

EFFECTS OF CHANGING CLIMATE ON ZOOPLANKTON AND JUVENILE SOCKEYE SALMON GROWTH IN SOUTHWESTERN ALASKA

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Abstract. Detecting and forecasting the effects of changing climate on natural and exploited populations represent a major challenge to ecologists and resource managers. These efforts are complicated by underlying density-dependent processes and the differential responses of predators and their prey to changing climate. We explored the effects of density-dependence and changing climate on growth of juvenile sockeye salmon and the densities of their zooplankton prey in the Wood River system of southwestern Alaska. We fit dynamic time-series models to data collected between 1962 and 2002 describing growth of juvenile sockeye, timing of spring ice breakup, and summer zooplankton densities. The timing of spring breakup has moved about seven days earlier now than it was in the early 1960s. Our analyses suggest that most of this shift has been a response to the warm phase of the Pacific Decadal Oscillation that persisted from the mid-1970s to the late 1990s. This progression toward earlier spring breakup dates was associated with warmer summer water temperatures and increased zooplankton (especially *Daphnia*) densities, which translated into increased sockeye growth during their first year of life. The number of spawning adults that produced each year class of sockeye had a strong negative effect on juvenile sockeye growth rates, so that the size of the density-dependent effect was, on average, twice as large as the effect of spring breakup date. These results highlight the complexity of ecological responses to changing climate and suggest that climate warming may enhance growing conditions for juvenile salmonids in large lakes of Alaska.

Key words: *Bristol Bay, southwest Alaska, USA; climate change; cryophenology; fish; global change; global warming; ice phenology; Pacific Decadal Oscillation; sockeye salmon; Wood River, southwest Alaska, USA; zooplankton.*

INTRODUCTION

Predicting the effects of future climate change on the dynamics of freshwater biota is a critical goal for ecology (Carpenter et al. 1992, Naiman et al. 1995). Recent synthesis efforts have produced somewhat-confident predictions about future changes in hydrologic patterns and associated chemical responses (e.g., Melack et al. 1997, Schindler 1997). Forecasts about the future status of freshwater biota are much less compelling and, in fact, there is more confusion than consensus about the responses of fish and plankton to climate warming. For fishes, the most widely accepted forecasts predict that there will be northward shifts in the distributions of cool- and warm-water fishes as climate warming improves thermal habitat for these species (Shuter and Post 1990). In contrast, many cold-water species like trout and salmon are expected to lose substantial amounts of their current habitat (Schindler et al. 1990, Rahel et al. 1996, Stefan et al. 2001). Physiological models predict that growth rates of some fish-

es should improve as climate enhances the thermal regimes of lakes (Magnuson et al. 1990). However, in contrast, decreased growth rates of fishes are expected if their metabolic demands increase faster than the rates of prey production in response to climate warming (Magnuson et al. 1990, McDonald et al. 1996).

Forecasts about how zooplankton populations will respond to climate warming are also mixed. For example, DeStasio et al. (1996) predicted that spatial overlap between zooplankton and their fish predators will either increase or decrease, depending on location, lake morphometry, and the species involved. Chen and Folt (1996) demonstrated that warming in autumn can disrupt life-history strategies of zooplankton, which has the potential to alter their biogeographic ranges. In central Europe, spring warming associated with the North Atlantic Oscillation has been associated with increased densities of many zooplankton species (e.g., Gerten and Adrian 2000, Straile and Adrian 2000, Benndorf et al. 2001). Biomass of marine zooplankton off the coast of southern California declined by 80% in the second half of the 20th century associated with surface temperature warming producing increased thermal stratification, and thus, reduced plankton productivity (Roemmich and McGowan 1995). Similar observations from long time series in North America freshwaters remain unreported.

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Adding to the uncertainty about how fishes and plankton will respond to changes in climate are confounding variables that mask long-term responses to physical conditions. One key variable that may confound population responses to climate is density dependence in growth and mortality processes. Others include species interactions, habitat degradation, eutrophication, resource exploitation, and contamination by toxic substances (Breitburg et al. 1999). Long time series of climatic and biological variables enable us to begin to separate population responses to changing climate from potential confounding variables.

Pacific salmon (*Oncorhynchus* spp.) may be especially responsive to climate changes because they have complex life-history strategies, occupy a variety of stream, lake, estuarine, and marine ecosystems, and are widely distributed throughout the North Pacific Ocean—an ecosystem that has been shown to be highly sensitive to subtle climate shifts (Beamish and Bouillon 1993, Mantua et al. 1997). Forecasts of the responses of salmon populations to future changes in climate have not been encouraging. Thermal changes in the North Pacific Ocean are expected to substantially reduce the volume and productivity of oceanic habitat for salmon (Hinch et al. 1995, Welch et al. 1995). Forecasts for the responses of Pacific salmon to climate change during the freshwater phase of the life cycle also predict general declines in growth and survival. For example, Henderson et al. (1992) predicted that sockeye productivity in the Adams River of southern British Columbia (Canada) would decline under the climate scenarios projected for a doubling of atmospheric carbon dioxide. In a comprehensive review of expected climate effects on freshwater ecosystems of western North America, Melack et al. (1997) also predicted that sockeye salmon populations would exhibit reduced freshwater growth rates throughout their range in response to increased thermal challenges and to reduced plankton production in nursery lakes. Increased glacial runoff to lakes and rivers in southcentral Alaska may also increase turbidity and thus reduce primary production that supports salmon growth (Melack et al. 1997). Reduced juvenile growth should, in turn, reduce the marine survival rate of sockeye (Henderson and Cass 1991, Koenigs et al. 1993, Melack et al. 1997).

Sockeye salmon (*Oncorhynchus nerka*) have a unique life-history strategy associated with spending a substantial portion of their life cycle in lakes (Burgner 1991). After spending 1–3 years feeding in the ocean, adult sockeye salmon migrate to freshwater habitats associated with lakes that are used by juvenile sockeye usually for the first 1–2 years of life before they migrate to the marine environment. Spawning occurs in a wide variety of habitats including small streams, large rivers, and beaches on lakes (Quinn et al. 2001). Upon emergence from gravel in the early spring, roughly coincident with ice breakup, most sockeye fry move to lakes to feed on lentic insects and zooplankton (Burgner

1991). Comparative studies have shown that the growth of juvenile sockeye during their lake residency is positively related to the thermal budget, nutrient concentrations, and zooplankton production, and negatively related to their own density in lakes (Hyatt and Stockner 1985, Eggers and Rogers 1987, Edmundson and Mazumder 2001, Mazumder and Edmundson 2002). Nevertheless, formal analyses of the responses of juvenile salmon growth to changing climate regimes have yet to be published.

Ice phenologies of lakes and rivers represent an integrated response to changes in climatic conditions. Ice breakup date generally reflects spring warming rates for the previous 1–2 month period (Robertson et al. 1992, Wynne et al. 1996, Livingstone 1997, Magnuson et al. 2000). Water bodies throughout the Northern Hemisphere have exhibited consistent trends toward later autumn freezing and earlier spring breakup in the last 100 years (Magnuson et al. 2000). These changes in ice phenology have resulted in substantially longer ice-free seasons on lakes and rivers. In general, rates of change in spring warming have been greater than the observed changes in autumn cooling. Despite these pronounced changes in length of the open-water season, we have a very limited understanding of their significance for the productivity and organization of aquatic communities. There have also been few formal analyses to evaluate the relative contributions of long-term climate change and of periodic modes of climate variability on spring breakup dates. Notable exceptions include the analyses of Anderson et al. (1996) who showed that El Niño Southern Oscillation (ENSO) variability had strong effects on the date of spring ice breakup in southern Wisconsin (USA), and Yoo and D'Odorico (2002) who showed that the North Atlantic Oscillation (NAO) had strong effects on ice phenologies of lakes and rivers in Northern Europe. The Pacific Decadal Oscillation (PDO), a recently described climate oscillation, has been shown to have strong effects on climatological processes in western North America (Mantua and Hare 2002), but its effects on spring ice phenologies, or lake ecology in general, remain unexplored.

We used a previously unpublished time series of data collected from 1962 through 2002 on the growth of juvenile sockeye salmon in the Wood River system of southwestern Alaska (USA) to estimate the growth responses of juvenile sockeye to long-term changes in their density and the timing of spring ice breakup. We also relate the observed changes in sockeye growth and spring ice breakup dates to summer densities of zooplankton—the key prey for juvenile sockeye in lakes. Our analyses show that the largest effects on juvenile sockeye growth are negative and density dependent but that increases in the length of the growing season have also had substantial positive effects on growth rates. Similarly, zooplankton densities were higher in summers following early spring breakup dates. These re-

sults suggest that conditions for growth of sockeye salmon during their lake residency in southwestern Alaska are likely to improve if global climate continues to warm at the rates observed during the last four decades. How these changes in juvenile rearing conditions translate into changes in the overall productivity of the stocks remains uncertain.

MATERIALS AND METHODS

Study site

The Wood River system is a major tributary of the Nushagak River that flows into Bristol Bay in southwestern Alaska. Lake Aleknagik is the southernmost lake in a chain of five large lakes that serve as major nursery systems for sockeye salmon. The annual sockeye run to the Wood River system has averaged $4.7 \times 10^6 \pm 2.8 \times 10^6$ fish (mean \pm 1 SD) since 1960, of which about 50% are caught by fisheries before they enter freshwater. On average, about 30% of those fish that escape the fishery spawn in Lake Aleknagik or rivers and streams that flow directly into it. After adult spawning in July to September, eggs incubate through the winter, the fry emerge early the following spring, and then migrate to Lake Aleknagik. Juvenile sockeye generally spend one full summer in the lake before migrating to the ocean the following spring. In this paper we present data collected from Lake Aleknagik between 1962 and 2002 to characterize the patterns of growth in juvenile sockeye, and how this relates to the density of their parents, summer zooplankton densities, and the timing of spring ice breakup during their freshwater growth year.

Lake Aleknagik is 83 km² in surface area, has a maximum depth of 110 m, and is situated at an elevation of 10 m above mean sea level. The crustacean zooplankton community of Lake Aleknagik is composed of the calanoid copepods *Eudiaptomus gracilis*, *Eurytemora yukonensis*, and *Leptodiptomus pribilofensis*, the cyclopoids *Cyclops columbianus* and *Acanthocyclops brevispinosus*, and the cladocerans *Eubosmina longispina*, *Daphnia longiremis* and, *Holopedium gibberum*. The fish community is dominated by anadromous sockeye salmon, and by several resident freshwater species (*Salvelinus alpinus*, *Gasterosteus aculeatus*, *Pungitius pungitius*, *Dallia pectoralis*, *Oncorhynchus mykiss*).

Juvenile sockeye growth

Juvenile sockeye were sampled by tow net (Johnson 1956, Burgner et al. 1969) during the last week of August of every year since 1962. In brief, the 3×3 m square net was towed at the lake surface between two boats at about 3 km/h for 5 min at each survey site. A total of nine standard sites were surveyed in each year of the study. Surveys commenced about an hour after nightfall when sockeye have accomplished their nighttime migration to the surface waters (Scheu-

erell and Schindler 2003). Growth data presented in this paper are arithmetic means of all juvenile sockeye caught in all tow-net stations on Lake Aleknagik. Each year, at least 200 individuals were measured, and often more than 1000 fish were measured. Because there is a small amount of variability in the date that our surveys were conducted in any given year, all estimates of sockeye size were standardized to an expected size on 1 September by assuming that fish grow about 0.3 mm/d (D. E. Rogers, unpublished data). 1 September is near the end of the growing season for Lake Aleknagik and it can be assumed that estimates of size on this date are a good approximation of the size of fish entering the winter nongrowing season. Because there has been a general tendency for an extended ice-free season in the autumn (Magnuson et al. 2000), our estimates of changes in sockeye growth rates to warming trends should be considered as conservative. All methods have been consistent for the duration of this study.

We used the number of adult sockeye that spawned in the Lake Aleknagik system in the previous year as our metric of juvenile sockeye density in Lake Aleknagik due to a lack of reliable estimates of actual juvenile density. The tow-netting methods described above were not designed to estimate juvenile sockeye density, but rather, to obtain samples for characterization of the size distribution of fishes. Sockeye escapement numbers for the entire Wood River system were enumerated near the mouth of the Wood River. These total escapement numbers were then allocated among the five lakes in the system through a combination of ground surveys of creeks and aerial surveys of rivers and lake beaches once the sockeye established themselves on the spawning grounds. Ground surveys occurred during August and early September of each year, and aerial surveys were performed by the Alaska Department of Fish and Game during late August and September. These slight differences in survey timing reflect the differences in spawning timing among various habitats: stream fish spawn earlier than river and lake fish.

Zooplankton densities

Zooplankton were collected every year from 1967 through 2002 at six stations every two weeks between June and early September in Lake Aleknagik. Zooplankton were sampled with vertical tows of a 247- μ m mesh conical net with a mouth opening of 0.5 m and a width:length ratio of 1:3. A 6.8-kg weight was suspended from the bottom of the net to help ensure vertical tows. The net was retrieved either by hand or by gas-powered winch at a rate of \sim 0.5 m/s. Zooplankton were preserved in either 5% formalin or 50% ethanol. Vertical tows were all 60 m deep, except for one station off of Yako Creek that was towed from 20 m. Zooplankton were enumerated under a dissecting microscope. Consecutive subsamples obtained with a Stempel pipette were enumerated until \sim 500 individual zoo-

plankters were counted. Because juvenile sockeye move from littoral habitats to pelagic habitats in mid-summer, we only included the densities of zooplankton in August for the time-series analyses presented here. However, we do show the relationship between the timing of spring ice breakup and monthly zooplankton abundance with simple correlation analyses to capture some of the seasonal dynamics in the zooplankton community. Vertical temperature profiles from 0 to 60 m were taken on every date that zooplankton were sampled with either a bathythermograph or an electronic thermister. Prior to 1967, when zooplankton sampling was initiated, water temperatures were measured about every two weeks from early June through mid-September with a bathythermograph.

Timing of spring breakup

The timing of ice breakup in spring has been shown to be highly responsive to climate changes during the last century throughout North America (Magnusson et al. 2000). We used the timing of spring breakup as an integrated proxy of climatological changes in this region. Spring breakup date has been recorded since 1962 in the village of Aleknagik located at the south (outflow) end of Lake Aleknagik every year. Annual values of the Pacific Decadal Oscillation (PDO) were obtained from the University of Washington Joint Institute for Study of the Atmosphere and Ocean (*data available online*),⁵ and values for the El Niño Southern Oscillation index (ENSO) were obtained from the National Oceanographic and Atmospheric Administration Climate Diagnostics Center (*data available online*),⁶ to be tested as drivers of the spring breakup dates.

Time-series analyses

We used dynamic linear models (DLM, Pole et al. 1994) to explore the temporal relationships between the growth of juvenile sockeye in their first year of life, the density of their parents, the availability of their food (zooplankton), and the timing of spring ice breakup. This technique has been applied effectively to ecological data and the methodology has been described in detail elsewhere (e.g., Cottingham and Carpenter 1998, Lamon et al. 1998, Scheuerell et al. 2002) so we describe it only briefly here.

DLM are described by the following two general equations:

$$Y_t = \mathbf{X}_t \boldsymbol{\theta}_t + \mathbf{v}_t \quad \mathbf{v}_t \sim \mathcal{N}[0, V_t] \quad (1)$$

$$\boldsymbol{\theta}_t = \mathbf{G} \boldsymbol{\theta}_{t-1} + \boldsymbol{\omega}_t \quad \boldsymbol{\omega}_t \sim \mathcal{N}[\mathbf{0}, \mathbf{W}_t] \quad (2)$$

where Y_t is the value of the response variable at time t , \mathbf{X}_t is an $1 \times m$ vector of predictor variables, $\boldsymbol{\theta}_t$ is an $m \times 1$ vector of regression parameters, and \mathbf{v} is a vector of observation errors in the observation equation (Eq.

1). The observation errors \mathbf{v}_t have an unknown variance V_t that is time dependent. Therefore, as the analysis proceeds through time, V_t is estimated from all of the prior data by assuming it is equal to the inverse of the precision ($V_t = \phi_t^{-1}$). Following Pole et al. (1994), we assume that ϕ_t is gamma distributed as

$$\phi_t \sim G[n_{t-1}/2, d_{t-1}/2] \quad (3)$$

such that n_{t-1} is the degrees of freedom and d_{t-1} is the sum of squared errors. The discounting scheme described below also applies to V_t .

The system equation (Eq. 2) allows the $m \times 1$ vector of regression parameters ($\boldsymbol{\theta}_t$) to evolve through time according to a first-order Markov process that incorporates prior information through Bayesian learning. \mathbf{G} is the system evolution matrix that determines the configuration of the model and $\boldsymbol{\omega}_t$ is an $m \times 1$ variance vector that describes the stochastic change in each of the parameter estimates ($\boldsymbol{\theta}_t$) over time. The system variance matrix (\mathbf{W}_t) has the variance in $\boldsymbol{\omega}_t$ along the diagonal and zeros elsewhere. It is determined by the component discount factors applied to the previous time step's posterior covariance matrix (Pole et al. 1994).

One-step forecasts of the response variable are generated at each time step and the parameters are updated as new information becomes incorporated into the model. Through the use of discounting, priors are given weights that determine how influential the earlier data are when updating the parameter estimates. These discounts represent the rate of exponential decay of useful information such that when the discount is 1 (its maximum value) all of the prior information is retained whereas a discount of 0 means no prior information is used at all. The lower the discount value, the faster parameters can change through time, but at a cost of higher model uncertainty. We selected discounts by varying them systematically between values of 0.8 and 1 and choosing the values that minimized the negative log likelihood of the overall forecast model (Pole et al. 1994). Once the optimum discounts for each model were set, we calculated the retrospective fits of each model to the data. The performance of each model for explaining the historical variation in each of the response variables was assessed from these retrospective fits (Pole et al. 1994). Pole et al. (1994) offer a more detailed discussion of the general model development, while Lamon et al. (1998) and Scheuerell et al. (2002) provide a comprehensive example of the methodology applied to ecological data.

We compared each competing model to a reference model containing only an underlying level and no regression effects (i.e., an autocorrelated random-walk model). We assessed model performance with the likelihood-ratio test, which is appropriate for testing nested models (Hilborn and Mangel 1997). To compare any full model A with a reference model B, the test statistic

⁵ (<http://jisao.washington.edu/pdo/PDO.latest>)

⁶ (<http://www.cdc.noaa.gov/~kew/MEI/>)

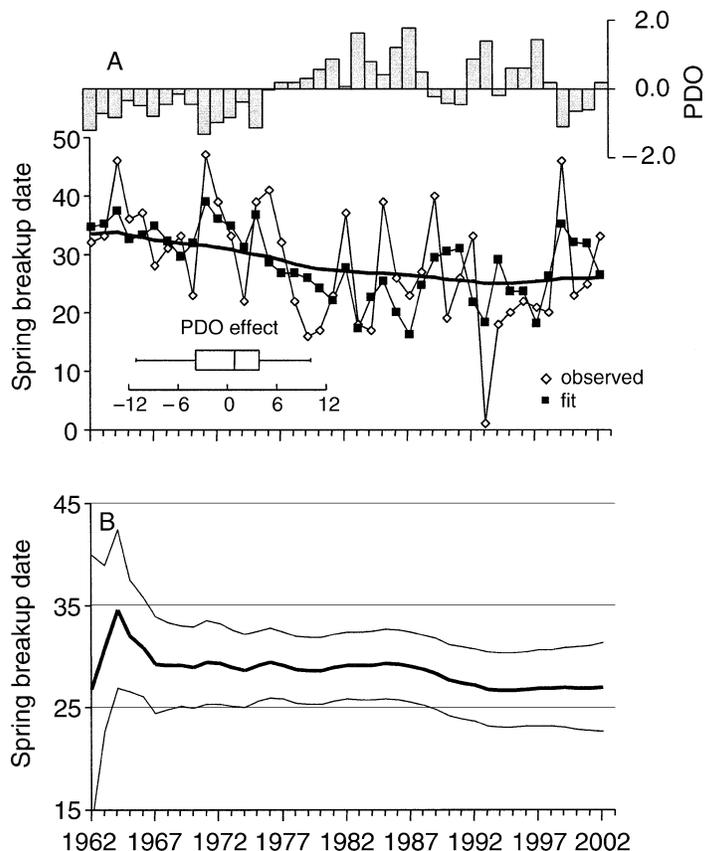


FIG. 1. Spring ice-breakup date on Lake Aleknagik (southwestern Alaska, USA). (The breakup date is the first day enough ice has broken up that a boat can navigate the length of the lake; day 1 is 1 May.) (A) Time series of the date of spring breakup from 1962 through 2002 (open diamonds), the best-fit simple trend model (heavy solid line), and the overall best model including trend and the Pacific Decadal Oscillation (PDO) as a regressor (solid squares). The inset is a box-and-whisker plot of the values of the PDO effect size (see *Materials and methods: Time-series analyses* for details). Bars show the strength of the PDO, standardized by subtracting the long-term mean for this time period. (B) The fitted values (heavy line) and 90% credible limits on the underlying intercept of the PDO model shown in panel (A).

(R) was computed as twice the difference in negative log likelihood, $L(x|\cdot)$, as follows:

$$R = 2[L(x|B) - L(x|A)] \quad R \sim \chi^2(df). \quad (4)$$

The degrees of freedom (df) for the test equal the difference in the number of parameters between models A and B.

We then ranked the competing predictive models in order of increasing performance according to the Bayes information criterion (BIC):

$$\text{BIC} = 2L(x|\cdot) + p \log_e(n) \quad (5)$$

where L is the negative log likelihood, p equals the number of parameters in the model, and n is the sample size (Box et al. 1991). Models with the lowest BIC provide the most parsimonious fit to the data. We used these criteria to assess the performance of various models for describing variation in the length of juvenile sockeye at the end of their first growing season, summer zooplankton densities, and the timing of spring breakup.

To compare the magnitude of the effect of each regressor on the dependent variable of each model, we calculated effect sizes as the product of the regression coefficient and the value of the independent variable in each year of the time series. Effect sizes are expressed in units of the dependent variable and thus provide a simple indication of the magnitude of each explanatory variable on the response variable in each model.

RESULTS

Changes in timing of spring ice breakup

There has been a significant trend toward earlier spring ice breakup date since 1962 in Lake Aleknagik, despite substantial interannual variation in the timing of this event (Fig. 1A). A simple, single-parameter random-walk model predicted that the spring breakup date has progressed seven days in the last four decades; from 2 June in 1962 to 26 May in 2002 (Fig. 1A). However, a more complex model with the Pacific Decadal Os-

TABLE 1. Summary statistics from dynamic linear models to explain historical variation in (A) the timing of spring ice breakup, (B) *Daphnia* density in August, (C) total crustacean zooplankton density in August, and (D, E) average juvenile sockeye salmon length on 1 September.

Response variable	Regressor variable(s) [†]	m^{\ddagger}	NLL [§]	BIC	P^{\parallel}
A) Spring ice-breakup date (1962–2002)	PDO	6	143.4	309.1	0.018
	PDO, ENSO	7	143.1	312.2	0.035
	ENSO	6	145.4	313.1	0.135
	random walk	4	147.4	309.7	
B) <i>Daphnia</i> density (1967–2002)	breakup date	6	9.8	41.1	0.008
	sockeye density	6	11.3	44.1	0.037
	breakup date, sockeye density	7	10.0	45.1	0.027
	random walk	4	14.6	43.5	
C) Zooplankton density (1967–2002)	breakup date, sockeye density	7	-36.5	-47.9	0.000
	breakup date	6	-27.9	-34.3	0.03
	random walk	4	-24.4	-34.5	
	sockeye density	6	-24.4	-27.3	NS
D) Sockeye length (1962–2002)	breakup date, sockeye density	7	105.4	236.8	0.000
	breakup date	6	109.6	241.5	0.000
	sockeye density	6	110.1	242.5	0.000
	random walk	4	125.0	264.9	
E) Sockeye length (1967–2002)	sockeye density	6	97.0	215.5	0.000
	breakup date, sockeye density	7	95.7	216.5	0.000
	sockeye density, zooplankton	7	96.9	218.9	0.000
	breakup date, sockeye density, zooplankton	8	95.9	220.5	0.000
	zooplankton	6	101.6	224.7	0.000
	breakup date, zooplankton	7	99.9	224.9	0.000
	breakup date	6	103.4	228.3	0.000
random walk	4	109.5	233.3		

Notes: The time period to which each model is fit is given in parentheses. Models are sorted according to their performance as indicated by their Bayesian information criterion (BIC).

[†] PDO = Pacific Decadal Oscillation; ENSO = El Niño Southern Oscillation.

[‡] Number of parameters in the model.

[§] Negative log likelihood.

^{||} Based on likelihood-ratio test comparing each model to the random-walk model; NS indicates “not significant.”

cillation (PDO) as an additional independent variable performed substantially better than the random-walk model, and had a lower BIC (Bayes information criterion) than either the El Niño Southern Oscillation (ENSO) model or the combined PDO and ENSO model (Table 1A). This model estimated a strong negative effect of PDO on the timing of spring breakup (i.e., high PDO values produce earlier springs) overlaid on an underlying trend associated with a spring breakup date that is approximately four days earlier in 2002 than it was in the early 1960s (Fig. 1B). The central 50% of the distribution of PDO effect sizes on ice breakup date spanned about eight days (Fig. 1A).

Summer water temperatures were strongly correlated with the timing of spring ice breakup (Fig. 2); earlier spring breakup dates were associated with warmer lake temperatures for both the 0–20 m strata and that 0–60 m strata in June, July, August, and September (Table 2, Pearson correlation, $P < 0.02$). The strength of PDO was also positively correlated with summer water temperatures in all months in both the 0–20 m and 0–60 m strata ($n = 41$ years, $P < 0.05$), except for during July in the 0–20 m stratum.

Zooplankton densities

The timing of spring ice breakup had important effects on densities of *Daphnia*, and weak effects on the

entire crustacean community (Tables 1 and 2, Figs. 3 and 4). The timing of spring ice breakup was strongly associated with the densities of *Daphnia* observed in all months from June to September; earlier spring breakup dates were associated with higher *Daphnia* densities (Fig. 3, Table 2). The strongest correlation occurred during August, even though *Daphnia* get progressively more abundant as the summer progresses from June to September. Unlike *Daphnia*, simple correlations between spring breakup date and total crustacean zooplankton densities were not significant (Fig. 3, Table 2).

The best dynamic linear model (DLM) explaining variation in August *Daphnia* densities included only

TABLE 2. Pearson correlation coefficients between the date of spring ice breakup and monthly zooplankton densities ($n = 36$ years) and water temperatures ($n = 41$ years) for Lake Aleknagik (southwestern Alaska, USA). All boldface numbers are significant at $P < 0.02$.

Month	Zooplankton density		Water temperature	
	<i>Daphnia</i>	Crustaceans	0–20 m	0–60 m
June	-0.491	-0.283	-0.78	-0.79
July	-0.481	-0.154	-0.60	-0.81
August	-0.574	0.011	-0.65	-0.70
September	-0.350	0.094	-0.53	-0.55

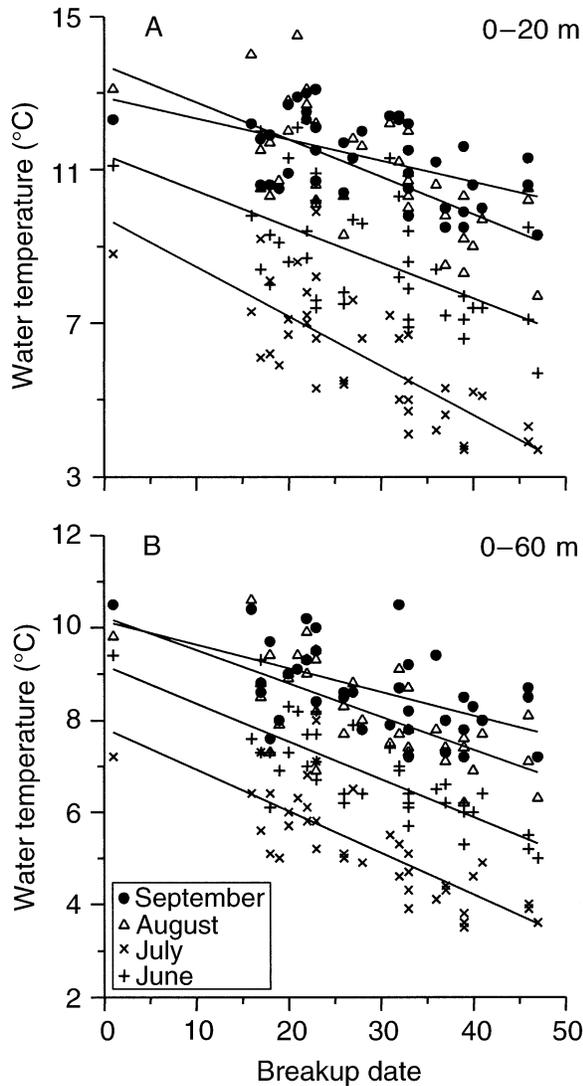


FIG. 2. Relationship between monthly average water temperature and spring ice-breakup date in Lake Aleknagik for (A) the 0–20 m depth stratum and (B) the 0–60 m stratum between 1962 and 2002.

an effect of spring breakup date and indicated that earlier springs were associated with higher August peaks in *Daphnia* populations (Fig. 4A). Other significant models for *Daphnia* densities included a negative effect of sockeye density, and a combination of a negative sockeye-density effect and a breakup-date effect but neither of these models performed as well as the breakup-date-only model (Table 1B). For total crustacean zooplankton densities, the best DLM included both the effect of earlier breakup date and sockeye density (Table 1C). A model with breakup date alone was also a significant model, but a model with sockeye density alone was not significantly different from the reference model (Table 1C). The effect sizes of density and spring breakup date on total crustacean densities were ap-

proximately equal and relatively small (Fig. 4B). The effect size of spring breakup date on August *Daphnia* abundance was approximately five times larger than the effect on the entire crustacean community (Fig. 4).

Juvenile sockeye growth dynamics

DLM that included combinations of sockeye density, spring breakup date, and summer zooplankton densities were all substantially better at describing the dynamics in juvenile sockeye growth than a random-walk model (Fig. 5, Table 1D and E). For the period from 1962 through 2002, models with either spring breakup date or sockeye density as single regressors performed substantially better than the random-walk model. However, the performance of these was not nearly as good as a model with both spring breakup date and sockeye den-

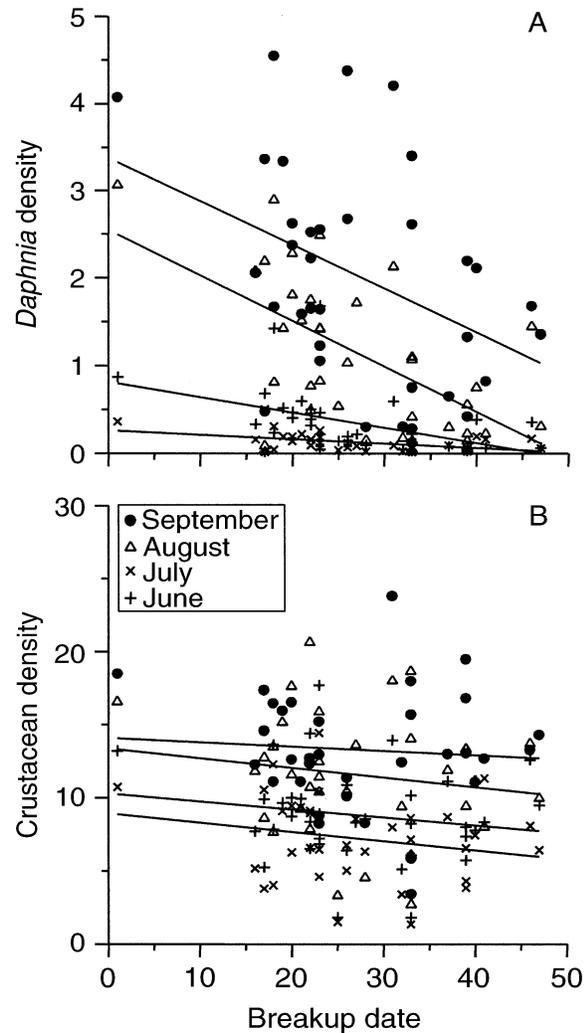


FIG. 3. Relationship between monthly zooplankton densities and spring breakup date in Lake Aleknagik between 1967 and 2002: (A) *Daphnia* densities and (B) total crustacean community densities. Units are thousands of organisms per square meter.

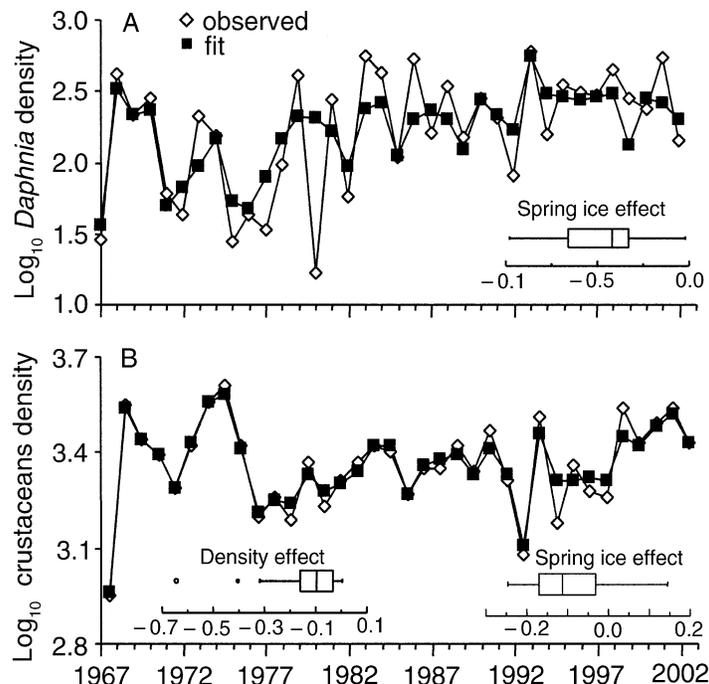


FIG. 4. Density of *Daphnia* and crustaceans in Lake Aleknagik (Alaska, USA). Density measurements were made in thousands of organisms per square meter. (A) Time series of observed August *Daphnia* density (open diamonds) from 1967 through 2002, and the overall best-fit model with the timing of spring ice-breakup date as a regressor (solid squares). The inset is a box-and-whisker plot of the values of the spring-breakup-date effect sizes. (B) Time series of observed August crustacean zooplankton density (open diamonds), and the overall best-fit model with the timing of spring ice-breakup date and the density of adult sockeye as regressors (solid squares). The insets are box-and-whisker plots of the values of the density and spring-ice effect sizes.

sity as regressors (Table 1D, Fig. 5A). In this case sockeye density had a negative effect on growth while earlier spring-breakup dates enhanced sockeye growth. In this model, the effect sizes of density were about twice as large as the effect sizes of spring breakup dates. For the shorter time series for which zooplankton data exist (1967–2002), the best models had either sockeye density alone or in combination with the spring breakup date as regressors (Table 1E). All models including crustacean zooplankton density as a regressor were statistically significant, but generally did not perform as well as the density and spring breakup-date models. All zooplankton effects were positive, and the best model using zooplankton as a predictor also included a negative term for sockeye density (Table 1E). The positive effect sizes of zooplankton density were substantial and about twice as large as the negative effects of density (Fig. 5B).

DISCUSSION

As has been demonstrated elsewhere (e.g., Magnuson et al. 2000), the phenology of spring ice breakup showed a distinct trend toward earlier dates over the last forty years in Lake Aleknagik of southwestern Alaska (USA). Our analyses suggest that much of this change has been driven by a combination of the Pacific Decadal Oscillation (PDO) and a longer term shifting

baseline in climatic conditions (Fig. 1). After accounting for the effects of the PDO on spring breakup date, the underlying trend in spring breakup date has shifted about four days earlier over the last forty years. Without accounting for the effects of PDO, the underlying breakup date progressed about seven days earlier over this same time period.

Anderson et al. (1996) showed that interannual changes in spring ice-breakup date for southern Wisconsin (USA) lakes were strongly correlated with El Niño Southern Oscillation (ENSO) events, while lakes at higher latitudes were only weakly correlated with ENSO. Our results support this finding inasmuch as ENSO had only weak effects on breakup date for our study site compared to the effects of PDO. As far as we know, we are the first to consider the effects of the PDO on lake ice phenology. Similarly, Yoo and D'Odorico (2002) showed that the North Atlantic Oscillation (NAO) had strong effects on ice phenologies in Northern Europe that were overlaid on an underlying trend associated with global warming. We suspect that the ice records for Lake Aleknagik reflect analogous effects; over the last four decades we estimate that the progression toward earlier spring breakup has been driven about equally by the recent warm phase of the PDO and large-scale climate warming. Thus, our results reinforce the suggestion that spring ice breakup

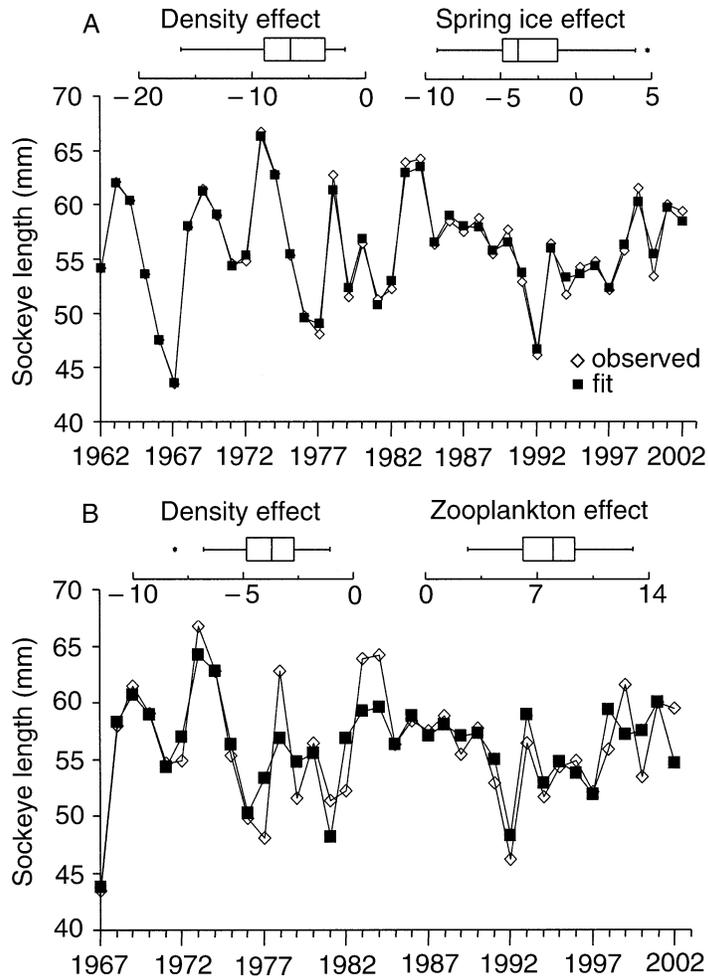


FIG. 5. Length of juvenile sockeye salmon in Lake Aleknagik (Alaska, USA). (A) Time series of the observed length of juvenile sockeye on 1 September (open diamonds) from 1962 through 2002, and the overall best-fit model with sockeye density and the spring ice-breakup date as regressors (solid squares). The insets are box-and-whisker plots of the values of the density and spring-ice effect sizes for this model. (B) Observed lengths of juvenile sockeye on 1 September (open diamonds) from 1967–2002, and the best model that included zooplankton as a regressor (solid squares). In this case, the zooplankton regressor was only significant when sockeye density was also included as a predictor. The insets are box-and-whisker plots of the values of the adult-density and zooplankton-density effect sizes for this model.

is driven by multiple modes of meteorological forcing, the strengths of which vary depending on geographic position and especially latitude (Wynne et al. 1996).

Our analyses quantified the effects of the progression toward earlier spring breakup on zooplankton populations and growth of juvenile sockeye salmon in their first year of life. Dynamic time-series models showed that earlier spring breakup dates were strongly associated with increased summer densities of *Daphnia* and weakly with the entire crustacean zooplankton community. This result confirms comparative studies demonstrating the sensitivity of *Daphnia* to water temperature (Gillooly and Dodson 2000). In the case of modeling *Daphnia* populations, the best time-series model included only spring breakup date as a predictor of summer density (Table 1B), which was surprising given

the strong effects of sockeye fry on *Daphnia* populations in other Alaska lakes (Kyle et al. 1988, Mazumder and Edmundson 2002). However, for both the aggregate zooplankton community and the size of sockeye at the end of the growing season, the best models included the additional negative effects of adult sockeye density (Table 1C–E). As has been documented elsewhere (Burgner 1987, Koenings and Burkett 1987, Kyle et al. 1988, Mazumder and Edmundson 2002), growth of sockeye fry demonstrated strong negative density dependence, an ecological response that confounds the effect of changes in the timing of spring breakup on sockeye growth rates. Similarly, the climatic effects on zooplankton densities were strongest when the effect of sockeye density was also accounted for. Because sockeye fry exert strong top-down effects on zooplank-

ton (O'Neill and Hyatt 1987, Kyle et al. 1988, Mazumder and Edmundson 2002), high densities of sockeye should reduce zooplankton densities, thereby masking effects of climate shifts on zooplankton. However, by accounting for the negative effects of sockeye density, the models detected strong positive effects of earlier spring-breakup timing on summer zooplankton densities.

Our analyses demonstrate that the spring warming trends observed during the last four decades were correlated with improved growing conditions for juvenile sockeye in Lake Aleknagik. This enhancement of growing conditions is associated with a longer growing season, increased summer water temperatures, and increased densities of zooplankton, their preferred prey. Application of a bioenergetics model of sockeye growth and consumption (Beauchamp et al. 1989) would be the best way to sort out the relative importance of each of these factors for enhancing the growth of juvenile sockeye during their lake residency. Previous bioenergetics analyses of lake trout responses to climate warming in Alaska predicted that increased temperatures would cause a decline in fish growth rates unless increased temperature also enhanced prey production (McDonald et al. 1996). Clearly, in Lake Aleknagik the warming trend has also enhanced zooplankton resources for juvenile sockeye and thus has been associated with increased growth of sockeye during their lake residency. More mechanistic analyses of the relative effects of growing-season length, prey availability, and water-temperature effects on metabolic rates will further enrich our understanding of the causal factors that produce the enhanced growing conditions we have highlighted in this paper.

How will continuing climate changes affect future population dynamics in this sockeye population? Much of the trend toward early spring breakup in the 1980s and 1990s that we document here was associated with the warm phase of the PDO (Mantua and Hare 2002). In the late 1990s the PDO shifted back to a cool phase that was also reflected in the relatively late spring-breakup dates observed in 1999 and 2002 (Fig. 1). However, these PDO effects were overlaid on an underlying trend that shifted spring breakup dates earlier by about one day per decade. Assuming this trend is a response to global climate warming (Magnuson et al. 2000, IPCC 2001), it may be obscured by the current cool phase of the PDO that could persist for a couple of decades (Mantua and Hare 2002). Nevertheless, our analyses suggest that the warming trend should actually continue to improve growing conditions in Lake Aleknagik for juvenile sockeye. Given the strong effect of body size on the marine survival rates of sockeye (Henderson and Cass 1991, Koenings et al. 1993), increased juvenile growth rates should increase production rates of this population. In fact, annual estimates of recruits per spawner in the Wood River System generally increased in the 1980s and 1990s (Hilborn et al. 2003).

We do not know whether the increasing trend in productivity of this stock resulted from increased survival in the freshwater or marine environment. However, if anything, increasing freshwater growth rates should have increased early marine survival during this latter phase of the life cycle of Lake Aleknagik sockeye.

Commercial fisheries for sockeye salmon were among the most valuable in North America throughout the 20th century. Much of the global catch of sockeye salmon derives from the fisheries of Bristol Bay, Alaska, where catches have averaged about 22.5 million sockeye per year, and whose ex-vessel value (i.e., value at time of purchase from the fisherman) has been estimated at about US\$ 100 million annually in the last decade. Future management of these fisheries will ultimately depend on the responses of salmon populations to changing climate—dynamics that do not appear to be uniform across nursery systems in southwestern Alaska (Hilborn et al. 2003).

We estimated the joint effects of density dependence and climate change on first-year growth of juvenile sockeye during the last four decades in southwestern Alaska. Dynamic time-series models demonstrated that sockeye growth was affected by both negative density dependence and positively by a temporal procession toward earlier spring ice-breakup dates. Although statistically significant, models that did not account for density-dependent effects on growth performed poorly at linking changes in climate to changes in sockeye growth rates. These results exemplify the complexity of ecological responses to climate change and highlight the important issue that ecological interactions may obscure biological responses to changing climate. Understanding biological responses to climate change requires that we account for the ecological dynamics inherent to all ecosystems (e.g., density dependence, species interactions), that may be regulated by factors largely independent of climatic conditions.

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