

## A 500-year context for the recent surge in sockeye salmon (*Oncorhynchus nerka*) abundance in the Alagnak River, Alaska

Daniel E. Schindler, Peter R. Leavitt, Susan P. Johnson, and Curtis S. Brock

**Abstract:** Returns of sockeye salmon (*Oncorhynchus nerka*) to the Alagnak River in Bristol Bay, Alaska, during the last 3 years were unprecedented in the last five decades. Enumerated run sizes averaged about 1 million fish from 1955 to 2002 but surged unexpectedly to average 5.4 million fish in 2003–2005. These huge returns currently pose a challenge to management of Bristol Bay sockeye for several reasons, including that it is unclear whether the recent surge in abundance is a new phenomenon or if it has arisen as part of interdecadal population variability. To answer this question we used changes in lake sedimentary  $\delta^{15}\text{N}$  coupled with an isotope-mixing model to estimate historical abundances of sockeye salmon populations in this ecosystem. Our analyses show that periods of high salmon abundance have occurred every ~100 years during the last five centuries, interspersed by prolonged periods of substantially lower abundance. We suggest that the recent high returns are an expression of the long-term variability that is characteristic of this stock and will be a relatively transient phenomenon.

**Résumé :** Au cours des 3 dernières années, les retours de saumons rouges (*Oncorhynchus nerka*) de la rivière Alagnak dans la baie de Bristol, Alaska, ont été sans précédent pendant les cinq décennies antérieures. Les tailles moyennes des montaisons de 1955–2002 ont été estimées à 1 million de poissons; de façon inattendue en 2003–2005, elles ont augmenté à une moyenne de 5,4 millions de poissons. Ces retours massifs posent actuellement des problèmes pour la gestion des saumons rouges de la baie de Bristol pour plusieurs raisons, en particulier parce qu'il n'est pas clair si cette augmentation récente de l'abondance est un phénomène nouveau ou si elle fait partie de la variabilité de la population au cours des décennies. Afin de répondre à la question, nous utilisons les changements dans le  $\delta^{15}\text{N}$  des sédiments conjointement à un modèle de mélange des isotopes afin d'estimer les abondances passées des populations de saumons rouges dans cet écosystème. Nos analyses révèlent qu'il s'est produit des périodes de fortes densités de saumons environ tous les 100 ans au cours des cinq derniers siècles avec de longs intervalles d'abondances substantiellement plus basses. Nous croyons que les retours importants actuels sont l'expression de la variabilité à long terme de ce stock et qu'ils représentent un phénomène relativement transitoire.

[Traduit par la Rédaction]

### Introduction

Fisheries management often assumes that fish abundance can be quantified as a stationary parameter (constant mean and variance) that is characteristic of a particular ecosystem. In addition to the convenience of assuming stationarity, stock assessment data are often too poor in quality or too short in duration to properly assess whether abundance varies over long time periods (Walters 1987). Management strategies assuming stationarity can result in suboptimal harvest if the

underlying abundance is changing (Walters and Parma 1996) and can increase the risk of overharvesting the population under certain management strategies (i.e., those that attempt to maintain high harvested biomass). Although environmentally driven changes in the abundance of fish stocks is a critical component of sustainable fisheries, management rarely considers how this aspect of ecosystems varies over long time scales.

Sockeye salmon (*Oncorhynchus nerka*) populations in Bristol Bay, southwest Alaska (Fig. 1a), have been characterized

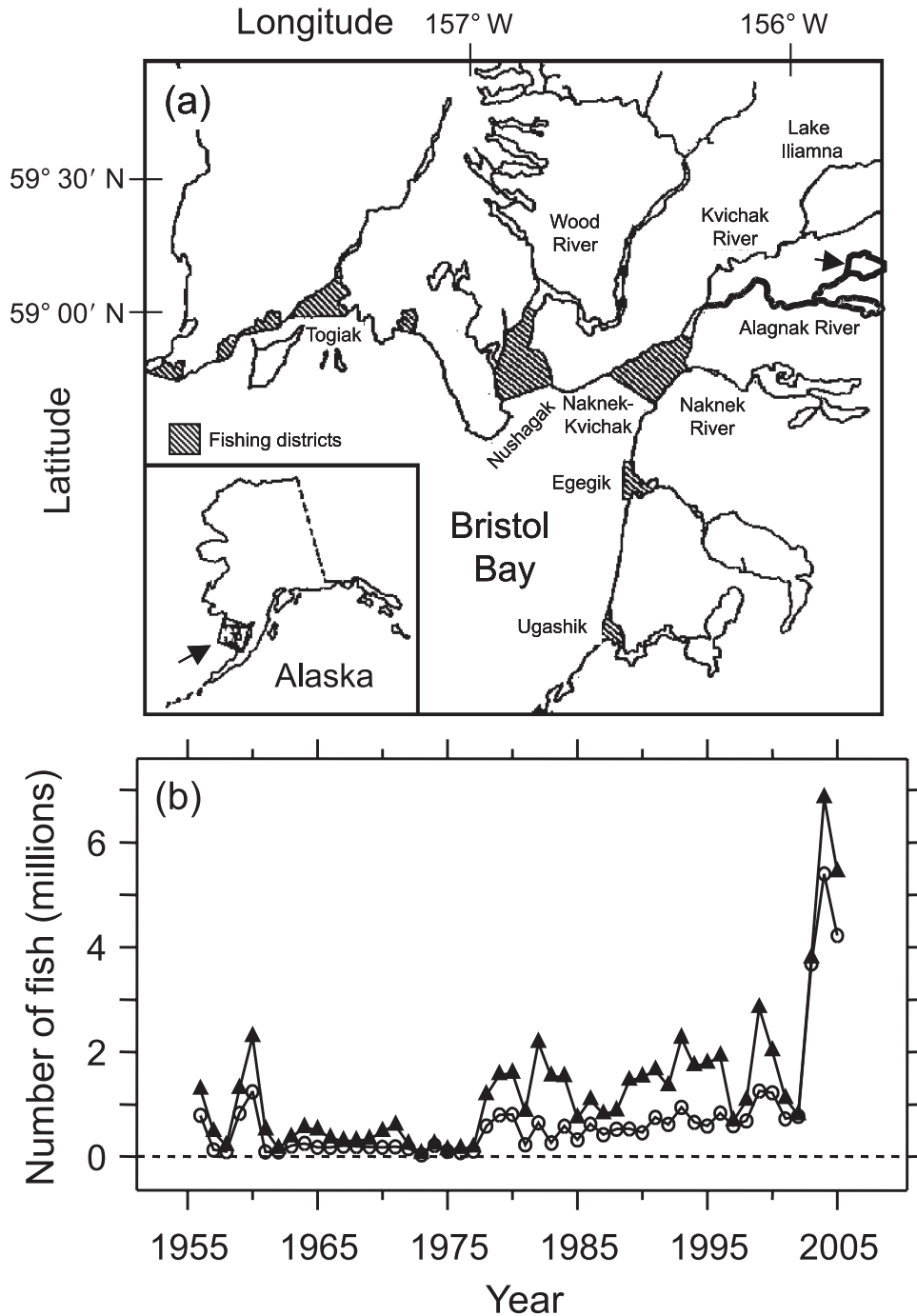
Received 1 February 2006. Accepted 21 April 2006. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 18 May 2006.  
J19145

**D.E. Schindler<sup>1</sup> and S.P. Johnson.** School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195, USA.

**P.R. Leavitt and C.S. Brock.** Department of Biology, University of Regina, Regina, SK S4S 0A2, Canada.

<sup>1</sup>Corresponding author (e-mail: [deschind@u.washington.edu](mailto:deschind@u.washington.edu)).

**Fig. 1.** (a) Map of Bristol Bay, Alaska, showing the major fishing districts for sockeye salmon (*Oncorhynchus nerka*; hatched regions) and the location of the Alagnak River. The arrow in the large panel points to Kukaklek Lake, the site where the lake sediment core was extracted to reconstruct sockeye salmon populations in the Alagnak system. (b) Total run and escapement dynamics of sockeye salmon in the Alagnak River from 1955 to 2005. Data are from the Alaska Department of Fish and Game (Clark 2005).



by long-term variation in abundance that, in general, has correlated with the major phases of the Pacific Decadal Oscillation (Mantua et al. 1997). However, when total sockeye abundance is divided into the major river districts that provide spawning and nursery habitats for the stock complex, the performance of individual stock components has differed during the last century (Hilborn et al. 2003; Peterman et al.

2003), with some populations (e.g., Egegik River) having had distinct periods of high abundance, interspersed by periods of distinctly lower abundance. Others (e.g., Wood River) have been building slowly throughout most of the last century. In contrast, the Kvichak River stock, which was the single largest sockeye population in the world for most of the last century, has recently shown a substantial decline in

abundance to the point at which the fisheries on this river are now severely restricted in an attempt to conserve this stock component (Fair 2003).

One of the biggest surprises in the dynamics of Bristol Bay sockeye has been the substantial and abrupt increase in the Alagnak River sockeye population in recent years (Clark 2005). Enumerated run sizes averaged ~1 million fish during 1955–2002 but surged to an average of 5.4 million fish in 2003–2005 (Fig. 1b). Because the fish from this stock are caught in a mixed-stock fishery, i.e., combined with those from the Naknek and Kvichak rivers (Fig. 1a), it is unclear whether the recent huge returns to the Alagnak River are the result of reduced fishing pressure to conserve the Kvichak stock or whether the productivity of the freshwater and marine habitats used by Alagnak River fish has increased abruptly. This uncertainty has prevented development of a rational long-term management strategy for the Alagnak stock.

We used paleolimnology to reconstruct the long-term changes in the abundance of sockeye salmon returning to the Alagnak River system to put the recent population changes into a five-century historical context. Because death of salmon after spawning releases nitrogen enriched in the  $^{15}\text{N}$  isotope in proportion to the number of fish returning to a system, and because this isotope signature is preserved in lake sediments (Finney et al. 2000), estimates of changes in sedimentary N isotope ratios can be used to reconstruct historical population dynamics of sockeye salmon (Schindler et al. 2005). Our reconstructions show that the abundance of the Alagnak River sockeye stock has varied considerably at centennial time scales over the last five centuries, and the recent stock buildup coincides with the periodicity of past production peaks.

## Materials and methods

### Site description

The Alagnak River, a tributary of the Kvichak River flowing into Bristol Bay, Alaska (Fig. 1a), is a major spawning and nursery system for sockeye salmon. Most of the sockeye spawning occurs in the tributaries flowing into two large lakes (Kukaklek and Nonvianuk), which are also used as nursery grounds for juvenile sockeye before their migration to the ocean (Clark 2005). Kukaklek Lake receives about 70% of the spawning run (Clark 2005); therefore, we used this site for paleolimnological reconstructions of past sockeye runs in the Alagnak system. We used Tazimina Lake in the upper Kvichak drainage and Grant Lake from the upper Wood River drainage as reference sites to establish background variability in sediment characteristics independent of sockeye populations. These lakes have substantial waterfalls on their outflows that render them inaccessible to anadromous fishes.

One sediment core was collected from a depth of 35 m in Kukaklek Lake and another from a depth of 30 m in Tazimina Lake by float plane in September 2004 using a Glew gravity corer (John Glew, Paleolimnological Environment Assessment and Research Laboratory, Queens University, Kingston, Ontario). Previous analyses of the spatial heterogeneity of the  $\delta^{15}\text{N}$  in surface sediments of similar Bristol Bay sockeye nursery lakes demonstrated that a single, repre-

sentative core was adequate to reconstruct historical variation in sedimentary  $\delta^{15}\text{N}$  because spatial variation in  $\delta^{15}\text{N}$  was low within any single lake (coefficient of variation ~16%; Brock et al. 2006). Grant Lake was previously cored in August 2003 as described in Schindler et al. (2005). All cores were separated into 1.7 mm slices in the field and frozen immediately at  $-10\text{ }^\circ\text{C}$  in the dark. This sectioning interval translated into data intervals that averaged 3.4 years (standard deviation (SD) = 1.7 years) and, as a result of sediment compaction, were of slightly shorter duration in the upper sections of the core than in the deeper sections. Within 3 months, core samples were thawed, freeze-dried to constant mass, and analyzed for isotope content.

### Sediment chronology

Sediment ages were estimated from down-core declines in  $^{210}\text{Pb}$  activity using the CRS (constant rate of supply) model of Binford (1990). Samples for analysis of  $^{210}\text{Pb}$  activities were dried to constant mass at  $50\text{ }^\circ\text{C}$ , homogenized, and analyzed for  $^{210}\text{Pb}$  using alpha-spectrometric analysis by Flett Industries (Winnipeg, Manitoba, Canada). All counting times were 8.3 h. The standard deviations of estimated sediment ages from the CRS model increased down-core to about  $\pm 17$  years by 1830 (i.e., coefficient of variation ~10%). Ages of older strata were extrapolated from the equilibrium sedimentation rate estimated from the CRS model (Binford 1990).

### Stable nitrogen isotopic composition

Stable nitrogen isotope distributions were determined by continuous-flow isotope ratio mass spectrometry using a Delta XL isotope ratio mass spectrometer with an automated Carlo Erba elemental analyzer inlet device. Analytical precision of this instrument was  $\pm 0.08\text{‰}$  for  $\delta^{15}\text{N}$ , well below the variation in  $\delta^{15}\text{N}$  observed among and within lakes attributable to variation in salmon abundance. Stable isotope ratios were expressed as  $\delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$ , where  $R_{\text{sample}}$  represents  $^{15}\text{N}/^{14}\text{N}$  in the sample, and  $R_{\text{standard}}$  is the corresponding isotope ratio from the atmospheric nitrogen.

### Isotopic mixing model and salmon run sizes

We used a two-member mixing model (Schindler et al. 2005) to translate changes in sedimentary  $\delta^{15}\text{N}$  into historical variation in escapement ( $E_t$ ) within the Alagnak River system. We assumed that sockeye returns to the tributaries of Kukaklek Lake were a reasonable indicator of sockeye abundance throughout the entire Alagnak system (Clark 2005).

The mixing model is expressed as

$$E_t = N_{\text{ws}}R_t + e_t$$

where

$$R_t = \left( \frac{\delta^{15}\text{N}_{\text{sed},t} - \delta^{15}\text{N}_{\text{ws},t}}{\delta^{15}\text{N}_{\text{salm}} - \delta^{15}\text{N}_{\text{sed},t}} \right)$$

$N_{\text{ws}}$  is the amount of N loaded from the watershed to the lake expressed in the same units as escapement,  $\delta^{15}\text{N}_{\text{sed},t}$  is the  $\delta^{15}\text{N}$  of the sediments from Kukaklek Lake representing a mixture of nitrogen loaded from salmon and from the watershed at time  $t$ ,  $\delta^{15}\text{N}_{\text{ws},t}$  is the  $\delta^{15}\text{N}$  from watershed sources

at time  $t$ ,  $\delta^{15}\text{N}_{\text{salm}}$  is the  $\delta^{15}\text{N}$  of sockeye salmon tissue, and  $e_t$  are random normal errors with mean equal to zero. Thus,  $N_{\text{ws}}$  is the only unknown term and can be estimated by regressing  $E_t$  against  $R_t$  for the period when  $E_t$  was enumerated directly.

We used the enumerated escapement ( $E_t$ ) to the Alagnak system for the period 1955–2002 (Clark 2005) and the corresponding changes in  $R_t$  to estimate  $N_{\text{ws}}$ . Escapement to the Alagnak River is monitored by the Alaska Department of Fish and Game using a combination of tower-count and aerial surveys. Tower counts were performed from 1955 to 1976 and from 2001 to present by enumerating fish migration upstream on the main stem of the river for 10 min on each bank for every hour throughout the spawning run (Clark 2005). Aerial surveys during 1977–2000 were expanded to total escapement numbers based on the relationship between escapement based on tower counts and escapement based on aerial surveys derived for years when both methods were used ( $n = 9$  years; Clark 2005). Because the values of  $R_t$  are obtained from sediment samples that include more than 1 year of time, and because sediment mixing causes some blurring of the salmon-derived nitrogen signature in the sedimentary record, we smoothed the enumerated escapement data with a 5-year running mean before estimating  $N_{\text{ws}}$ . Values of  $E_t$  from the smoothed series were selected to match the average age of each of the 25 sediment samples from Kukaklek Lake between 1955 and 2003.

We ran four different model scenarios to account for variation in  $\delta^{15}\text{N}_{\text{ws}}$  in the calculation of  $R_t$ . Two scenarios simply used the average value for each of the two reference systems and assumed that this parameter was constant. We also ran two additional scenarios that accounted for the observed changes in  $\delta^{15}\text{N}$  in the sediment cores from the reference lakes. For these latter scenarios, the  $\delta^{15}\text{N}$  values from each of the reference systems were linearly interpolated to establish values for  $\delta^{15}\text{N}_{\text{ws},t}$  that matched the dates for each sample from the Kukaklek core. We assumed that  $\delta^{15}\text{N}_{\text{salm}}$  was constant through time and equal to 11.2‰ (Schindler et al. 2005).

We used a Morlet wavelet transform (Torrence and Compo 1998) to evaluate periodicity in the historical time series of sockeye abundance in the Alagnak River. To accomplish this we combined the enumerated abundances (sum of catch and escapement, smoothed with a 5-year running mean) from 1955 to the present with the historical abundances from 1507 to 1955 determined from our paleo-reconstructions. This combined time series was then interpolated to obtain abundance values corresponding to a regular 4-year interval (i.e., approximate average time interval represented by the sediment core analyses). The power spectrum was calculated according to Torrence and Compo (1998; software available at <http://paos.colorado.edu/research/wavelets/>).

## Results and discussion

Sediments from the sockeye salmon nursery lake (Kukaklek) were more enriched in  $^{15}\text{N}$  than the sediments from either reference lake (Fig. 2a). The  $\delta^{15}\text{N}$  from Kukaklek Lake averaged 4.3‰ (SD = 0.6‰) compared with 2.8‰ (SD = 0.5‰) and 3.1‰ (SD = 0.2‰) for Tazimina and Grant

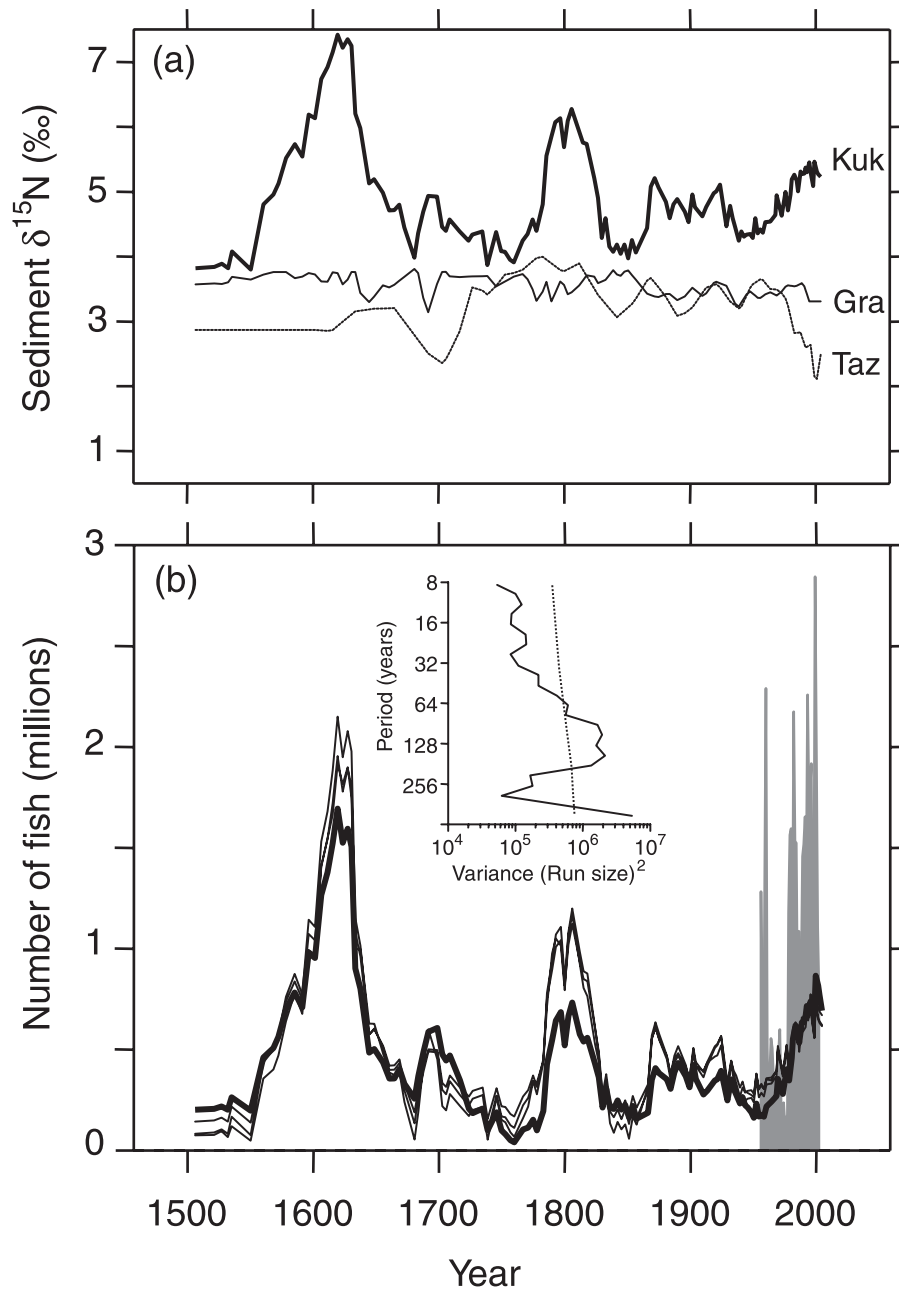
lakes, respectively. This enrichment of  $^{15}\text{N}$  is indicative of the deposition and retention of salmon-derived nutrients (SDN) in the sediments of Kukaklek Lake. In addition, the substantial increases in escapement to the Alagnak River from 1955 to the present provided a convenient contrast in SDN deposition to test whether these escapement increases were faithfully archived in the sedimentary record. Indeed, the upswing in escapement during this time period was paralleled by a substantial increase in the  $\delta^{15}\text{N}$  in the recent sedimentary record of Kukaklek Lake (Fig. 2a).

The best model fit to the smoothed escapement data was obtained using the observed dynamics in  $\delta^{15}\text{N}_{\text{ws}}$  from the Tazimina Lake reference core. This yielded a value of  $1.66 \times 10^6$  sockeye equivalents for  $N_{\text{ws}}$ , which produced model predictions in good agreement with historical escapements for the last five decades ( $r^2 = 0.69$ ,  $n = 25$ ). This value of  $N_{\text{ws}}$  was then applied throughout the 500-year reconstruction of  $E_t$ . Values of  $N_{\text{ws}}$  fit from the other three model scenarios were somewhat higher (mean  $2.28 \times 10^6$ , SD =  $0.19 \times 10^6$ ) and did not produce fits to the data that were as good as the Tazimina scenario ( $r^2$  range 0.46–0.6) but were used to produce historical model reconstructions for comparison purposes.

Our reconstructions of historical population dynamics of sockeye salmon in the Alagnak River suggest that this stock has been highly variable and distinctly periodic during the last five centuries (Fig. 2b). There were three major peaks of enhanced abundance: the first around 1600, the second around 1800, and the last around 2000. These major peaks were interspersed by two smaller abundance peaks centered about 1700 and 1900. Each of the major abundance peaks lasted about 20–50 years and was interspersed by several decades of substantially reduced abundance. A wavelet analysis (Torrence and Compo 1998) performed on the combined time series shown in Fig. 2b demonstrates that sockeye abundances have varied with a centennial oscillation during the last five centuries (Fig. 2b, inset). Thus, the recent buildup of the population, culminating in the record returns observed in the last 3 years, has occurred at about the expected time based on the periodicity in the abundances over the last five centuries. In light of this pattern, the buildup of the Alagnak stock since 1955 (Figs. 1b, 2b) is revealed as part of a long-term cycle, the cause of which is presently unknown. If the historical cyclical nature of the stock still applies to the current dynamics, our analyses suggest that returns observed in the last few years occurred near the expected production peak and that we should begin to see abundance taper off again in the near future.

The increase in abundance of Alagnak sockeye since the mid-1970s is generally consistent with both the increased abundances in several other Bristol Bay stocks during this time period (Hilborn et al. 2003; Peterman et al. 2003) and the centennial-scale periodicity observed in the Kukaklek Lake sediment record. Temporal changes in sockeye abundance from the Alagnak system also show some of the same general patterns of interdecadal variation observed in two other Bristol Bay salmon stocks over the last three centuries (Finney et al. 2000). However, the extent of the recent surge in Alagnak sockeye abundance compared with other Bristol Bay stocks and the fact that some Bristol Bay stocks have

**Fig. 2.** (a) Chronologies of sedimentary  $\delta^{15}\text{N}$  from Kukaklek Lake (Kuk) and the two reference lakes with natural blockages to sockeye (*Oncorhynchus nerka*): Grant Lake (Gra) and Tazimina Lake (Taz). (b) Reconstructed time series of sockeye salmon abundance in the Alagnak River from the four different baseline scenarios discussed in Materials and methods. The heaviest line is from the scenario with the best fit to the data (i.e., using Tazimina Lake as the reference). The shaded region represents the total enumerated annual run size to the Alagnak River from 1955 to 2002 (Clark 2005). Values for 2003–2005 were omitted because they were off scale. Note that the total enumerated run size greatly exceeds the reconstructed escapement since 1955, because fish that were intercepted by fisheries (average, 47% of run; range, 3%–83%) are included in the enumerated run size but are not archived in the lake sediments. Also note that fishery catch data are not available before 1955 but that commercial fisheries have been in operation since the 1890s. Inset shows the global wavelet power spectrum for the combined time series relative to the 5% significance boundary (dotted vertical line).



shown declines in abundance during this same time period emphasize the heterogeneity of population responses to changing environmental conditions within the Bristol Bay stock complex (Hilborn et al. 2003; Peterman et al. 2003). Thus, the recent surge in Alagnak sockeye abundance should

be viewed as one expression of the biocomplexity within Bristol Bay sockeye salmon.

Inspection of the last five decades of Alagnak sockeye abundance within the context of the last five centuries of historical dynamics suggests that this stock was more abundant

since the late 1970s than during most of the last 500 years. However, total run size during the last 20 years has been about two million fish (Clark 2005), which is very comparable with the peak densities that occurred for about two decades in the early 1600s (Fig. 2*b*). Taken together, our results suggest that the record returns to the Alagnak River observed recently were not simply a result of the conservation measures recently placed on Kvichak River fish. Instead, the recent surge in abundance of Alagnak River sockeye appears to be an expression of their long-term population dynamics and is likely to be a transient phenomenon.

## Acknowledgements

This is a contribution of the University of Washington – Alaska Salmon Program. Funding was provided by the National Science Foundation (Biological Oceanography). We thank Troy Hamon of the National Park Service for coordinating access to Kukaklek Lake, Monika Winder, Jackie Carter, David Wilbur, Gordon Holtgrieve, and Jennifer Griffiths for assistance with field and lab work, and Lowell Fair, Bryan Pyper, and four anonymous reviewers for helpful comments on an earlier version of the manuscript. DES thanks the Department of Ecology and Evolutionary Biology at Cornell University for hosting him while writing this paper.

## References

- Binford, M.W. 1990. Calculation and uncertainty analysis of  $^{210}\text{Pb}$  dates for PIRLA project lake sediment cores. *J. Paleontol.* **3**: 253–267.
- Brock, C.S., Leavitt, P.R., Schindler, D.E., Johnson, S.P., and Moore, J.W. 2006. Spatial variability of stable isotopes and fossil pigments in surface sediments of Alaskan coastal lakes: constraints on quantitative estimates of past salmon abundance. *Limnol. Oceanogr.* **51**(4). In press.
- Clark, J.H. 2005. Abundance of sockeye salmon in the Alagnak River System of Bristol Bay Alaska. Alaska Department of Fish and Game, Fishery Manuscript No. 05-01, Anchorage, Alaska.
- Fair, L.F. 2003. Critical elements of Kvichak River sockeye salmon management. *Alaska Fish. Res. Bull.* **10**: 95–103.
- Finney, B.P., Gregory-Eaves, I., Sweetman, J., Douglas, M.S.V., and Smol, J.P. 2000. Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. *Science (Washington, D.C.)*, **290**: 795–799.
- Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. *Proc. Nat. Acad. Sci.* **100**: 6564–6568.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**: 1069–1079.
- Peterman, R.M., Pyper, B.J., and MacGregor, B.W. 2003. Use of the Kalman filter to reconstruct historical trends in productivity of Bristol Bay sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* **60**: 809–824.
- Schindler, D.E., Leavitt, P.R., Brock, C.S., Johnson, S.P., and Quay, P.D. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. *Ecology*, **86**: 3225–3231.
- Torrence, C., and Compo, G.P. 1998. A practical guide to wavelet analysis. *Bull. Am. Meteorol. Soc.* **79**: 61–78.
- Walters, C.J. 1987. Nonstationarity of production relationships in exploited populations. *Can. J. Fish. Aquat. Sci.* **44**: 156–165.
- Walters, C., and Parma, A.M. 1996. Fixed exploitation rate strategies for coping with effects of climate change. *Can. J. Fish. Aquat. Sci.* **53**: 148–158.