Climate effects on inter-annual variation in growth of the freshwater mussel (*Anodonta beringiana*) in an Alaskan lake

NEALA W. KENDALL, HARRY B. RICH, LESLIE R. JENSEN AND THOMAS P. QUINN
School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, U.S.A.

**SUMMARY**

1. Warming trends are evident in many parts of the globe but are especially marked at higher latitudes, with complex effects on the biota that include direct effects on growth potential and indirect effects through food webs.
2. Air temperatures have been increasing over the past 50 years in southwestern Alaska, affecting the growth and population dynamics of many organisms, including a variety of aquatic species such as the freshwater mussel *Anodonta beringiana*.
3. We collected freshwater mussels from Iliamna Lake, in the Bristol Bay region of Alaska, and measured their shells to examine climatic effects on growth patterns.
4. Linear mixed effects models and ordinary least square linear regressions revealed strong positive correlations between local air temperatures (especially in May, October and the summer months) and inter-annual variation in mussel growth. Slower mussel growth was also significantly correlated with later date of ice break-up, which was linked to air temperatures in late spring.

**Keywords**: Alaska, *Anodonta*, climate change, freshwater mussels, growth variation

**Introduction**

Changing climatic conditions can have complex and diverse effects on organisms, including but not limited to changes in range, phenology (e.g. timing of migration and breeding), growth and abundance. Many of these effects are especially marked in high-latitude systems, including lakes (Magnuson *et al.*, 2000; Root *et al.*, 2003; Berteaux *et al.*, 2004). Northern lakes have experienced significant reductions in the duration of ice cover, increases in peak temperature and changes in important temperature-related biotic processes (Schindler *et al.*, 1990; Straile, 2000; Scheffer *et al.*, 2001; Winder & Schindler, 2004a). Indeed, the effects of climactic warming can be amplified in polar lakes because of these factors, especially ice cover (Moritz, Bitz & Steig, 2002; Holland & Bitz, 2003; Smol *et al.*, 2005). Lakes are sensitive to climatic change and can serve as sentinels because of their position within drainage basins and their capacity for integrating biotic and abiotic processes (Adrian *et al.*, 2009; Schindler, 2009; Williamson *et al.*, 2009). In contrast to conditions elsewhere, where warming trends may lead to stress or extirpation of species, increased temperatures and longer growing seasons in high-latitude lakes may enhance growth rates. For example, the growth of juvenile sockeye salmon (*Oncorhynchus nerka* Walbaum) in lakes of the Bristol Bay region of Alaska has been accelerated by early ice break-up and warmer summer temperatures (Schindler *et al.*, 2005; Rich *et al.*, 2009).

Research on climatic effects has tended to consider such commercially exploited species as salmon but effects should be evident across diverse taxa. In freshwater ecosystems, unionid mussels can play an important role as a food source and as filter feeders. They can compose up to 90% of the bottom fauna, reflecting their ecosystem function (Mann, 1965).
Mussel shells, like other bivalves, expand as they regularly lay down thin layers of new shell over the existing shell, extending from the umbo to the outside edge. When they are growing quickly, the edge expands, creating a wide, opaque ring that is visible on the external side. During the winter, when growth decreases, the layers pile up on the edge without expanding, creating a thicker shell in a narrow band. The annuli created by these growth patterns can be used to age individuals and measure mollusc growth rates (Negus, 1966; Schöne et al., 2004; Strom et al., 2004; Albuquerque et al., 2009; Helama et al., 2009), though external examination of annuli can underestimate the true age of a mussel (e.g. Kesler & Downing, 1997). To the extent that the date of ice break-up and summer temperatures affect growth, inter-annual variation in annuli spacing should be correlated with climatic conditions (e.g. Schöne et al., 2004; Menge, Chan & Lubchenco, 2008; Albuquerque et al., 2009).

Accordingly, the purpose of this study was to estimate the growth of the Yukon floater mussel (*Anodonta beringiana* Middendorff) and test the hypothesis that their growth was positively related to climatic conditions in a given year. We sampled mussels from Iliamna Lake, Alaska, where there has been a clear warming trend in recent decades that is known to have affected the growth of juvenile sockeye salmon (Rich et al., 2009).

**Methods**

Mussels were collected by hand from the head of Finn Bay, on Porcupine Island, in the eastern end of Iliamna Lake (Fig. 1) in water about 1 m deep in August of 2007 and 2008. Finn Bay is a long, narrow bay sheltering and separating the mussel population from the windy, rocky shoreline of the island. The mussels were identified as *A. beringiana*, though we acknowledge that there is some ambiguity regarding the taxonomy of this genus (Nedeau et al., 2009). In 2007 and 2008, we collected 32 and 59 mussels, respectively, for use in growth measurements. Mussels were not collected at random but rather we sought to collect more old than young mussels to allow calculation of growth further back in time. The specimens were brought to the laboratory where the flesh was removed and the shells cleaned and dried at room temperature for a week. The right valve of each mussel was measured for standard height and length at each external ring, corresponding to a given year, only counting rings with a complete path around the shell. From the measurements collected, area was indexed as length × height (rather than a more complex estimate to take into account the shell’s variable shape). Shell area was used for statistical analysis and modelling rather than either of the individual measurements because each yielded different information; mussels grew more in length than in height each year.
Annual growth increment was the difference in mussel shell area from 1 year to the next.

We predicted annual mussel shell growth patterns using linear mixed effects models (Zuur et al., 2009) to account for sampling of a given individual multiple times and avoid shortcomings associated with fixed effects models (e.g. Smith, Jones & Van Montfrans, 2008; Weisberg, Spangler & Richmond, 2010). In our mixed effects models, the random effect was individual mussel, because of the repeated shell area growth measurements from a given individual (one measurement for each year), and the fixed effects were monthly air temperature, average summer air temperature and ice break-up date. The latter was calculated as the date when ice was gone from a reference point in Iliamna Lake and is reported by airplane pilots, local residents and Alaska Department of Fish and Game personnel. These data have been compiled by University of Washington researchers in most years since 1960 (Rich, 2006). Most of our models included only single parameters because we wanted to understand how each parameter affected growth. Temperatures in many months were correlated, so we only ran multi-parameter models for a subset of parameters that were not correlated.

These models (Eqn 1) calculated the predicted growth increment ($I_{iy}$) for individual $i$ in year $y$ from an individual month’s ($m$) air temperature deviate ($T_{ym}$), the annual average air temperature deviate ($T_y$) or ice break-up date ($D_y$). In Eqn 1, $X$ represents one of the above climatic variables.

$$I_{iy} = a + n_i + Xb + e_{iy}$$  

(1)

In this equation, $n_i$ represents a random effect because of mussel individual $i$, and $e_{iy}$ are errors for mussel $i$ in year $y$. Thus, mussel shell growth is the sum of a baseline value (the intercept $a$), a random effect because of the individual mussels and a fixed effect. Each model was adjusted with a first-order autoregressive process, abbreviated AR(1), which implies that the errors were correlated over time as a given mussel shell was measured annually for multiple years. The annual growth increment data were log normally distributed. Because of the uncertainty of generalised linear mixed effects models (Zuur et al., 2009), we log transformed the mussel shell growth data to make it normally distributed and used a linear mixed effects model (lme in the nlme package) with a normal error distribution and restricted maximum likelihood as the parameter-estimation method in the program R (R Development Core Team, 2008).

Air temperature data are available from the Iliamna airport from 1960–2009 (Fig. 2). We do not have long-term records of water temperature in Finn Bay, but it is shallow and protected and so should be strongly related to air temperatures. Continuous records from Finn Bay in summer 2009 indicated that daily mean water temperatures approached $19 ^\circ C$ in parts of July (mean of daily means $= 14.5 ^\circ C$) and decreased in August (mean of daily means $= 12.8 ^\circ C$). We examined air temperature of all months because temperatures at different times have the potential to influence shell growth directly and/or indirectly. We also averaged temperatures across multiple months to see how these were correlated with mussel shell growth. Each year’s and month’s temperature effect was calculated as a deviate from the long-term yearly and monthly average, as in Eqns 2 & 3, where $T_{ym}$ is the average temperature in a given month in a given year, $T_y$ is the average temperature for a given month across all years, $T_{ym}$ is the average temperature in a given year and $T_y$ is the average temperature across all years.

$$T_{ym} = T_{ym} - T_m$$  

(2)

$$T_y = T_y - T_y$$  

(3)

We used the Akaike Information Criterion with a second-order correction for small sample sizes (AICc;
Burnham & Anderson, 2002) to understand how well each model fit the data. The models that fit the data best (highest likelihood) had the lowest AICc values. To understand how each parameter affected mussel shell growth, we determined whether its coefficient value differed significantly from zero. Finally, the standard deviations of the random effects (the individual mussels) were very small (ranging from $2.08 \times 10^{-5}$ to $3.3 \times 10^{-5}$), allowing us to perform simple ordinary least squares regressions to understand how much variation in annual shell growth was explained by each environmental factor.

## Results

Our mussels ranged in age from 6 to 20, so we had 5–19 years (1989–2007) of growth information from individual mussels. Thus, our oldest mussels were older than the average maximum age reported by Nedeau et al. (2009) for other Anodonta species but much younger than long-lived freshwater species such as pearl mussels (Margaritifera margaritifera Linnaeus). The average age of the mussels was 9 and the median was 8. Growth rates varied but could be approximated as a linear function (Fig. 3a). Thus, ontogenetic growth trends did not need to be removed, as is common for longer-lived molluscs (e.g. Schöne et al., 2004). Growth rate increased rapidly from ages 1 to 4, decreased and then stabilized around age 9 (Fig. 3b).

Annual average mussel shell growth varied a great deal over time, ranging from $145 \text{ mm}^2$ in 1996 to $443 \text{ mm}^2$ in 2005 (mean = $314 \text{ mm}^2$, SD = $99 \text{ mm}^2$). Single-parameter linear mixed effects models indicated that mussel shell growth had the strongest correlation (positive) with May air temperature (Table 1). October air temperature and the average summer (May–September) air temperature AICc values were 38 and 39, respectively, more than May alone. Their slope coefficients were also positive and significantly different from zero, as were the slope coefficients for January, February, June, July and August, but not September, November or December. Thus, mussels grew faster when temperatures were warmer than average and slower when temperatures were below average. Warm October temperatures may be important if they allow Finn Bay to remain ice-free longer, allowing continued mussel shell growth. Warm conditions in January and February may lead to earlier dates of ice break-up.

![Box plots of (a) annual average shell size and (b) average shell growth of mussels sampled from Finn Bay, Iliamna Lake, Alaska (n = 91 mussels). The smallest and largest observations (in the range not considered as outliers) are shown as the error bars; the lower and upper edges of the box are the lower and upper quartiles (25th and 75th percentiles, respectively); the line in the middle of the box is the median and the circles represent data points considered to be outliers (1.5 times the inter-quartile range).](image)
The year effect also had a positive and significant regression coefficient, suggesting that mussels have grown more in recent years than in earlier years. The ice break-up date was available for only a subset of years for which we had mussel growth data. Thus, we used a smaller data set in our regression for this parameter, so its AICc value is not comparable to those obtained from models for the other parameters. The ice break-up date regression coefficient was significantly negative, indicating that in years when the ice melted later, mussels grew less (Table 1).

Linear mixed effect models that included multiple variables had significantly larger AICc values than single-variable models, so were less correlated with mussel shell growth.

Ordinary least squares regressions yielded R² values indicating how much of the variation in mussel shell growth among years was explained by different climatic factors. May air temperature explained almost 31% of mussel growth variation between 1989 and 2007 (Fig. 4), while average summer air temperature explained 32% of the variation and the date of ice break-up explained 20%.

Owing to variation in growth of mussels of different ages (Fig. 3b), we wanted to confirm that our results were not because of the age distribution of the mussels in our sample. Thus, we used only mussel growth from ages 3 to 4 and 8 to 9 in our linear models to test the generality of our findings. When only growth of mussel shells from age 3 to 4 was compared with air temperature, August temperature was most strongly correlated with growth and the slope coefficient was positive. The second strongest correlation (also positive) was for summer months (average of

![Fig. 4](image_url) Relationships between average annual mussel shell growth (across all ages) in Finn Bay, Iliamna Lake, Alaska and average May air temperature in that year (n = 19 years).
May–September). The results were similar for growth of mussel shells from age 8 to 9; March temperature was most strongly correlated with shell growth, followed by the average temperature in March–June. Thus, different monthly temperatures were most strongly correlated with mussel shell growth when different ages were assessed but the overall patterns remained: warmer temperatures were significantly correlated with accelerated growth.

Discussion

Air temperatures in May, October and the summer months and date of ice break-up were strongly related to growth of the freshwater mussel *A. beringiana* via processes that might be direct and indirect. If warmer temperatures increase the organism’s scope for growth and food is not limiting, then growth should be more rapid when temperatures are above average (Newell, 1969; Schöne et al., 2004; Menge et al., 2008; Albuquerque et al., 2009). However, sequences of events in northern lakes can affect growth in more complex ways.

The strong statistical effect of May air temperature probably occurs, not because the mussels grow rapidly in that month, but rather because May temperature affects the date when ice breaks up. Ice break-up in a large lake such as Iliamna, especially in the eastern end where there are many islands and inlets, is somewhat imprecisely measured because ice does not leave all areas simultaneously. Regardless, when the lake is covered with ice it remains cold, stratified and comparatively dark while day length increases rapidly. When the ice leaves, the lake quickly warms, turns over with the prevailing winds and blooms of phytoplankton and zooplankton follow. Lake Aleknagik, also in Bristol Bay, has experienced a general advancement of ice break-up, longer ice-free season, warmer temperatures and higher zooplankton densities in summer (Schindler et al., 2005). Similar processes may be occurring in Iliamna Lake, and they would all tend to contribute to faster growth of mussels. We note that temperate lakes may show different effects. For example, in Lake Washington, a monomictic lake in Washington State, the trend towards warmer conditions and earlier stratification has been associated with earlier phytoplankton blooms (Winder & Schindler, 2004a) but densities of the cladoceran *Daphnia* spp. have decreased (Winder & Schindler, 2004b). During the 20-year period for which we had mussel growth data, Iliamna Lake has not shown a significant warming trend, but the overall trend in the longer time series is significantly upward (Fig. 2). As Schindler et al. (2005) pointed out, this trend seems to result from the combination of general warming and the recent phase of the Pacific Decadal Oscillation (Mantua et al., 1997). Thus, projections of future conditions depend on the mix of regional and global processes.

Extrapolated ordinary least squares regression results indicated that for each 1 °C increase in summer temperature, mussels grew an additional 46 mm². Given the 1.8 °C temperature increase from 1960–2009, mussel shells are projected to be now growing approximately 82 mm² more each year than in the past. Whether such increases will be sustained in the future will depend on whether temperatures continue to rise and on the physiology and ecology of the species at such temperatures. Sclerochronological studies such as ours can provide information on climate conditions prior to human records if the organism is sufficiently long-lived, but in this case, human records encompass the lifespan of even the oldest mussels that we measured. Therefore, the results are more important for their insights into the thermal ecology of mussels than past climate.

Finally, it should be noted that there is some measurement error when counting and measuring mussel shell rings, especially for older individuals. Previous studies suggested that ageing of bivalves using external annuli may result in fewer bands being counted than if internal annuli are used and that errors increased for more mature mussels (Veinott & Cornett, 1996). However, even the accuracy of internal annuli has been questioned (Kesler & Downing, 1997). Such errors, however, would be unlikely to affect our overall conclusions. We used data from all ages and then also the least ambiguous ages (3–4). Results with both sets of data indicated positive effects of temperature on growth, so even errors in estimation of maximum age would not alter these findings.

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References

Adrian R., O’Reilly C.M., Zagares H. et al. (2009) Lakes
as sentinels of climate change. Limnology and Oceanog-
rapy, 54, 2283–2297.

Albuquerque F.S., Peso-Aguiar M.C., Assunção-Albu-
and human density affect Achatina fulica (Bowditch)
(Gastropoda: Pulmonata) shell length, total weight and

Keeping pace with fast climate change: can arctic life
count on evolution? Integrative and Comparative Biology,
44, 140–151.

and Multimodel Inference: A Practical Information-Theo-

Helama S., Nielsen J.K., Macias Fauria M. & Valovirta I.
(2009) A fistful of shells: amplifying sclerochronolo-
gical and palaeoclimate signals from molluscan death

climate change in coupled models. Climate Dynamics,
21, 221–232.

yield inaccurate growth estimates in the freshwater
mussels Elliptio complanata and Lampsilis radiate. Fresh-
water Biology, 37, 325–332.

Magnuson J.J., Robertson D.M., Benson B.J. et al. (2000)
Historical trends in lake and river ice cover in the

Mann K.H. (1965) Heated effluents and their effects on
the invertebrate fauna of rivers. Proceedings of the
Society of Water Treatment Examiners, 14, 45–53.

Mantua N.J., Hare S.R., Zhang Y., Wallace J.M. & Francis
with impacts on salmon production. Bulletin of the
American Meteorological Society, 78, 1069–1079.

rocky intertidal ecosystem engineer and community

Moritz R.E., Bitz C.M. & Steig E.J. (2002) Dynamics of
recent climate change in the Arctic. Science, 297, 1497–
1502.

Freshwater Mussels of the Pacific Northwest, 2nd edn.
The Xerces Society for Invertebrate Conservation, Portland,
OR.

Negus C.L. (1966) A quantitative study of growth and
reproduction of unionid mussels in the River Thames

Newell R.C. (1969) Effect of fluctuation in temperature on
the metabolism of intertidal invertebrates. American
Zoologist, 9, 293–307.

R Development Core Team (2008) R: A Language and
Environment for Statistical Computing. R Foundation for
Statistical Computing, Vienna, Austria. ISBN 3-900051-

Controls over Growth, Distribution, and Life History of
Juvenile Sockeye Salmon in Iliamna Lake, Alaska.

Rich H.B. Jr, Quinn T.P., Scheuerell M.D. & Schindler
control the growth and life history of juvenile sockeye
salmon (Oncorhynchus nerka) in Iliamna Lake, Alaska.
Canadian Journal of Fisheries and Aquatic Sciences,
66, 238–246.

Root T.L., Price J.T., Hall K.R., Schneider S.H., Rosen-
warming on wild animals and plants. Nature, 42, 57–
60.

Climatic warming causes regime shifts in lake food
webs. Limnology and Oceanography, 46, 1780–1783.

for the effects of climate change on watersheds, airsheds, and landscapes. Limnology and Oceanography,
54, 2349–2358.

Schindler D.W., Beatty K.G., Fee E.J., Cruikshank D.R.,
DeBruyn E.R., Findlay D.L., Lindsey G.A., Shearer J.A.,
warming on lakes of the central boreal forest. Science,
250, 967–970.

Schindler D.E., Scheuerell M.D., Rogers D.E. & Abrey
and growth of juvenile sockeye salmon in southwestern

217-year record of summer air temperature recon-
structed from freshwater pearl mussels (M. margarit-
era, Sweden). Quaternary Science Reviews, 23, 1803–1816.

and temporal variability of juvenile spotted seatrout
Cynoscion nebulosus growth in Chesapeake Bay. Journal
of Fish Biology, 73, 597–607.

Smol J.P., Wolfe A.P., Birks H.J.B. et al. (2005) Climate-
driven regime shifts in the biological communities of
arctic lakes. Proceedings of the National Academy of
Sciences USA, 102, 4397–4402.


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