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1 May 2000; accepted 21 September 2000

Impacts of Climatic Change and Fishing on Pacific Salmon Abundance Over the Past 300 Years

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The effects of climate variability on Pacific salmon abundance are uncertain because historical records are short and are complicated by commercial harvesting and habitat alteration. We use lake sediment records of $\delta^{15}\text{N}$ and biological indicators to reconstruct sockeye salmon abundance in the Bristol Bay and Kodiak Island regions of Alaska over the past 300 years. Marked shifts in populations occurred over decades during this period, and some pronounced changes appear to be related to climatic change. Variations in salmon returns due to climate or harvesting can have strong impacts on sockeye nursery lake productivity in systems where adult salmon carcasses are important nutrient sources.

Historical records of air and ocean temperature, as well as atmospheric pressure fields, show significant interdecadal fluctuations in the North Pacific region (1–3). These climatic fluctuations appear to have had large impacts on marine ecosystems (1, 3–5). Salmon catch records suggest a correlation between the intensification of the Aleutian Low, increased coastal sea surface temperatures in the eastern North Pacific, and increased pro-

duction of Alaskan salmon during the 20th century (6). However, the historical record is of insufficient length or quality to assess the representativeness of these recent observations. Because Pacific salmon are important economic and cultural resources, their viability in response to future climatic change is of great concern (7). Here, we present high-resolution records of diatoms, cladocerans, and sedimentary $\delta^{15}\text{N}$ to explore the sockeye salmon–climate connection over the last ~300 years in sockeye nursery lakes located on western Kodiak Island and near Bristol Bay, Alaska.

Sockeye salmon (*Oncorhynchus nerka*) typically spend 2 to 3 years feeding in the North Pacific and subsequently migrate to their home lake–stream system where they spawn and die. Sockeye often return in tre-

mendous numbers, and it is not uncommon for densities to reach the equivalent of 5000 to 30,000 adult fish (average weight ~2.7 kg) per km² of lake surface area (8). After hatching, juvenile sockeye spend 1 to 3 years in their home nursery lake feeding primarily on pelagic zooplankton; however, >99% of the biomass of adult sockeye is accumulated in the marine environment (8). Therefore, the nutrients originating from carcasses of post-spawning adults are almost exclusively of marine origin. These carcass-derived nutrients are often significant sources of nutrients to these oligotrophic systems (9). For example, in Karluk Lake, Kodiak Island (Fig. 1), carcass-derived nutrients typically contribute more than half of the lake-water phosphorus (P) and nitrogen (N) annually (10). Atmospheric and anthropogenic inputs to the lakes we studied are insignificant (10); the catchments are virtually undisturbed by human activities, and many are not forested, thus reducing the confounding effects of forest fires.

Adult sockeye salmon carcasses have high $\delta^{15}\text{N}$ (~12‰) relative to terrestrial N in Alaskan nursery lakes, which typically have values close to atmospheric levels (0‰) (11). Stable N isotopes thus can be used to track the salmon-derived N into the biota of freshwater and terrestrial ecosystems (11–13). In the lakes we studied, there is a strong association between zooplankton $\delta^{15}\text{N}$ and salmon-derived nutrient (SDN) loading (Fig. 2A). These nutrients are subsequently transferred to higher trophic levels, as demonstrated by the relation between juvenile sockeye salmon $\delta^{15}\text{N}$ and the SDN loading in their nursery lakes (Fig. 2B). Lake sediments faithfully archive this information, as shown by the relation between surface sediment $\delta^{15}\text{N}$ and SDN loading (Fig. 2C). Factors known to influence sedimentary $\delta^{15}\text{N}$ in other settings

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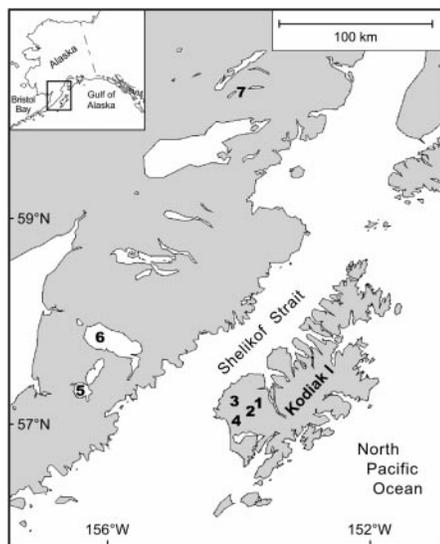


Fig. 1. Locations of seven Alaskan lakes discussed in this study: 1, Karluk; 2, Frazer; 3, Red; 4, Akakura; 5, Ugashik; 6, Becharof; and 7, Tazimina.

were evaluated with the use of water chemistry, limnological, and sedimentary data for the study lakes and found to be of minor importance relative to SDN loading (14). Diatom valves and cladoceran body parts are dominant microfossils in these sediments. Diatom species composition can be used to reconstruct past nutrient dynamics (15), and cladoceran microfossils provide important information on secondary production (16). Fossils of salmon, notoriously patchy and incomplete (17), were not found in our cores.

In Karluk Lake (57°25'N, 154°05'W), the $\delta^{15}\text{N}$, diatom, and cladoceran records (Fig. 3) (18) show a striking concordance with each other and with the sockeye escapement data (the number of fish that return to spawn) (19). Large sockeye escapements are recorded by high sedimentary $\delta^{15}\text{N}$ values and the dominance of meso-eutrophic to eutrophic diatoms (*Stephanodiscus minutulus/parvus* and *Fragilaria crotonensis*), at the expense of more oligotrophic taxa (20). The strong decrease in escapement beginning in 1939 and sustained until 1984 is recorded in the sediments by a marked decline in $\delta^{15}\text{N}$ and an increase in benthic diatoms (particularly small benthic *Fragilaria* spp. such as *F. brevistriata* var. *inflata*), reflecting the relative decline in planktonic production with the decreasing SDNs. *Bosmina longirostris* averaged 87.3 \pm 5.6% of the cladoceran microfossils in the Karluk Lake core. The concentration of *Bosmina* track the changes in $\delta^{15}\text{N}$ and the above diatom-inferred nutrient changes, indicating higher secondary production concurrent with increased SDN loading.

The recent increase in escapement, beginning in 1985, coincides with a distinct diatom signature (Fig. 3). This observation, however,

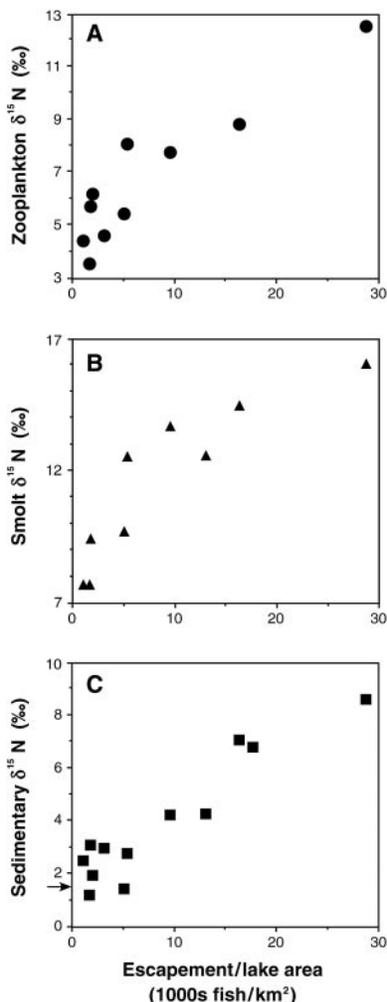


Fig. 2. The influence of SDN loading, as represented by the escapement/lake area ratio (i.e., the density of adult sockeye returning to the lake ecosystem to spawn), on the $\delta^{15}\text{N}$ signature of components of the nursery lakes' food web (zooplankton and juvenile sockeye salmon) and surface sediments. Relations between the escapement/lake area ratio and (A) the $\delta^{15}\text{N}$ of zooplankton ($r = 0.92$, $P < 0.01$), (B) the $\delta^{15}\text{N}$ of juvenile sockeye (smolts) ($r = 0.88$, $P < 0.01$), and (C) the $\delta^{15}\text{N}$ of sediments ($r = 0.94$, $P < 0.01$). The arrow on the vertical axis of (C) is the average $\delta^{15}\text{N}$ of sediments from 33 lakes in Alaska without salmon ($1.5 \pm 0.9\text{‰}$). These nursery lakes span a large gradient in SDN loading and cover a large portion of the range of sockeye in Alaska. Sampling and analytical methods, sample variability, and site locations are described in (18). Samples of zooplankton and juvenile sockeye were not available from all 12 sites.

was expected because of the confounding influence of a lake fertilization program, implemented from 1986 until 1990. The program was designed to increase summer primary and secondary production in an effort to increase salmon production (21). The increase in *Cyclotella pseudostelligera*, a taxon known to respond to artificial fertilization (22), clearly demarks this period. The $\delta^{15}\text{N}$

signature was also influenced by fertilization, because the fertilizer had a $\delta^{15}\text{N}$ value of zero (10).

After inception of commercial fishing on the Karluk system in 1882 (23), the production of sockeye salmon declined; total production averaged more than 2 million fish until about 1910, and about 500,000 fish in the 1970s. Our data suggest that the prolonged 20th-century collapse of the Karluk sockeye fishery was driven in part by reductions in carcass-derived nutrients from overharvest. The sediment data infer a positive-feedback system, in which higher adult salmon abundance leads to increases in nutrient (P and N) loadings. This enrichment, in turn, increases lake primary and secondary productivity. Completing the cycle, the increase in lake carrying capacity for juvenile salmon may ultimately result in higher numbers of adult salmon. The declines in $\delta^{15}\text{N}$ and primary and secondary production during the 20th century (Fig. 3) suggest a disruption of this feedback loop.

High $\delta^{15}\text{N}$ values and dominance of more eutrophic diatom taxa indicate that sockeye abundance in Karluk Lake was relatively high at the time the commercial fishery began. Secondary production, as indicated by *Bosmina* remains, was also high at this time. A marked decline in sockeye abundance of similar magnitude to the recent collapse occurred between ~1810 to 1835, as evidenced by the low $\delta^{15}\text{N}$ and a decrease in relatively eutrophic diatom taxa and *Bosmina*. The $\delta^{15}\text{N}$ and microfossil data during the early 1700s indicate another period of relatively low salmon abundance. The positive covariation between $\delta^{15}\text{N}$ and proxies of primary and secondary production indicate that the nursery lake–nutrient feedback cycle was tightly linked.

The pattern observed in $\delta^{15}\text{N}$ in Karluk Lake is similar to that in ^{210}Pb and tephrodated cores from four other salmon nursery lakes (Red, Akakura, Ugashik, and Becharof). These lakes include two of the most important sockeye salmon–producing regions of the North Pacific (Fig. 1). The $\delta^{15}\text{N}$ profiles suggest that salmon stocks were at high abundance in many systems when commercial harvesting was initiated and indicate marked declines in the early 1800s and early 1700s (Fig. 4). Our data are consistent with the few historical observations (24). There appears to be a positive relation between inferred sockeye abundance and tree-ring–reconstructed Gulf of Alaska SST (25) from about 1700 to 1850 (Fig. 4). The prominent decline in $\delta^{15}\text{N}$ in the early 1800s coincides with the period of the coldest sea surface temperatures and coastal air temperatures for the past 250 years (25–27). These observations are consistent with the relation inferred between temperature and salmon abundance

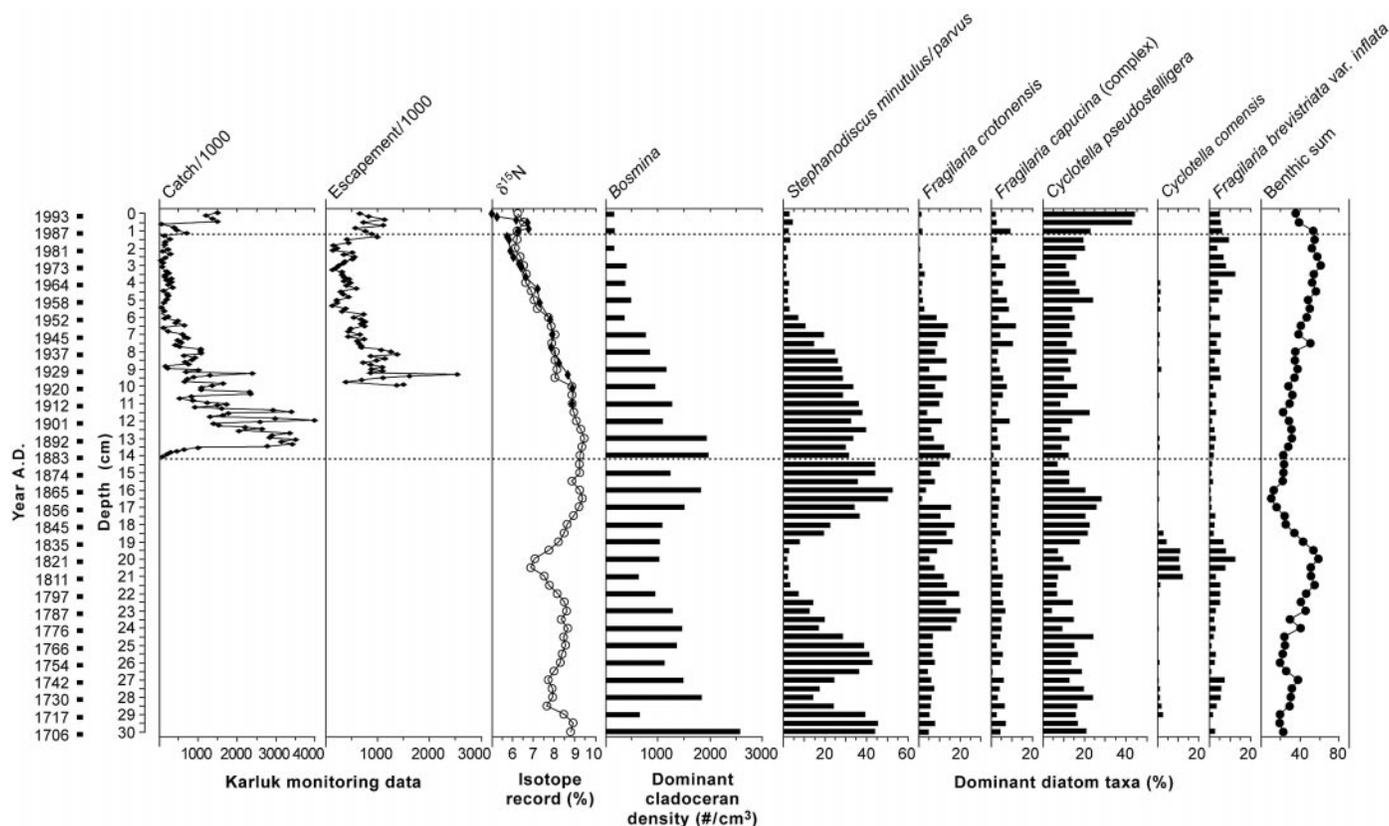


Fig. 3. Historical and paleolimnological evidence of sockeye salmon variation in Karluk Lake over the past ~300 years. The historical information for Karluk sockeye salmon includes commercial catch data beginning in 1882 and escapement counts from a weir on the Karluk River beginning in 1921. The paleolimnological data consist of $\delta^{15}\text{N}$ profiles from two replicated cores collected at the same sampling station showing the excellent reproducibility of the

coring, isotope and dating techniques, concentrations of cladoceran *Bosmina longirostris* microfossils, relative abundances of dominant diatom taxa (greater than 10% in at least one interval), and the relative abundance sum of all benthic diatoms. The data are divided into three different zones (from top to bottom): the fertilization period, the commercial fishing period, and the precommercial fishing period.

in this region during the 20th century (3). However, this relation seems to decouple from ~1850 to 1920, when temperature reconstructions indicate cooler than average temperatures, and salmon stocks had above average abundances. As expected, the low $\delta^{15}\text{N}$ recorded in the last two decades does not track overall sockeye abundance, because the stocks were managed for constant escapement and a large proportion of the fish was harvested (28).

As controls, we analyzed $\delta^{15}\text{N}$ in sediments from two nearby lakes (Frazer and Tazimina) (Fig. 1) that match the nursery lakes as closely as possible in morphometry and geographic location, but are isolated from salmon access by waterfalls. The $\delta^{15}\text{N}$ profiles are relatively depleted and are constant over time (Fig. 4). In Frazer Lake, a fish bypass was constructed, and sockeye salmon began to flourish in the 1980s (21). The $\delta^{15}\text{N}$ enrichment near the core top clearly records the recent delivery of SDN into this lake. Diatom and cladoceran analyses of cores from this lake also show very little change before the introduction of salmon.

Marked, regionally coherent variability in

sockeye salmon populations occurred over decadal scales both before and after the onset of commercial fishing. This suggests that large-scale forcing from the ocean-atmosphere system contributes to fluctuations in sockeye abundance. The lack of a simple relation between salmon abundance and SST suggests that complex interactions exist between climatic change and sockeye salmon ecosystems. Both climatic change and commercial harvesting can reduce inputs of SDNs to sockeye nursery lakes, which can decrease lake productivity, and ultimately influence salmon production. In Karluk Lake, where the SDNs are a high proportion of nutrient loading, the drop in sockeye in the early 1800s was followed by a swift recovery when the natural nutrient feedback loop was operating. In contrast, the disruption of this nutrient cycle during the commercial fishing period appears to have had a strong negative impact on lake productivity, thereby preventing a similar recovery in the 20th century. However, our work also shows that a gradient exists in the relative importance of carcass-derived nutrients between sockeye nursery lakes (Fig. 2), and thus the productivity of

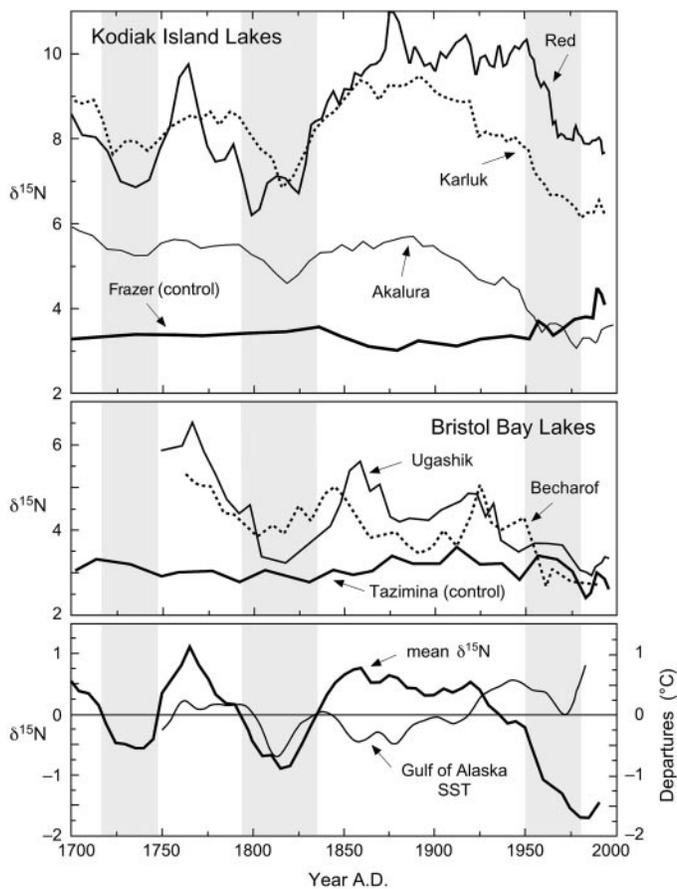
some systems may be less impacted by changes in SDN loading. This may be the case in the Bristol Bay lakes, where SDNs are a low proportion of total nutrient input, and the recent record catches (3) suggest that any disruption of their nutrient cycle had minor impacts on salmon production. This further highlights the need to assess the implications of both climatic change and altered nutrient cycles in determining management strategies for Pacific salmon stocks.

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Fig. 4. Comparison of $\delta^{15}\text{N}$ profiles from sockeye and control lakes from the Kodiak Island and Bristol Bay regions of Alaska over the past ~300 years (upper two panels). The sockeye lake profiles have many common trends in $\delta^{15}\text{N}$, including lower values in the early 1700s, early 1800s, and the mid- to late 1900s. The two control lakes (Frazer and Tazimina) are similar to the sockeye lakes in morphology and geography, but have waterfalls at their outlets impassable to sockeye. However, the construction of a fish ladder over the Frazer River waterfalls in the 1950s has allowed the migration of sockeye into this lake, and the associated SDN loading is faithfully tracked by the recent $\delta^{15}\text{N}$ enrichment in the Frazer Lake sediment profile. The lower panel compares $\delta^{15}\text{N}$ anomalies of the composite sockeye lake record with a reconstruction of Gulf of Alaska sea surface temperature (SST) (25) over this period. The composite sockeye lake record (calculated as the average deviation from the record mean of each of the five sockeye lake profiles) highlights the consistency of the variation in the sockeye lakes' $\delta^{15}\text{N}$ profiles. The SST reconstruction for the Gulf of Alaska (25-year smoothed) is based on coastal tree-ring data.



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 14. A number of potential factors, other than SDN input, may control sediment $\delta^{15}\text{N}$ variations, including nitrate utilization (29), ammonia volatilization (30), denitrification (31), N fixation (30), and organic matter source (30). We used limnological [nitrate, ammonia, total phosphorus (TP), and chlorophyll a concentration, phytoplankton composition] and sedimentary data (C/N ratio) to statistically evaluate these variables and found that SDN loading (escapement/lake area ratio) was the only significant factor ($P < 0.01$). Ammonia volatilization is probably minor because it is in low concentration, and the lakes are of near-neutral pH. N-fixing plankton are generally minor constituents. Denitrification rates are probably low in most lakes, as they generally have high oxygen levels throughout the water column. Relatively high nitrate levels imply that utilization rates may be low in some systems, possibly because of P limitation. In addition, the high $\delta^{15}\text{N}$ ratios observed in the biota of some lakes (Fig. 2) indicate an enriched source of N. The long-term trends over the 300-year period (Figs. 3 and 4) cannot be explained by diagenetic changes; control lake Tazimina is very constant over this period, and Frazer Lake demonstrates that core-top increases can occur with recent SDN enrichment. The

trends cannot be explained by changes in organic matter source, as the C/N ratios are very constant and low (between 7 and 9), indicating the dominance of aquatic sources in these cores. Long-term changes in the $\delta^{15}\text{N}$ of salmon carcasses could influence our profiles. However, there was no significant difference in $\delta^{15}\text{N}$ in four stocks of adult Alaskan sockeye before and after the mid-1970s climate shift (on the basis of scale isotope analysis, a reliable proxy for carcass composition).
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above correlations do not include the recent artificial lake fertilization period.

20. Autecological data for the dominant diatoms of Karluk Lake strongly support the inference of substantial nutrient shifts over the past 300 years. *Stephanodiscus minutulus/parvus* and *Fragilaria crotonensis*, which are abundant during intervals of high sockeye abundance (e.g., early 1900s), are meso-eutrophic to eutrophic indicators [e.g. (32, 33)]. Increasing dominance of *S. minutulus/parvus* over *F. crotonensis* suggests lower Si:P conditions, which are likely to have been brought about by greater diatom productivity (34). In contrast, *Cyclotella comensis* and *F. brevisstriata* var. *inflata*, which are more abundant during periods of fewer sockeye spawners, are oligotrophic to slightly meso-eutrophic indicators [e.g. (32, 33)]. From a 51-Alaskan lake diatom study, Gregory-Eaves *et al.* (35) calculated TP optima for *C. comensis* and *F. brevisstriata* var. *inflata* of 7.0 and 10.4 $\mu\text{g/liter}$, respectively. The autecology of *C. pseudostelligera* is described in (22). SDNs appear to influence not only diatom species composition but also life form. Periods of low sockeye escapement are tracked by greater abundances of benthic diatoms. These changes may occur because the benthic community is situated in or close to sockeye spawning areas (i.e., tributary streams and lake shores) where carcasses are most likely to decompose.
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40. Supported by the Alaska Sea Grant College Program, National Oceanic and Atmospheric Association (NOAA)—Auke Bay Lab Ocean Carrying Capacity (OCC) Program, Alaska Department of Fish and Game, U.S. Fish and Wildlife Service, NSF-NOAA GLOBEC Program (NSF grant OCE-9711427 to B.P.F.), Natural Sciences and Engineering Research Council of Canada (NSERC), the Northern Studies Training Program (NSTP), and the Ontario Graduate Scholarship program. We thank J. Adams, D. Andrews, D. Barto, K. Condon, S. Honnold, T. LaPorte, J. Larson, S. McNeil, S. Schrof, and M. Willette for field assistance and M. Billington, N. Haubenstock, A. Hiron, T. Howe, A. Krumhardt, M. Luoma, S. McNeil, C. Restrepo, and F. Satterfield for laboratory assistance. This paper has benefited from discussions with D. Barto, J. Blais, B. Cumming, P. Dillon, J. Edmundson, J. Goering, P. Hamilton, T. Johnston, T. Kline, D. Mann, O. Mathisen, S. McNeil, D. Schmidt, B. Sherwood-Lollar, C. Stager, as well as many scientists in our labs. We thank R. D'Arrigo, G. Wiles, and G. Jacoby for sharing tree-ring data. This is contribution number 166 of the U.S. GLOBEC program, jointly funded by the NSF and NOAA.

5 July 2000; accepted 14 September 2000

Antiphase Oscillation of the Left and Right Suprachiasmatic Nuclei

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An unusual property of the circadian timekeeping systems of animals is rhythm "splitting," in which a single daily period of physical activity (usually measured as wheel running) dissociates into two stably coupled components about 12 hours apart; this behavior has been ascribed to a clock composed of two circadian oscillators cycling in antiphase. We analyzed gene expression in the hypothalamic circadian clock, the suprachiasmatic nucleus (SCN), of behaviorally "split" hamsters housed in constant light. The results show that the two oscillators underlying the split condition correspond to the left and right sides of the bilaterally paired SCN.

Daily biological rhythms are governed by an innate timekeeping mechanism, a circadian clock. Such clocks have been localized to discrete sites and, in mammals, to the bilaterally paired SCN in the hypothalamus (1). The clock in the SCN is composed of multiple autonomous single-cell oscillators (2); within each cell, interacting transcription and translation feedback loops constitute the clock's actual oscillatory mechanism (3). It is less well understood how individual SCN cells interact to create an integrated tissue pacemaker that accounts for the circadian behaviors of whole animals.

One long-standing model of the rodent circadian clock describes it as a complex pacemaker consisting of two mutually coupled oscillators (4). The evidence for this idea rested initially on a phenomenon known as "splitting," which has been most extensively studied in hamsters exposed to constant light, in which an animal's single daily bout of locomotor (wheel-running) activity dissociates into two components that each free-run with different periods until they become stably coupled 180° (about 12 hours) apart. Circadian rhythms of drinking (5), body temperature (6), luteinizing hormone

secretion (7), and SCN electrophysiological activity (8) also split along with locomotion. Theoretical (9) and experimental (10–12) analyses suggest that the antiphase coupling of two equivalent oscillators is likely to be responsible for this phenomenon.

In this report, we present evidence that the two putative oscillators underlying the split condition correspond to the left and right sides of the paired SCN. This idea has been raised previously (9), supported by the observation that unilateral SCN lesions in split hamsters abolish behavioral splitting and produce a single bout of locomotion (13), although this interpretation is compromised by nonspecific surgical effects (14). We therefore assayed clock activity in unlesioned hamsters by measuring the expression of *Per1*, *Per2*, and *Per3*, which are homologous to the *Drosophila Per* gene that forms part of the clock's core oscillatory mechanism. The three mammalian *Per* genes encode mRNAs that oscillate with a circadian rhythm in the SCN (3), with high levels during both the light phase of a light-dark (LD) cycle and the subjective day in constant darkness and with low levels during both the dark phase and the subjective night. The cyclic expression of these genes is believed to be central to normal clock function in mammals, at least for *Per1* and *Per2* (15, 16).

Wheel-running activity was continuously recorded in male golden hamsters maintained in constant light. About 60% of our hamsters

develop stably split activity rhythms after 6 to 8 weeks in this lighting regimen (Fig. 1A). Individual animals were killed at various circadian times, and their brains were processed for in situ hybridization with antisense cRNA probes to each *Per* subtype and film autoradiography (17). When tissue sections were examined from behaviorally split hamsters killed during either of the two inactive phases of their locomotor activity cycles, *Per* gene expression within the SCN was markedly asymmetric (Fig. 1B), with hybridization signal observed unilaterally on either the left or right sides of the SCN. This asymmetry was especially striking for *Per1*, less so for *Per2*, and barely discernible for *Per3*. In each animal, the more pronounced hybridization signal for all three *Per* genes was on the same side of the SCN, although randomly on the left or the right.

The magnitude of left-right asymmetry was quantitated from the autoradiographs by calculating an optical density (OD) ratio [OD from the "high" (whether left or right) half-SCN/OD from the "low" half-SCN] (Fig. 1C). The ratio for *Per1* peaked about 6 to 8 hours after the offset of the last locomotor activity bout; for *Per2*, the asymmetry was less prominent and appeared delayed by about 2 to 4 hours relative to *Per1*. This relation between *Per1* and *Per2* resembled that in the SCN of animals entrained to an LD cycle (or free-running in constant darkness), in which the peak level of *Per2* lagged that of *Per1* by several hours (18–20). In two groups of behaviorally split hamsters killed at either the 6- or 10-hour time points in Fig. 1C, the rank order of OD ratios was *Per1* (3.84 ± 0.35) > *Per2* (2.16 ± 0.35) > *Per3* (1.25 ± 0.12) at the 6-hour point, whereas it was *Per2* (1.83 ± 0.30) > *Per1* (1.54 ± 0.14) > *Per3* (1.17 ± 0.08) at the 10-hour point (mean \pm SE) ($n = 5$ animals per group; for *Per1* and *Per2*, the 95% confidence interval of these means was greater than 1.00). In hamsters maintained in constant light but with unsplit locomotor activity rhythms, *Per* hybridization signal was present on both sides of the SCN and unilateral expression was not observed (OD ratio for *Per1* of 1.10 ± 0.06 for three animals killed in the middle of the inactive phase of their locomotor activity cycles).

These findings indicate that the left and

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