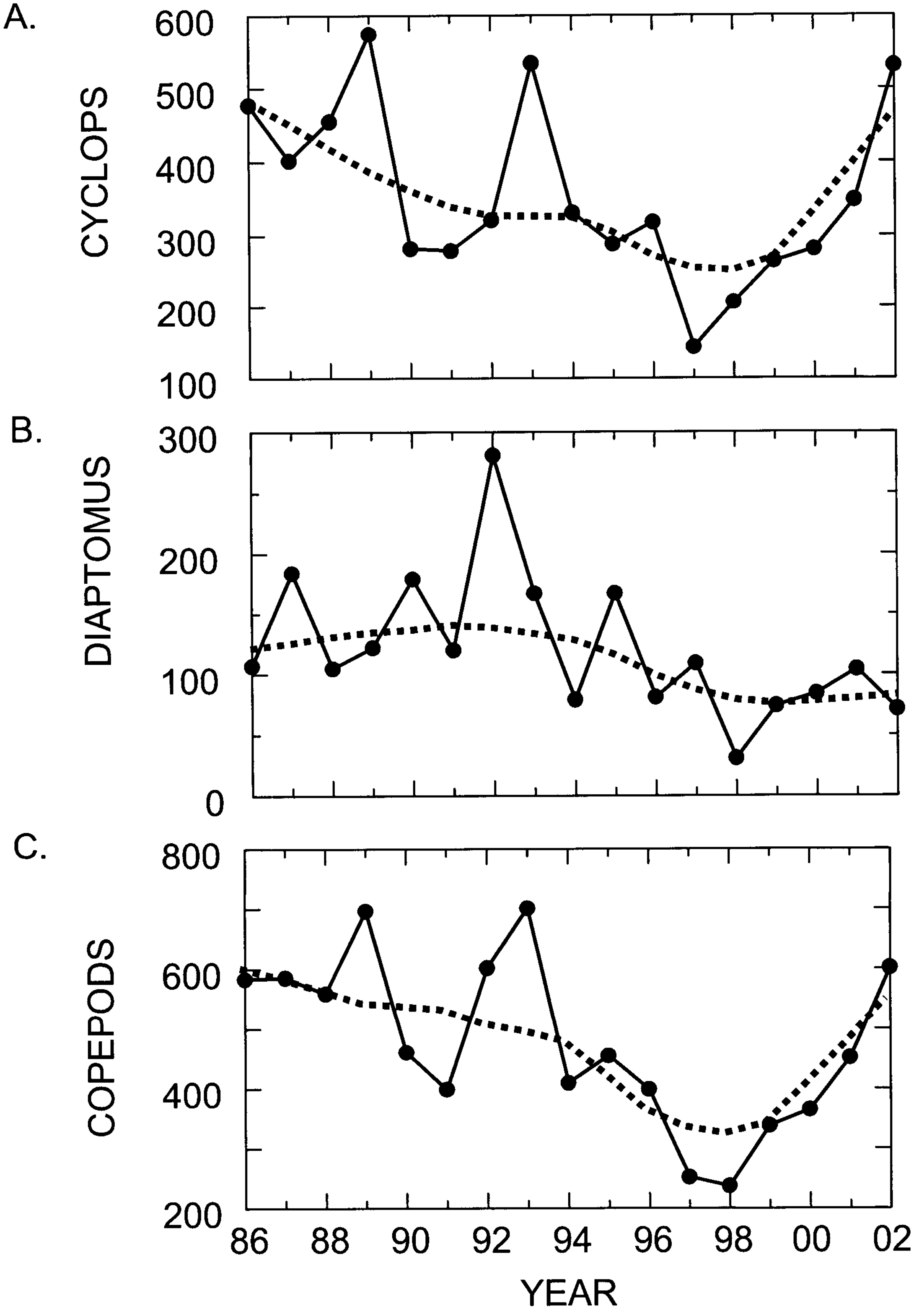

Figure 10. Time series of mean biomass (mg m^{-2}) of (A) *Cyclops*, (B) *Diaptomus*, and (C) total copepods (*Cyclops* + *Diaptomus*) in Skilak Lake, 1986-2002. Dashed lines are LOWESS fits to the data.

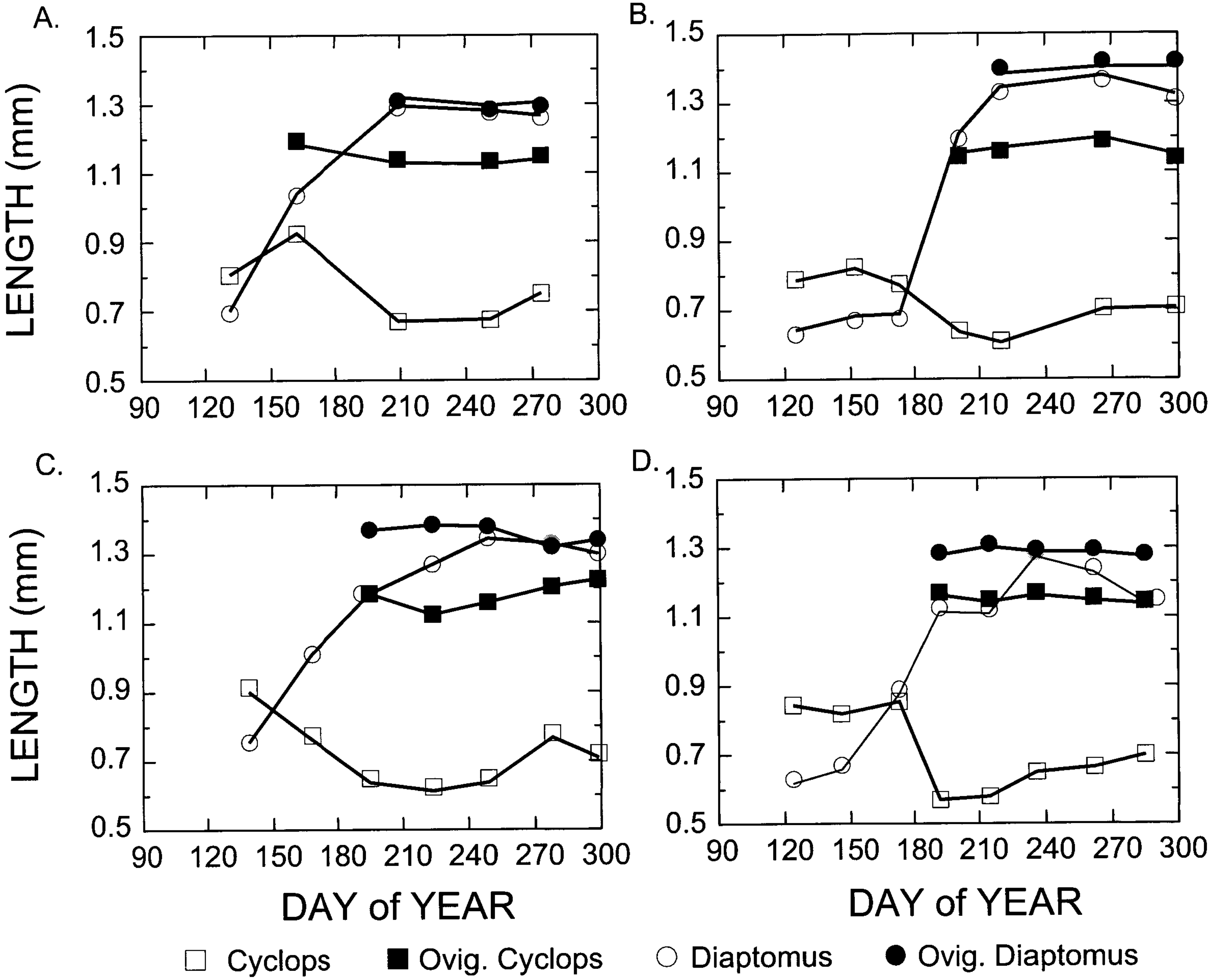

Figure 11. Seasonal changes in mean length of *Cyclops* and *Diaptomus* including ovigerous animals in Skilak Lake; (A) 1997, (B) 1998, (C) 1999, and (D) 2000.

mm to 0.9 mm, whereas the length of ovigerous animals ranged from 1.1 mm to 1.3 mm. Furthermore, the length-frequency distribution of *Cyclops* over the course of a year (from one spring period to the next), as represented by the 1992-1993 and 1993-1994 time series, indicated the presence of two age-class cohorts that began in July (Figures 12-13). That is, the temporal pattern in mean length of *Cyclops* revealed a bimodal distribution. The larger size distribution agreed well with the mean length of the ovigerous *Cyclops* component (Figure 11A-D). In addition, the length-frequency distribution of *Cyclops* during the subsequent spring (April-May) indicated that *Cyclops* individuals held over from the previous fall (October) because the mean size in the fall was essentially the same, 0.7-0.9 mm. Together these data indicate that *Cyclops* have a two year life history in Skilak Lake with few individual reaching sexual maturity in the first year (summer).

Copepods, fry growth, and recruitment

The biomass of copepods in the spring (SpC) together with the number of age-0 fall fry (FN) accounted for 60% of the variance in average fall fry (age-0) weight (FW) (Figure 14A). The regression equation was $FW = 1.34 - 2.57\times10^{-8}FN + 0.8.8\times10^{-4}SpC$ (R^2=0.60; P<0.001). Coefficients of the multiple regression had the expected signs (i.e., negative for FN and positive for SpC) suggesting density effects on growth and positive effects of food supply (zooplankton). The model seemed diagnostically well behaved in that there were no influential outliers as evidenced from the plot of observed versus predicted values, the greatest deviation from the model corresponded to the 1997-1998 rearing years (Figure 14B).

We also examined the relationship between fall fry abundance as a function of seasonal (spring, summer, fall) *Cyclops*, *Diaptomus*, and total copepod (*Cyclops* + *Diaptomus*) biomass and the number of sockeye spawners using stepwise multiple regression. Taken together, spawners (MS) and spring (May-June) copepod biomass (SpC) in Skilak Lake accounted for 45% of the variation in total age-0 fry (Skilak + Kenai) abundance (Figure 15A). None of the other zooplankton variables met the minimum significance requirements for inclusion in the model. The multiple regression equation was $FN = -4.21\times10^{6} + 2.15\times10^{4}MS + 2.35\times10^{4}SpC$ (R^2=0.45; P=0.021). Besides being a significant variable, spring copepod biomass greatly improved the ability to predict fall fry abundance over using just number of spawners. Including copepod biomass in the multiple regression model accounted for 18% more of the variance in fall fry abundance than did spawners alone. The largest residuals (observed minus predicted values) occurred in brood years 1995 and 1996 (rearing years 1996 and 1997) (Figure 15B). Results of ANOVA suggested that copepod biomass in the spring was lower (mean 287 mg m^{-2}) when fall fry abundance the previous year was greater than 20 million compared to the biomass levels (mean 432 mg m^{-2}) when fry abundance was less than 20 million (Figure 16). However, the reported P-value (P=0.13) was slightly greater than our prescribed significance level. Therefore, grazing by large fry populations in Skilak Lake may reduce copepod biomass the following spring.

Copepods and environmental variables

There were important fluctuations and trends in water turbidity in Skilak Lake (Figure 17A-B). During 1986-1992, turbidity in the near-surface water (1 m) averaged 4.6 NTU.

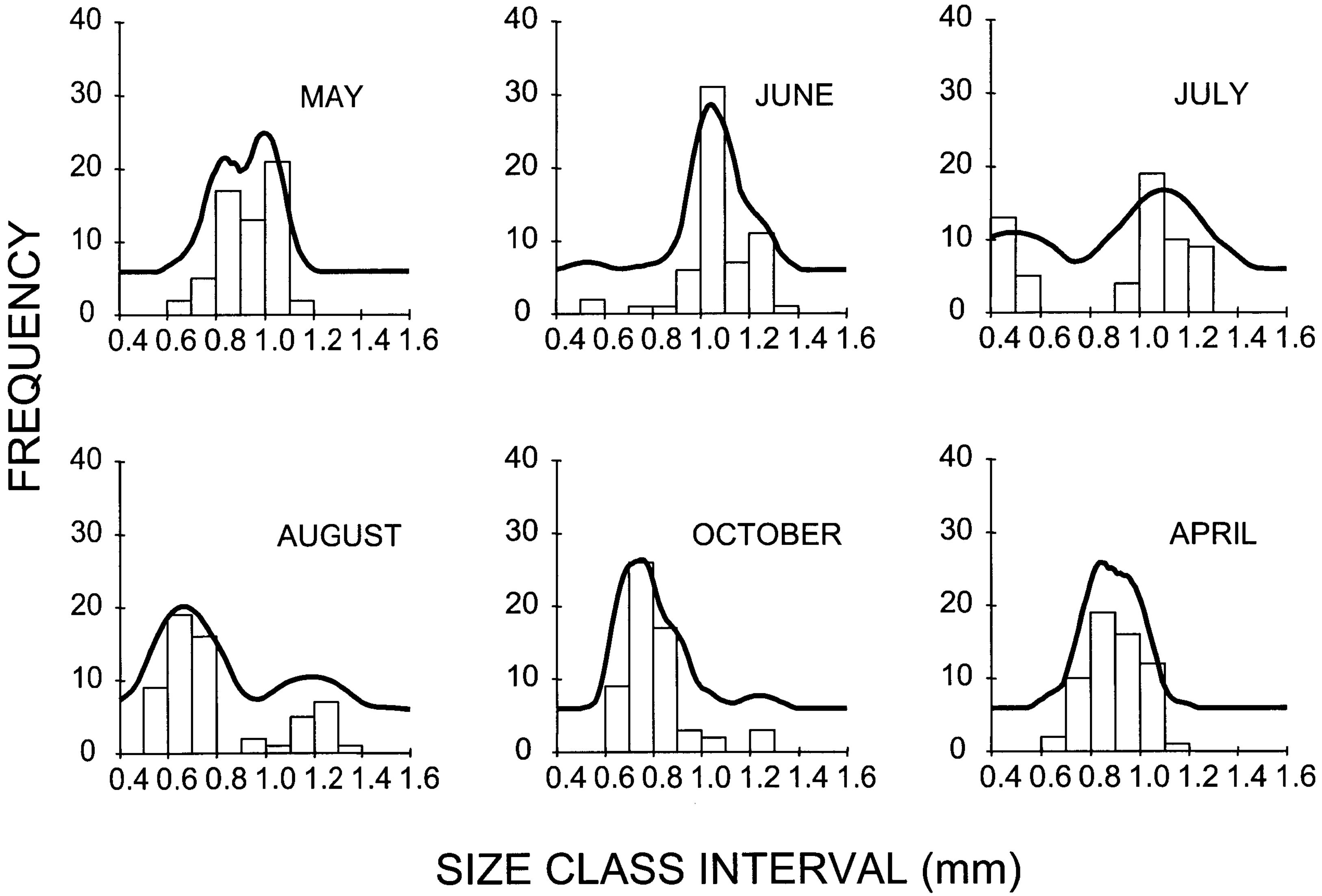

Figure 12. Comparison of monthly length-frequency distributions (n = 60) of *Cyclops* collected from May 1992 to April 1993.

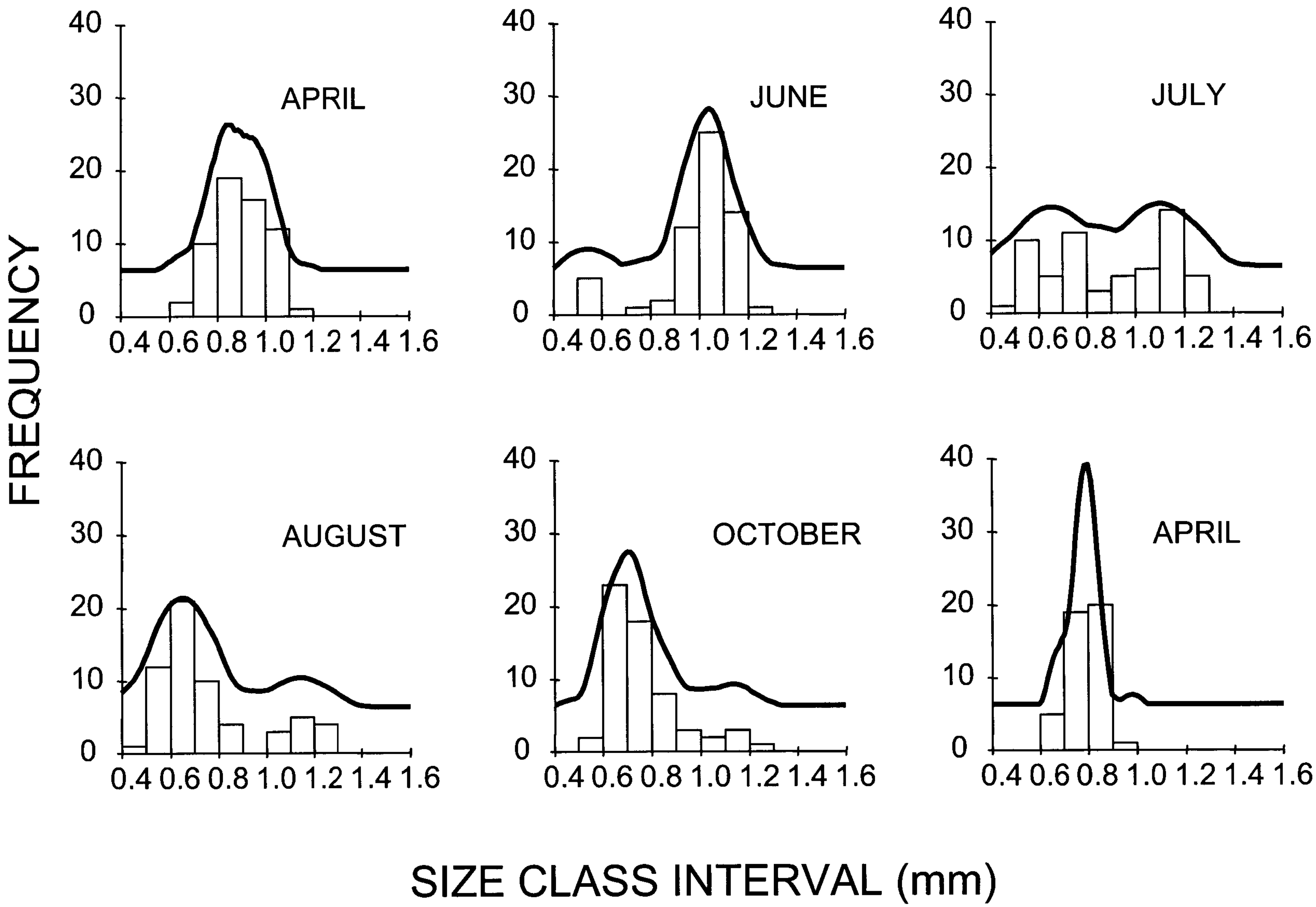

Figure 13. Comparison of monthly length-frequency distributions (n = 60) of *Cyclops* collected from May 1993 to April 1994.

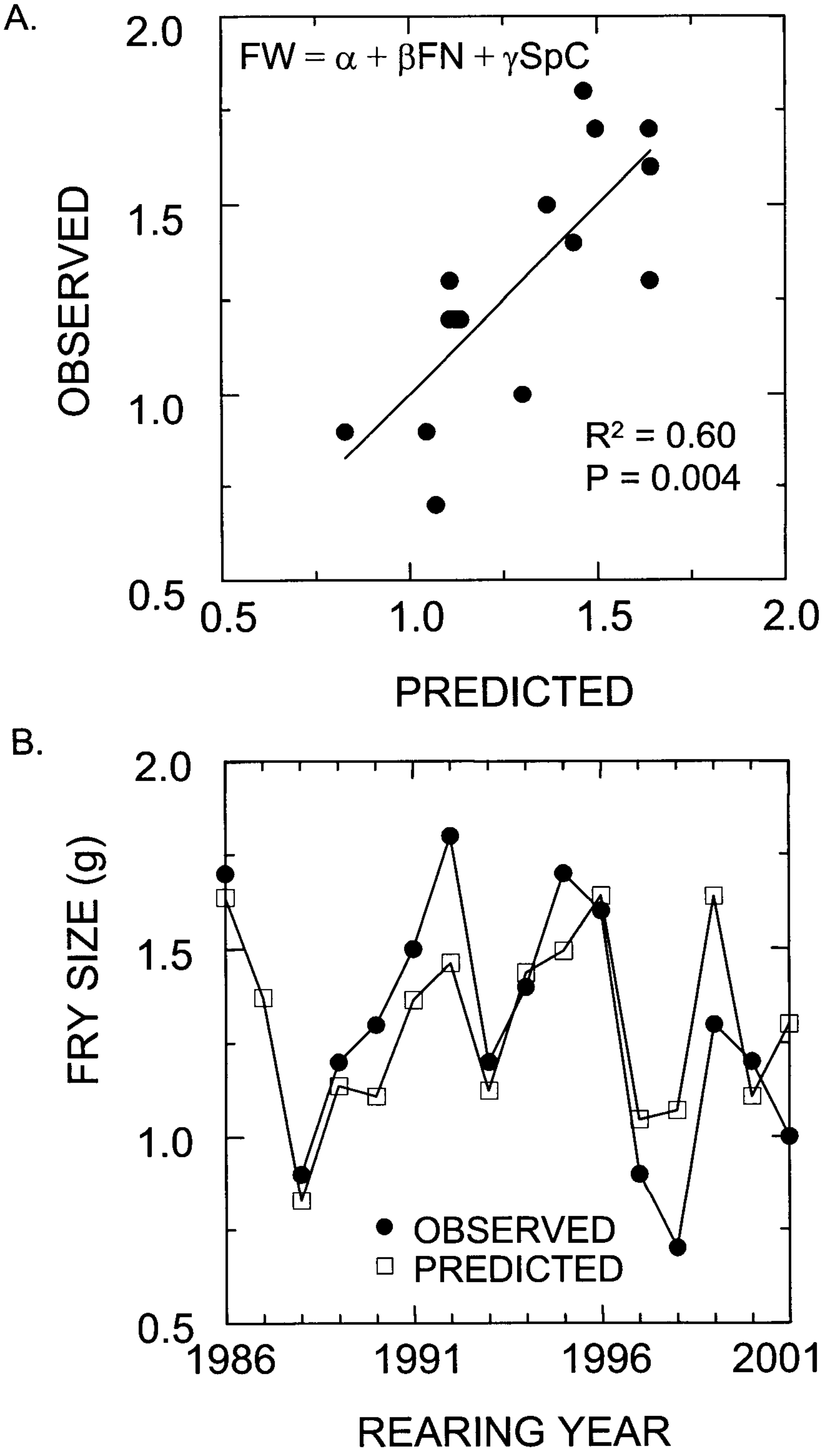

Figure 14. Plot of (A) predicted versus observed values from multiple regression for predicting age-0 fall fry weight (*FW*) from fry abundance (*FN*) and spring copepod biomass (*SpC*) in Skilak Lake; (B) temporal pattern by rearing year of observed and predicted fry weight values.

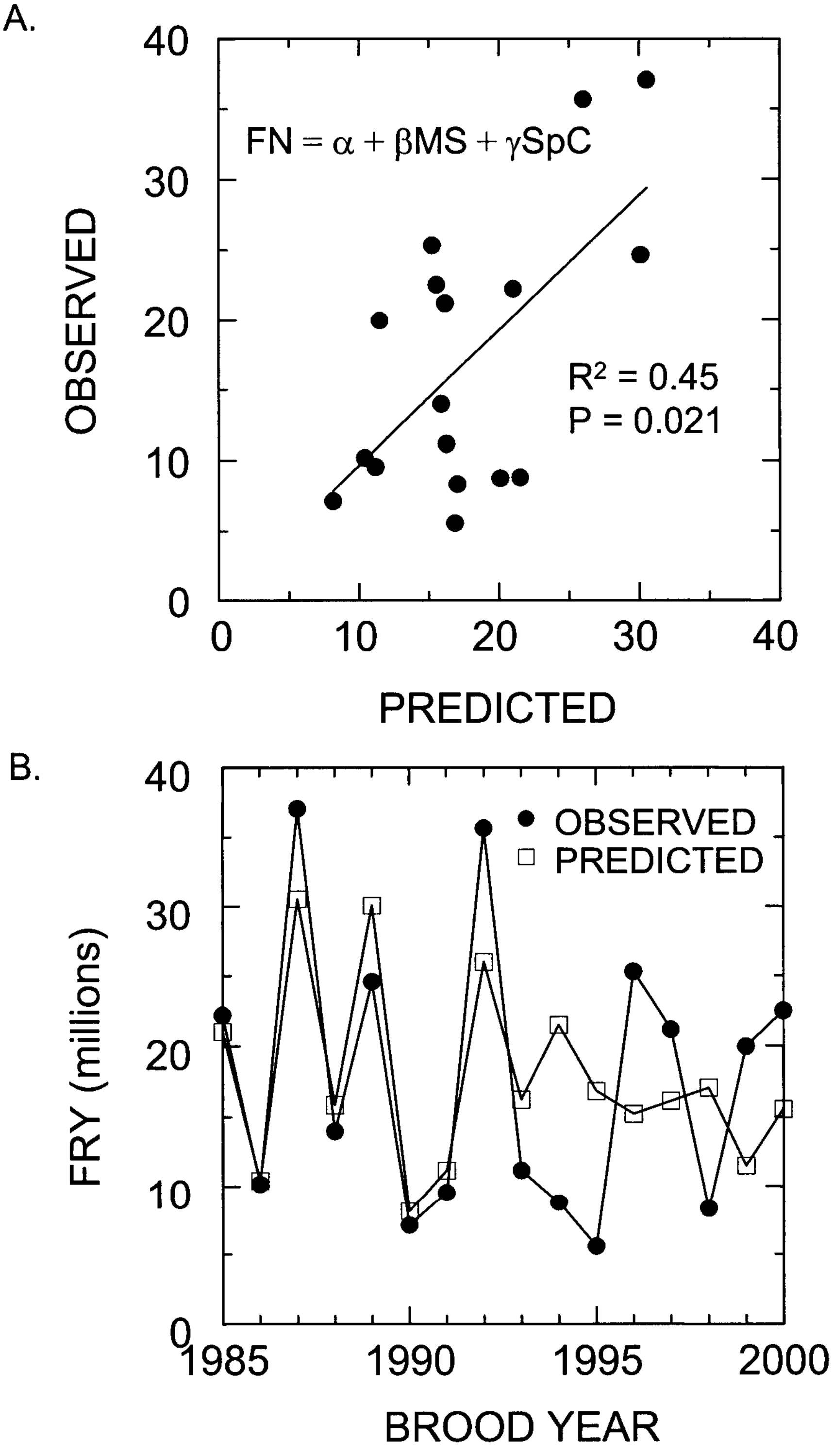

Figure 15. Plot of (A) predicted versus observed values from multiple regression for predicting the total number (Skilak + Kenai) age-0 fall fry (*FN*) from mainstem spawners (*MS*) and spring copepod biomass (*SpC*) in Skilak Lake; (B) temporal pattern by brood year of observed and predicted fry abundance values.

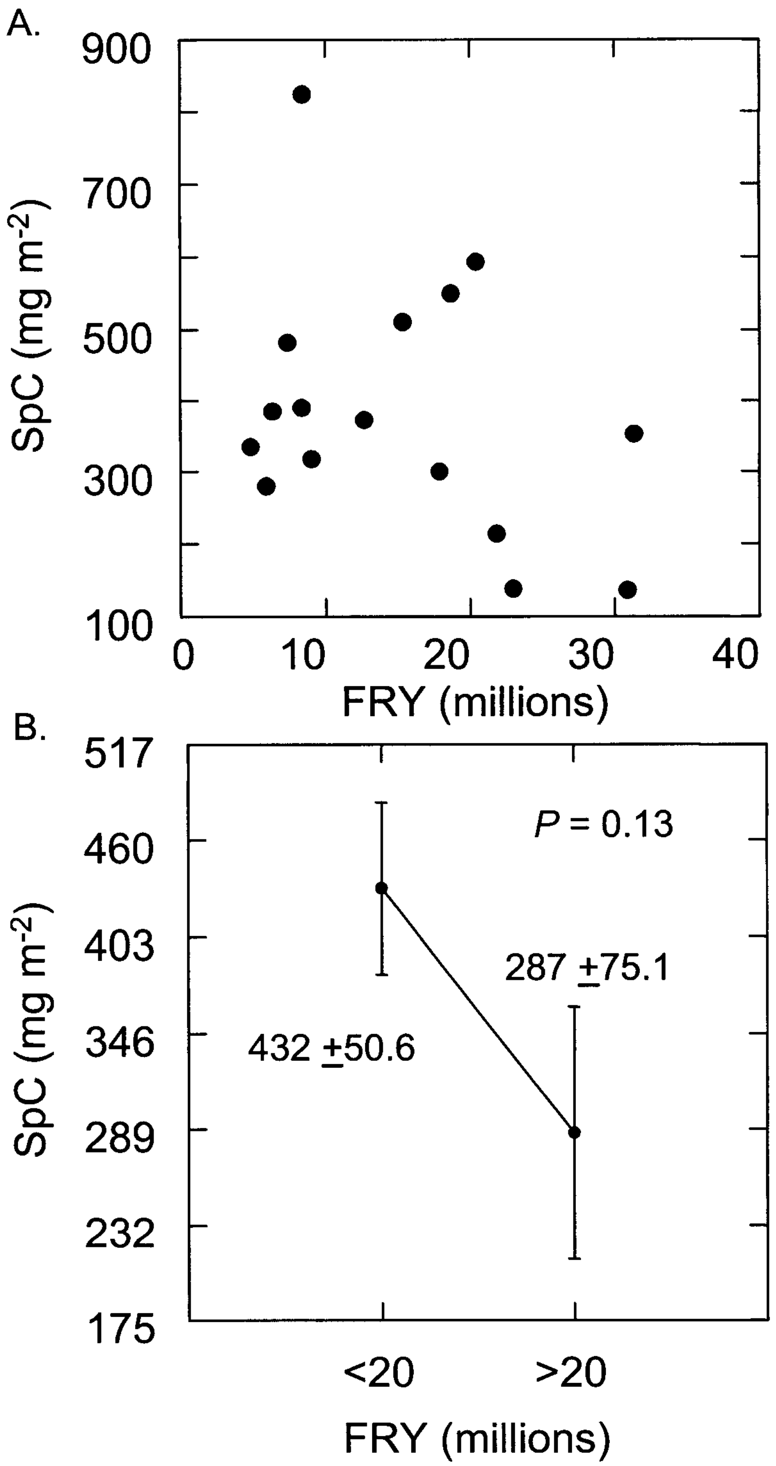

Figure 16. Plot of (A) age-0 fall fry abundance versus average copepod biomass the following spring (*SpC*); (B) least squares means and standard errors from ANOVA to test for differences in *SpC* when fall fry abundance is less than or greater than 20 million.

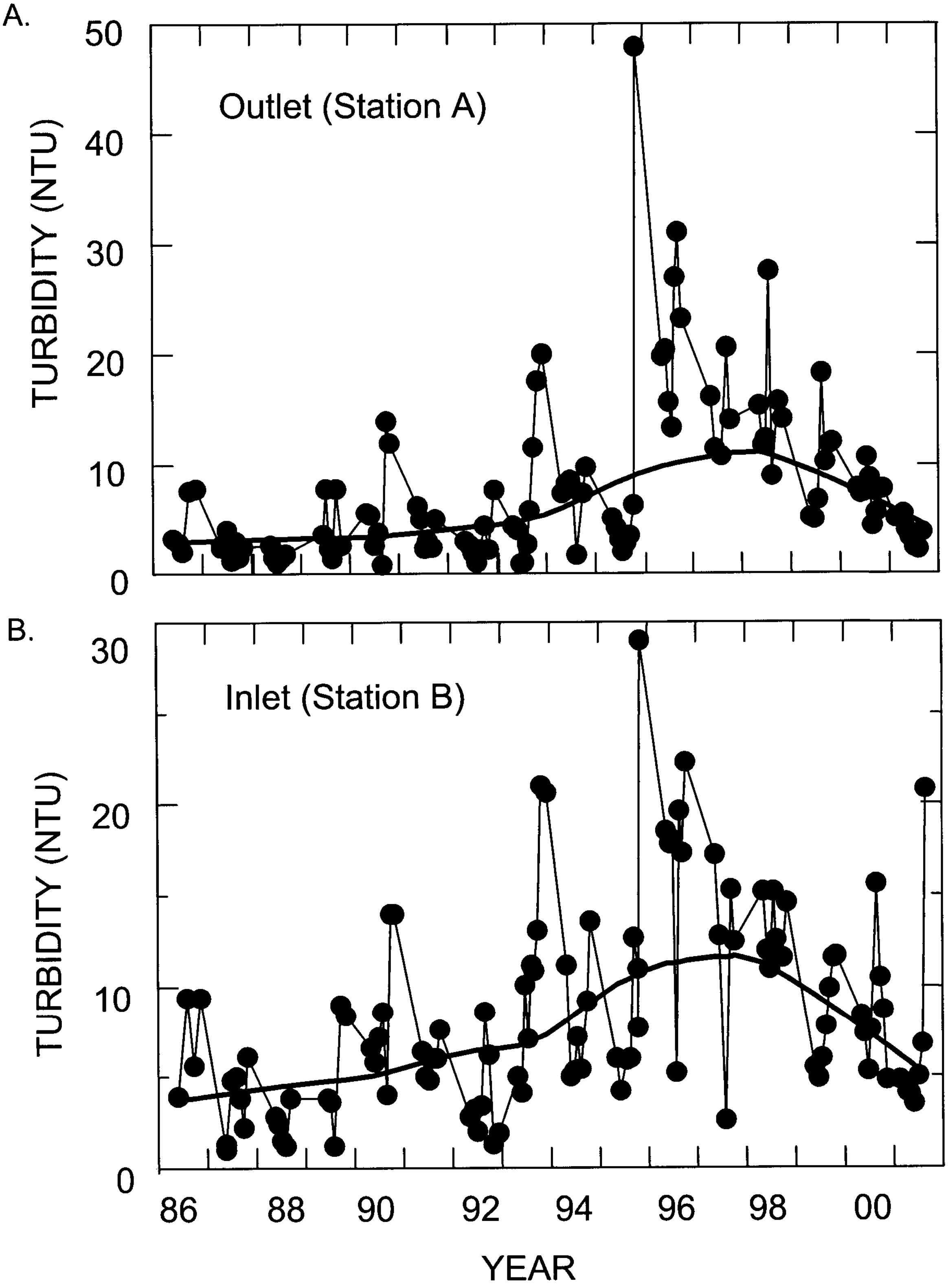

Figure 17. Temporal pattern of turbidity within the 1-m stratum near (A) the outlet and (B) inlet of Skilak Lake, 1986-2001. Also shown are LOWESS fits to the data.

Over the next five years (1993-1998), turbidity levels increased more than two-fold (mean 11. 6 NTU). In the past few years, water turbidity decreased to an average of about 7.4 NTU; however, these levels were 60% higher than water turbidity in the late 1980s and early 1990s. Turbidity levels were more variable in the part of the lake basin (Station B) nearest the glacier input (Figure 17B) compared to levels nearer the outlet (Station A) of the lake (Figure 17A). As expected, mean euphotic zone depth (EZD) showed a general decreasing trend over the same time period and more importantly the interannual fluctuations and long-term pattern tracked reasonably well with the summer ice balance (SIB) of Wolverine Glacier (Figure 18A). That is, EZD was strongly correlated (r^2=0.59; P=0.009) with SIB in the previous year (Figure 18B) suggesting that increasing glacier melt (smaller SIB) was associated with greater turbidity and a shallower EZD in Skilak Lake. The regression equation was $EZD = 14.0 + 2.11SIB$.

Although a time series plot of annual air temperature anomalies between 1950 and 2001 exhibited a gradual warming trend, there was no discernable trend in the temperature for the 1986-2001 portion of the time series (Figure 19A) during which water turbidity was measured. However, a plot of summer (June-August) air temperature anomalies for the available years showed evidence of a warming trend that began in the mid 1980s, as seen by the LOWESS fit to the data (Figure 19B). The increase was in the range of 1.0-1.5 °C. Between 1986 and 1998, annual (May-October) annual copepod and EZD showed a general downward trend (Figure 20A) and there appeared to be a one-year lag in copepod biomass with respect to EZD. We found a strong positive relationship (r^2=0.53; P=0.001) (Figure 20B) between EZD and total copepod biomass in the subsequent year ($COPB_{y+1}$). The regression equation was $COPB_{y+1} = 132.1 + 45.0EZD$. EZD and *Cyclops* biomass in the subsequent year ($CYCB_{y+1}$) were more strongly related ($r^2 = 0.59$; $P<0.001$). This regression equation was $CYC_{y+1} = 43.5 + 40.5EZD$ ($r^2 = 0.59$; $P<0.001$). On the other hand, no such significant relationship was found between EZD and *Diaptomus* biomass.

DISCUSSION

Copepod-sockeye linkage

Many studies have shown that when populations of planktivorous fish are abundant, heavy grazing reduces the number of large-bodied zooplankton such as *Daphnia* (Brooks and Dodson 1965; McQueen et al. 1986; Northcote 1988; Mazumder and Lean 1994). In Frazer Lake (Alaska) large sockeye escapements and subsequent recruitment of planktivorous fry led to top-down control of zooplankton, particularly of the cladoceran (daphnid) component (Kyle et al. 1988). Kyle and colleagues found the major switch in the zooplankton community from large herbivores to more predator resistant taxa (e.g., small-bodied *Bosmina* and copepods) of this clear water lake resulted in large decreases in juvenile sockeye recruitment (fewer smolts) and lower total returns of adults from the affected brood years. In some sockeye nursery lakes, the effects of excessive planktivory continued beyond the immediate fry-rearing year because cropping was associated with a failure of cladoceran zooplankton populations to recover, at least in clear and organically stained systems (Koenings and Kyle 1997).

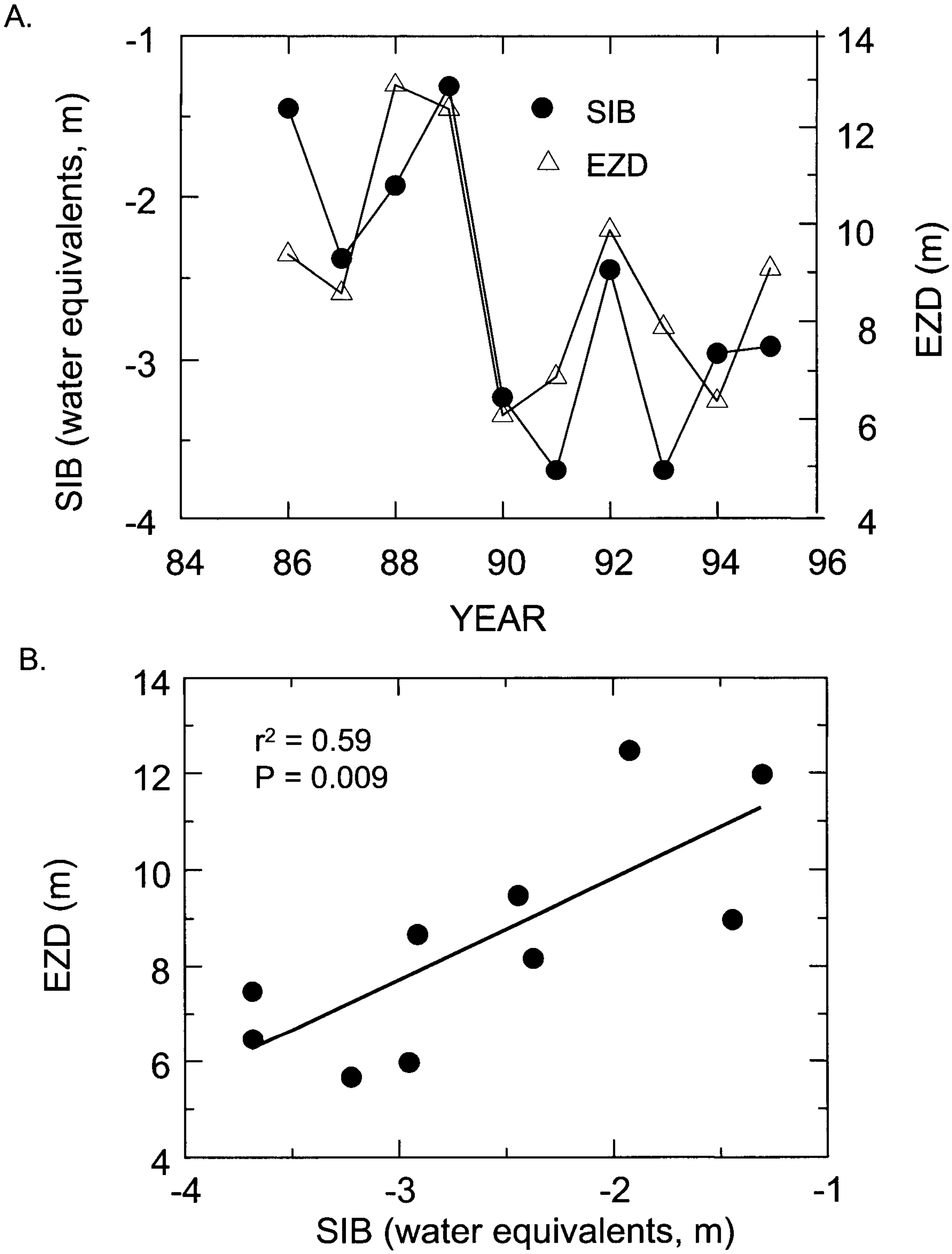

Figure 18. (A) Time series of the summer ice balance (*SIB*) of Wolverine Glacier and average euphotic zone depth (*EZD*) in the following year for Skilak Lake; (B) *EZD* as a function of *SIB*.

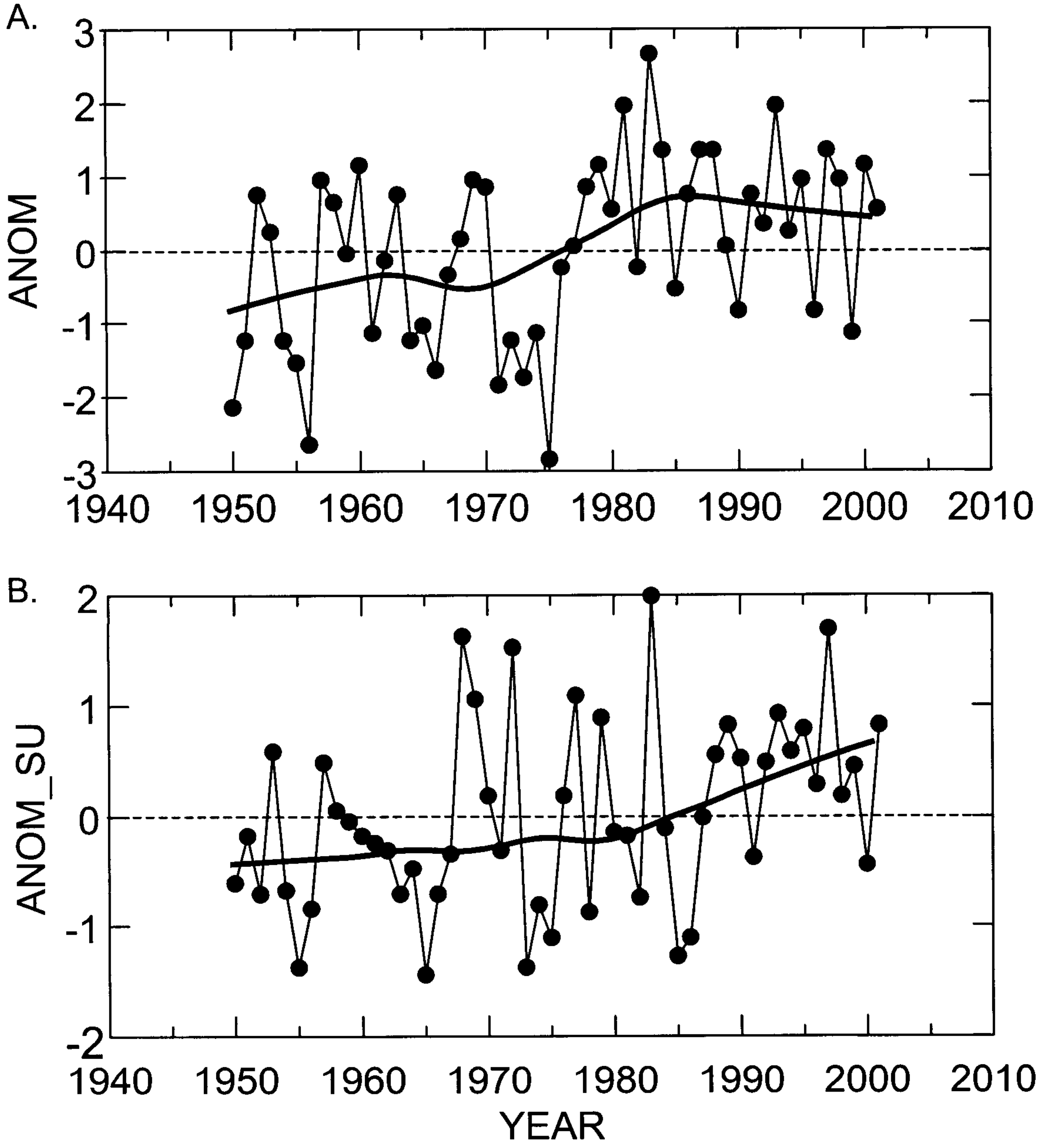

Figure 19. Time series of (A) annual (*ANOM*) and (B) summer (June-August) (*ANOM_SU*) air temperature (°C) anomalies for Kenai, Alaska (1950-2001). Dashed lines are the 52-year means and curved lines are LOWESS fits to the data.

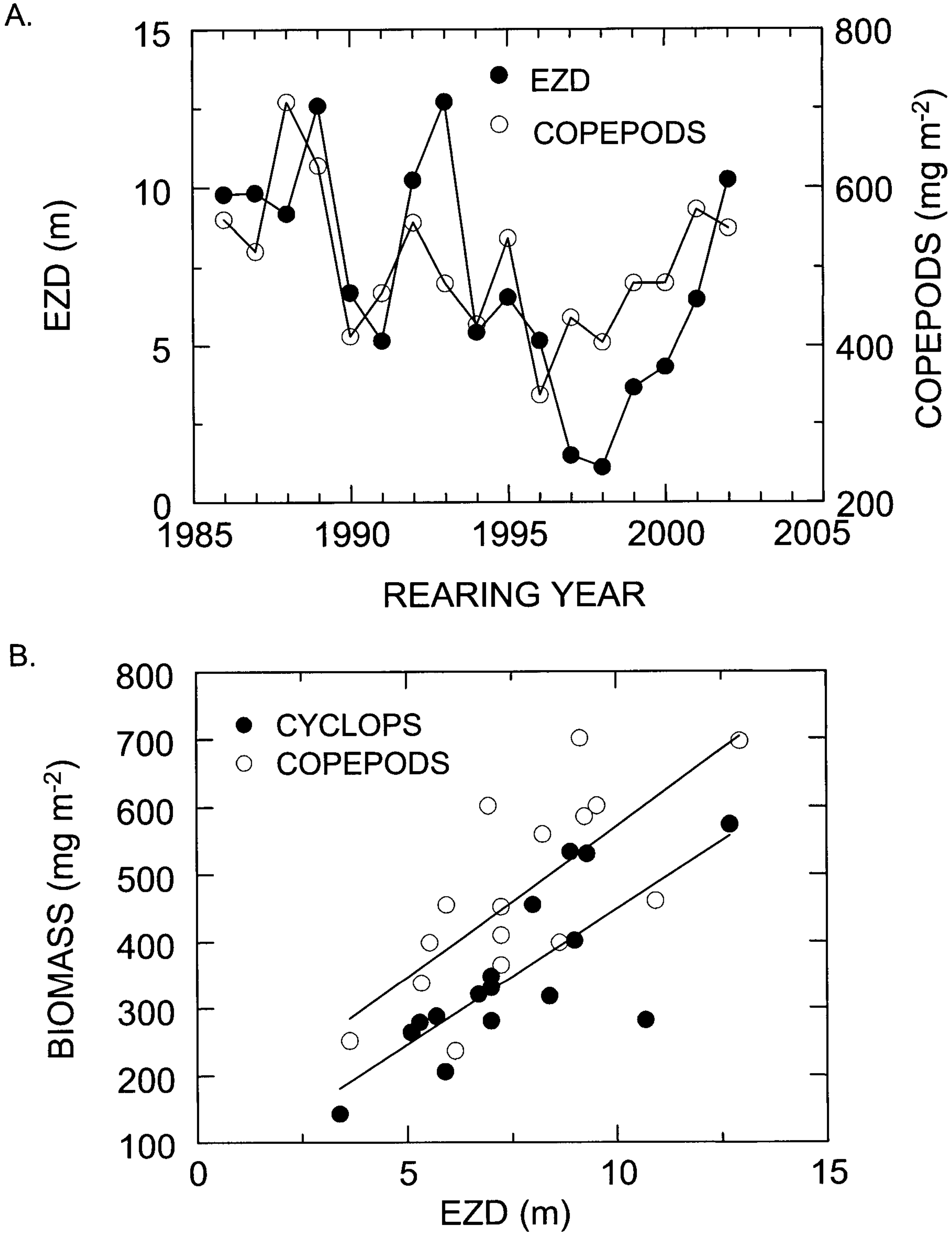

Figure 20. Time series of (A) mean annual euphotic zone depth (*EZD*) and (May-October) copepod biomass in Skilak Lake; (B) the relationship between *EZD* and the biomass of *Cyclops* and total copepods in the subsequent year.

Koenings et al. (1990) showed that in glacial (turbid) lakes the size distribution of inorganic silt particles within the water column largely overlaps that of the edible microphytoplankton (20-200 µm) so that the mixture of particles consumed by zooplankton through filter feeding is of low nutritional value. As a result, glacial lakes cannot support abundant populations of filter-feeding cladocerans such as *Daphnia*, and instead are dominated primarily by the copepods *Cyclops*, a raptorial feeder, and *Diaptomus* that grazes on smaller nanophytoplankton (10-20 µm), which in turn comprises the bulk of the total algal biomass in glacial lakes (Stockner and McIsaac 1996). These two copepod taxa are the only prey for rearing sockeye juveniles in the limnetic zone of Skilak and Kenai lakes. To date, there are few if any studies within glacial lakes that demonstrate size-selective predation by planktivorous fish on copepods or a strong copepod-fish linkage (but see Schmidt et al. 1994). Edmundson et al. (1997) hypothesized that excessive foraging on zooplankton (mainly cyclopoid copepods) by juvenile sockeye salmon produced from large escapements caused a decline in sockeye salmon production in glacially turbid Coghill Lake (Prince William Sound, Alaska). In nearby Crescent Lake (Upper Cook Inlet), which has similar glacial turbidity levels as in Skilak and Kenai lakes, Edmundson and Edmundson (2002) suggested heavy predation by sockeye juveniles held *Cyclops* densities at low levels, which may have led to long-term decline in stock productivity (i.e., low adult recruit-per-spawner values). Over the available time series of data for the Kenai River system, the number of spawners increased on average (Figure 3A) and *Cyclops* and total copepod biomass in Skilak Lake, the major nursery area for young salmon, decreased (Figure 10A,C). This provides at least some circumstantial evidence of a grazing effect; however, increasing water turbidity and associated decrease in EZD may also be contributing to the decline in cyclopoid copepod biomass (Figure 20). Nonetheless, the seasonal availability of prey (zooplankton), temporal pattern of zooplankton size distributions in relation to fry, and the dependence of fry growth and survival on spring copepod biomass, provide a much more convincing picture of the strong interaction between copepods, mainly *Cyclops*, and sockeye juveniles.

The temporal changes in length-frequency and the relative changes in cohort dominance provided evidence that *Cyclops columbianus* in Skilak Lake has a life history that spans across two growing seasons (Figure 11-12), but *Diaptomus* has an annual life cycle with recruitment occurring somewhat earlier (i.e., June) than *Cyclop*s. Although copepods generally appear to have annual life-history patterns in freshwaters (Hairston and Bohonak 1998), Elgmork (1985) also described *Cyclops scutifer*, a close relative of *C. columbianus*, as having a multi-year life history in certain environments. The strong relationship between fall fry abundance and the biomass of total copepods (*Cyclops* + *Diaptomus*) in the spring (May-June) (Figure 14) suggests that the density of the previous years' cohort of *Cyclops* largely determines survival of emergent fry in the spring. This model differed somewhat from that originally developed by Schmidt et al. (1997). In their multivariate model, fall fry abundance was strongly related (R^2=0.95, n=10) to number of spawners plus spring and summer *Cyclops* biomass. In our model, *Cyclops* biomass was not by itself a significant variable in predicting fry abundance.

The significance of spring copepod biomass, rather than spring *Cyclops* biomass, as a predictor of fall fry abundance is not clearly understood. Although earlier studies found that the diet of sockeye juveniles in Skilak Lake in the spring (May-June) composed mostly age-1 *Cyclops* (Schmidt and Tarbox 1995), the dietary composition also included *Diaptomus*, particularly in stomach samples collected later in the growing season. In addition, in some years (e.g., 1990-1992 and 1997) *Diaptomus* composed as substantial fraction (approximately 40%) of the total in-lake copepod biomass (Figure 10). While cyclopoid copepods are the most important taxon ingested by sockeye fry in Skilak-Kenai lakes, *Diaptomus* may also be an important supplemental food resource in years when cyclopoid copepods are in lesser abundance, particularly during the critical period of fry emergence in the spring. The effect of food (copepods) supply on growth and survival of sockeye fry probably represents interacting combinations of competitive effects between prey species, fish density, temperature, and turbidity. Thus, total (spring) copepod biomass was a better predictor of fall fry abundance than either *Cyclops* or *Diaptomus* alone. Furthermore, since *Cyclops* recruitment does not occur until July, we suggest that juvenile sockeye fry are largely dependent upon the survivors of the previous year's cohort of *Cyclops* as their primary food resource. Since this level of spring (age-1) *Cyclops* biomass is determined by mid-summer recruitment and grazing by fry during late summer and fall in the previous year, intense planktivory in a given year may reduce food resource availability and lower fry recruitment in the subsequent year. There was a an apparent reduction in spring copepod biomass associated with increasing fry abundance (Figure 16); though we concede the regression results were only marginally significant. However, there is some uncertainty in attempting to assign differences in spring copepod biomass to the predation pressures of the previous fall fry alone because there is also additional evidence supporting the hypothesis that copepod biomass is related to changing environmental (turbidity) conditions.

Short and long term impacts from overescapement

Evidence of an adjacent year interaction of juvenile sockeye salmon competing for a single cohort of *Cyclops* provides some basis for the one year lag in the recruit-per-spawner data (Figure 3C) for the Kenai River following the 1987, 1988, and 1989 large escapements (Figure 3A). The observation of lower adult returns from these brood-year escapements support the contention that overescapement occurred. Evidence for impacts from large escapements are (1) the low RPS values for the 1989 and 1990 brood years (Figure 3C), (2) the negative relationship between escapement and fry weight (Figure 6B), (3) the low lipid content of fry entering the overwinter period (Figure 7A-B), and (4) the dependence of both fry weight and fry abundance on spring copepod biomass, which suggests fish density effects (Figures 14-15). Our data support the notion that compensatory mortality of sockeye fry in these glacial nursery lakes contributes to reduced RPS following large escapement events. Clearly though, the magnitude of the effects and the extent to which they persist may be exacerbated or overridden by long-term changes in climate or water quality.

The influence of climate change on copepods and sockeye production

Although fish predation has long been recognized as a strong determinant of development and biomass of crustacean zooplankton, few studies have shown climatic influences on zooplankton in lakes. George and Harris (1985) found that pelagic zooplankton abundance and biomass in Lake Windermere (U.K.) was strongly tied to spring epilimnetic temperatures, but not to grazing by planktivorous fish. Temporal shifts in the occurrence of the spring clearwater phase, caused by the grazing of phytoplankton by zooplankton, were correlated with the North Atlantic Oscillation index for a set of shallow lakes in central Europe (Gerten and Adrian 2000; Scheffer 2001). It has been suggested that climatic warming would increase thermocline depth because of reduced loading of dissolved organic carbon and increased light penetration in north temperate (boreal) lakes (Schindler et al. 1996). On the other hand, King et al. (1997) found that warmer climatic conditions produced earlier stratification, steeper thermoclines, and thinner epilimnions in Lake Huron. Edmundson and Mazumder (2002) suggested that warmer climatic conditions could decrease temperatures in glacial lakes through higher light reflectance caused by turbidity increases. Whatever the response, such physical changes would in turn be expected to affect phytoplankton, zooplankton and fish communities in lakes (Schindler 2001).

Over the 17-year period of our studies on Skilak Lake, there was a trend of increasing glacier melt (Figure 18A) and water turbidity (Figure 17A-B) and decreasing EZD (Figure 18A) that was consistent with a general warming pattern in air temperatures (Figure 19B). In addition, *Cyclops* biomass was positively related to EZD (Figure 20A-B) suggesting that regional climatic effects (warming) and its attendant silt loading (turbidity) influence the interannual variations of copepod biomass. Zettler and Carter (1986) suggested higher abiotic turbidity in Lake Temiskaming (Ontario-Quebec) reduced predation by visually attuned planktivores, which resulted in larger zooplankton sizes. Sirois and Dodson (2000) showed that increasing turbidity in the St. Lawrence River, at least up to a point, increased the feeding efficiency of larval rainbow smelt by providing a greater contrast against which they can see their prey. However, increases in turbidity (shallower EZD) probably reduce the photosynthetic capacity of Skilak Lake and the amount of phytoplankton available for copepod grazing. Persistent levels of higher turbidity may also affect (lessen) vertical migration behavior of copepods and sockeye fry, which would certainly alter the bioenergetics of both predator and prey.

Although we found no studies that demonstrated altered vertical migration patterns in copepods in response to turbidity, Levy (1990b) found that turbidity dampened DVM in juvenile sockeye salmon in some British Columbia lakes. Under scenarios of climate warming, many complex abiotic and trophic interactions are expected in lakes (Schindler 2001; Gerten and Adrian 2002). Thus, in Skilak Lake simultaneous bottom-up and top-down ecological processes affect the production of *Cyclops*, the primary prey of juvenile sockeye salmon. Light penetration and primary production are affected by glacial run-off through changes in turbidity and EZD (Koenings and Edmundson 1991; Edmundson and Carlson 1998). Intense grazing by large fry populations reduces the biomass of *Cyclops* available to emergent sockeye salmon fry the following spring (Figure 16). Our statistical analyses support the notion that both of these processes affect the biomass of *Cyclops*, but these methods cannot reveal the magnitude of the affect of each process in any specific year. A mechanistic numerical model of the lake ecosystem should be developed to further examine these processes. Large escapements can reduce production from current and subsequent brood years. In conclusion, this multi-year response occurs because the primary copepod prey of juvenile sockeye salmon exhibits a two-year life history and prey abundance limits growth and ultimately survival rates of juvenile salmon. Climate changes affecting glacial run-off further modulate the interaction between copepods and juvenile sockeye salmon affecting salmon production.

Brood-year interaction

We observed a cyclic pattern in sockeye salmon returns for the Kenai River system (Figure 4A). Delayed density-dependence or brood interactions have been implicated in the cyclic fluctuations in salmon abundance and successfully modeled for some sockeye stocks (Collie and Walters 1987; Welch and Noakes 1990; Levy and Wood 1992; Myers et al. 1998). Under the brood interaction hypothesis, one possible mechanism is that nutrients from decaying salmon carcasses resulting from large escapements (i.e., peak years) may produce more food for juvenile sockeye the following rearing year compared to smaller escapements (off-peak years). Hence, more food resources lead to better growth and survival of young salmon in that year. Although nutrients (mainly phosphorus) released from salmon carcasses are an important factor affecting the productivity of some sockeye nursery lakes (Stockner 1987; Koenings and Burkett 1987; Kline et al. 1993ab; Schmidt et al. 1998), in glacial lakes such as Skilak and Kenai lakes, studies have shown that pelagic productivity is more limited by light penetration (turbidity) than nutrients (Edmundson and Carlson 1998). In particular, for 14 glacial lakes spanning a turbidity gradient from 5-45 NTU, which encompasses the range in turbidity for Skilak and Kenai lakes, Edmundson and Carlson (1998) found algal biomass (as indexed by chlorophyll *a* pigment concentration) was unrelated to changing phosphorus levels. Therefore, carcass nutrients probably do not cause brood interactions among sockeye salmon rearing in glacial lakes. An alternative hypothesis is that heavy grazing on crustacean zooplankton from large fry populations causes the survival of year classes that follow the more abundant line to be reduced (Eggers and Rogers 1987; Levy and Wood 1992).

The food supply hypothesis requires that a dominant year-class rearing in a common area (e.g., lake) deplete zooplankton available to one or more subsequent broods. For Kenai River sockeye salmon, this hypothesis is supported by (1) reduced spring copepod biomass when the abundance of fry the previous fall is greater than 20 million, (2) the dependence of fall fry abundance on spring copepod biomass and the number of spawners, and (3) the dependence of fall fry weight and thus subsequent overwinter survival on spring copepod biomass and fall fry abundance. Recently, Carlson et al. (1999) specified a brood-year interaction spawner-recruit model ($[R_i = S_i \exp(\alpha - \beta S_i S_{i-1} + \varepsilon]$) for the Kenai River (Kenai-Skilak lakes) sockeye stock, which contained a statistical interaction term (cross product) of the current (S_i) and prior years' (S_{i-1}) spawner abundance (i.e., $S_i \times S_{i-1}$). The fry growth and survival mechanisms we have described for this system are consistent with the brood year interaction model. That is, the adjacent year interaction of juvenile sockeye salmon competing for copepods in the spring, coupled with the two-year life-history of *Cyclops* provides a plausible biological explanation for significance of the interaction term in their (Carlson et al. 1999) spawner-recruit model. Simply put, predation on copepods (mainly *Cyclops*) by fry in a given year affects copepod biomass the following spring, which has a compensatory effect on fry survival and subsequent adult recruitment in the next year class.

Our spawner-recruit analyses supported the hypothesis that large sockeye salmon escapements into the Kenai River watershed cause reduced returns from current and future spawner populations. A relatively simple brood-interaction model with a single statistical interaction term best fit the Kenai sockeye salmon data (Table 2; Figure 4). Previous investigators using brood-interaction models including multiple lags but no statistical interaction terms have found only weak evidence of delayed density dependence (Eggers and Rogers 1987; Walters and Staley 1987; Welch and Noakes 1990; Myers et al. 1997). The statistical interaction term in our model indicates that multiple large escapements have the greatest compensatory effect on survival; whereas, a single large escapement followed by a small escapement may not produce such an effect.

The multiplicative effect suggested by the interaction term in our model could arise if *Cyclops* population sizes are linked between years. Our ecological data support the hypothesis that intense grazing by large fry populations in Skilak Lake reduces the biomass of *Cyclops* the following spring causing reduced survival of emergent fry. Presumably, survival of emergent fry is reduced due to food limitation and subsequent starvation during the first few weeks after entering the lake environment. Since the *Cyclops* population in the spring is composed of the progeny of the adult *Cyclops* population from the previous summer, a mechanism exists by which intense grazing on the adult population could affect the size of the *Cyclops* population the following spring. The relatively small clutch size of this copepod species (Williamson 1991) supports the notion that future *Cyclops* recruitment may be related to adult population size. In a system with such a linkage, a second large population of salmon fry would be much more likely to starve if they emerged into an environment depleted of *Cyclops* by intense grazing the previous year.

The relationship we observed between EZD in Skilak Lake and the residuals from our brood-interaction model (Figure 5) was consistent with our other observations in this system. Euphotic zone depth in Skilak Lake was correlated with *Cyclops* biomass (Figure 20B) indicating that light penetration affected primary and secondary production. Also, copepod biomass was correlated with fall fry abundance and size, which was in turn related to overwinter mortality of fry. These relationships are evidence of mechanisms that cause limitations in primary production to affect survival of sockeye salmon. Such mechanisms exist, because food abundance limits the growth of juvenile sockeye salmon in this system. Thus, large escapements and especially consecutive large escapements have the potential to substantially reduce stock productivity, and this potential is much greater when light penetration and primary production are reduced by elevated glacial runoff.

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