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**Constraints to growth of Lake Superior lake trout, *Salvelinus namaycush***

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*Abstract.*- We describe lake trout *Salvelinus namaycush* growth in Lake Superior management unit WI-2 between 1950 and 1999. Growth was described using both inter-annual and cohort based analyses employing size-at-age, instantaneous growth and vonBertalanffy growth models. Growth of lake trout has declined over the past 50 years. Reduction in growth was most notable after the early 1980s and was greater for wild than hatchery lake trout. In an attempt to explain the decline in growth, we evaluated several constraints including density-dependence, prey resource limitation, prey quality, thermodynamics and sea lamprey parasitism. We found little support for any of our expected hypotheses on growth constraints. A simplified bioenergetic and foraging model suggests that, while prey abundance and biomass are low in Lake Superior, they are sufficient to meet energetic demands in most years. The large thermal mass of Lake Superior may buffer against any significant inter-annual differences in climate that could affect lake trout thermal habitat volume and associated thermodynamic effects on growth. Future analyses such as these would benefit from more precise aging techniques, including using back-calculated growth rates from otoliths of single fish.

## **Introduction**

Lake trout stocks have fluctuated widely in Lake Superior during the past 70 years (Hansen et al. 1995). Expanding fisheries and sea lamprey induced mortality caused stocks to decline rapidly beginning in the mid-1940s. Fishing intensity declined between 1954 and 1961 culminating with the closure of non-indigenous commercial fisheries in 1962. Lake trout mortality remained high through this period as sea lamprey abundance continued to increase to its peak in 1961. Sea lamprey controls, initiated in 1953, were largely ineffective until 1958-60 when chemical treatment of streams reduced the lamprey population by 87% by the fall of 1961 (Smith et al 1974). Attempts to rebuild the lake trout population through stocking began in 1950, and increased rapidly to over 3 million yearlings annually by the late 1960s (Hansen et al. 1995). Reduced mortality combined with stocking and natural recruitment from remnant offshore stocks contributed to the gradual rebuilding of the population (Hansen et al. 1995). By 1998, fisheries managers from around Lake Superior recommended that satisfactory progress had been made towards rehabilitation, and that stocking be ceased in 9 of 13 U.S. management units in Lake Superior.

While lake trout abundance fluctuated so did the Lake environment. The abundance and composition of the piscivore community was in a continual state of flux as stocking programs for chinook and coho salmon and steelhead trout began in the mid 1960s and intensified to the present day (MacCallum and Selgeby 1987; Negus 1995). Species composition and size of the prey fish community switched from lake herring to rainbow smelt in the early 1960s before reverting back to lake herring in the 1980s (Dryer et al. 1965; Mason et al. 1998). Lake trout diets tracked the early change (Dryer

et al. 1965), but smelt remain the dominant prey to the present day (Negus 1995).

Interannual variation in climate, and sea lamprey abundance and scarring rates were also changing through this period.

Growth is a reflection of the environment occupied by the organism. Growth is expected to be better when environmental conditions are good, and poorer as the quality of the environment degrades. In light of the dynamic environment of Lake Superior over the past 50 years, we undertook this analysis to evaluate several hypotheses relating lake trout growth to potential constraints. Food and temperature are the primary determinants of fish growth (Mason et al 1995), although intrinsic factors (i.e. genetics) can also determine the rate and ultimate size of a given individual or stock. Temperature not only modifies growth through physiologic rates affecting metabolism and consumption (cf Brett and Groves 1979; Stewart et al. 1983) but also the interaction between predator and prey (Brandt et al 1992). The abundance, size and quality of the prey resources combine to affect the growth rate potential of the predator. Disease and parasitism can reduce the growth rate potential by increasing energetic costs.

The objectives of this study were therefore to describe the long-term growth of lake trout in Lake Superior and identify constraints to the realised growth. Growth was described using both inter-annual metrics and cohort based analyses. Our assumptions were that the inter-annual analyses (size-at-age, instantaneous growth) would identify large environmental signals that varied between years, but these results may be obscured by an underlying intrinsic growth response (i.e. poor growth at age “x” would be an expression not only of events in that year, but also any growth advantage or disadvantage incurred in all previous years). The cohort based analyses (vonBertalanffy growth

parameters) would help identify systematic differences affecting all ages, but would be unable to resolve inter-annual events. For each of the growth analyses, we explored the contribution of several potential constraints that had been proposed including: density-dependence (Walters et al. 1980; Ferreri and Taylor 1996); prey resource limitation (Eby et al 1995; Negus 1995); prey quality (Mason et al. 1998); thermodynamics (King et al. 1999) and sea lamprey parasitism (Kitchell and Breck 1980).

## Material and Methods

We used length-at-age data for wild and hatchery lake trout collected in Lake Superior Management Unit WI-2 during April or May from 1959-1999. No data were available for 1996. Weights were recorded for a subset of the fish collected since 1983. Fish were collected at 14 to 40 index stations using 305 to 3048m of 114-mm stretch-measure gillnets in all years. Aging techniques varied through time. From 1959-1968, all ages were derived from fin clips, so only hatchery lake trout were aged during this period. From 1969-1986, both wild and hatchery lake trout were aged using scales. From 1987-1999, either scales (total length <584mm) or otoliths (total length >584mm) were used. Age validation experiments on Lake Superior lake trout (Schram and Fabrizio 1998) have shown that lake trout greater than age 10 can not be reliably aged with scales. We therefore used only lake trout age 10 and younger in any of our analyses. Similarly, the size-selective nature of gillnets mean that very few fish younger than age 3 were captured in the gear in all years. We therefore, omitted any records for fish younger than age 4 in the analyses.

## Description of Growth

We evaluated changes in size-at-age (length and weight) and growth (instantaneous growth rate, von Bertalanffy growth coefficients) between hatchery and wild lake trout, and within a stock across years. Size-at-age and instantaneous growth rate ( $G$ ) were calculated and compared between years to assess inter-annual differences. As data were only available once per year, but were collected at approximately the same time each year, we estimated  $G$  as follows:

$$G_{a,y} = \ln\left(\frac{L_{a+1,y+1}}{L_{a,y}}\right)$$

where  $G_{a,y}$  is the instantaneous growth rate for a fish of age  $a$  in year  $y$ , and  $L$  (or  $W$ ) is the length (or weight) of that fish. Due to the limited number of young fish, instantaneous growth coefficients were only calculated for ages 5-10. We chose to include only estimates where the minimum sample size for both  $n_{a,y}$  and  $n_{a+1,y+1}$  were greater than 5 fish.

vonBertalanffy growth models were fit to cohorts (= year classes) of fish to evaluate intrinsic differences within a cohort of fish, recognising that smaller size-at-age at early ages would likely be maintained to older ages. The vonBertalanffy growth model takes the form:

$$L_a = L_\infty (1 - e^{-K(a-a_0)})$$

where  $L_a$  is the length (mm) at age  $a$  (years),  $L_\infty$  is the asymptotic length,  $K$  is the growth coefficient, and  $a_0$  is the hypothetical age when the fish would have been zero length.

Due to concerns over precision of aging older fish, we used the mean length of the 10 longest age 10 lake trout to estimate  $L_\infty$ . This assumption will underestimate the true  $L_\infty$ ,

but will ensure all cohorts are treated equally (model coefficients are not biased by the presence of a few very old or very large individuals in some years, but not in others). The absence of young fish in the samples yielded very imprecise estimates of  $a_0$ . We therefore assumed  $a_0=0$  for all cohorts. The final parameter of the vonBertalanffy growth model,  $K$ , was estimated using a nonlinear estimator in S-Plus.

### Constraints to growth

We generated time series for several biotic and abiotic factors to test hypotheses that these were constraints to growth of Lake Superior lake trout. These potential constraints included: density-dependence based on catch-per-unit-effort (CPUE) of lake trout; intra- and interspecific competition, expressed as abundance of lake trout, and chinook+coho salmon, respectively; prey dynamics; sea lamprey parasitism; and temperature.

CPUE data were available for wild and hatchery lake trout in management unit WI-2 from 1959-1999 (S. Schram, WDNR, unpubl. data). CPUE was expressed as mean number of lake trout per 1000-metre of 114-mm stretch-measure gillnet fished overnight during the spring (April-May). This was the same gear used to collect the aging structures.

The total number of salmonids stocked into Lake Superior was available for each jurisdiction (state / province) for each year since 1950 (MacCallum and Selgeby 1987; Hansen et al. 1995; D. Schreiner, MnDNR, pers. comm.). We considered only lake trout, chinook and coho salmon in our analyses. Owing to the extensive migration of these species throughout the lake (J. Peck, MiDNR, pers. comm.) we chose to combine all agency data into a single annual index.

Prey density (#/ha) and biomass (kg/ha) were derived from annual bottom trawl surveys conducted by the USGS since 1978. Details of the survey design can be found in Bronte et al. (1991). We considered only stations that were conducted in WI-2 for our analyses owing to sometimes large interannual variation in CPUE between different regions of the lake. Diet of lake trout is dominated by rainbow smelt *Osmerus mordax*, lake herring *Coregonus artedii* and chubs *C. hoyi* and *C. kiyi* (Dryer et al. 1965; Negus 1995). We therefore, included only these species in our analyses. We also used available prey length data collected during the trawl processing to estimate the density and biomass of prey available to lake trout assuming optimal sized prey were 25% of the lake trout length, the preference decreasing to zero at 10 and 50% (Power 1987).

Sea lamprey population estimates were available from 1957 to 1999 (Gavin Christie, GLFC, unpubl. data). The number of spawning phase lamprey was estimated from a regression relationship between river run size (from mark-recapture), larval abundance and river discharge for all US waters of Lake Superior. We approximated the size of the parasitic phase lamprey population by lagging the data back one year. Sea lamprey scarring rates (number of type A and B marks per 100 fish; King and Edsall 1979) were utilised for two size groups of lake trout approximating age 5 and age 9 lake trout (M. Ebener, COTFMA, unpubl. data).

Insufficient water temperature data were available to describe the thermal habitat for lake trout in Lake Superior. General trends in thermal indices derived for air temperature are often highly correlated with water temperatures (McCombie 1959; Shuter et al. 1983). We therefore used daily air temperatures recorded at the Madeline Island weather station (National Climate Data Center of NOAA) to estimate three thermal

indices: degree days  $<0^{\circ}\text{C}$  (assumed to be sub-optimal for lake trout growth), degree days  $>5^{\circ}\text{C}$  but  $<15^{\circ}\text{C}$  (assumed optimal lake trout growing conditions based on a thermal preference of  $10^{\circ}\text{C}$  (Wismer and Christie 1987), and degree days  $>20^{\circ}\text{C}$  (assumed to be too warm for lake trout growth). In cases where temperature data were not continuous (Lapse of 1 day to several weeks), missing values were estimated by linear interpolation. Insufficient temperature data were available in 1973, 1982 and 1983 to generate the needed thermal indices.

Data were analysed in S-Plus and Systat. Where necessary, data were appropriately transformed to normalise variance prior to analyses. General trends in size and growth parameters, and constraints were evaluated using general linear model procedures. Contrasts between ages and stocks were tested with paired t-tests, and/or analyses of covariance. Multivariate models were generated using stepwise linear regression, with lags of 1,2, 3, 5, and 10-years included in the cohort analyses to account for the pooling of age data across years (within a cohort). Statistical significance was evaluated at  $p<0.05$ .

## Results

Length- and weight-at-age declined significantly over time for most ages of lake trout, from both wild and hatchery stocks (Figure 1). Declines were most notable after the early 1980s, with little to no significant change during earlier years. Hatchery fish were larger than wild fish at younger ages ( $t=5.75$ ,  $p<0.01$ ,  $n=24$ ), while wild fish were larger at older ages ( $t=4.24$ ,  $p<0.01$ ,  $n=23$ ) (Figure 1). There were no significant

differences in length- or weight-at-age between males and females for the years where data were available.

Instantaneous growth coefficients (Table 1) varied without trend for both wild and hatchery fish. Growth coefficients tended to be higher for wild than hatchery fish when considering either length (1975-1998) or weight (1983-1998), although differences were only significant in 3 of the 10 possible contrasts (age 6 by weight  $t=3.04$ ,  $p=0.013$ ,  $df=10$ ; age 5 by length  $t=2.88$ ,  $p=0.012$ ,  $df=14$ ; age 7 by length  $t=2.69$ ,  $p=0.015$ ,  $df=18$ ).

Limited data prevented many comparisons in the 1970s and early 1980s but overall growth was poor in 1983, 1986, and 1997 and good in 1985, 1988, 1990, 1993 irrespective of stock or size metric (weight or length). Length based G estimates were lower in 1989 and 1993 than weight based estimates for the same years.

vonBertalanffy growth models were fit to hatchery (1961-1988) and wild (1965-1989) cohorts. Wild lake trout attained a larger asymptotic length but had a lower growth coefficient than hatchery lake trout. While asymptotic length ( $L_{\infty}$ ) declined linearly across all cohorts for both stocks (Figure 2), K tended to remain relatively constant until mid-1970s cohorts before increasing for both stocks (Figure 3). Analyses of covariance suggested significant stock effects for  $L_{\infty}$  ( $F=10.93$ ,  $p<0.002$ ). Lack of homogeneity of slopes prevented comparison of K between stocks ( $F=9.22$ ,  $p<0.005$ ).

### Constraints

CPUE for hatchery lake trout increased from 1959 until 1970 before declining to relatively stable levels in the mid 1990s (Figure 4a). Wild CPUE had increased from very low levels in the 1960s to approximately 20 fish per 1000 m by 1990 and remained relatively constant since (Figure 4a). Hatchery CPUE was correlated with numbers of

lake trout stocked until the mid 1970s, but the correlation is much weaker during the past 25 years as wild fish contributed much more to the overall lake trout CPUE. Chinook and coho salmon stocking (Figure 4b) increased steadily from the initiation of the program in 1966 to nearly 2 million fish annually in 1991. During the 1990s stocking rates have been steadily reduced to approximately 1 million salmon per year.

Density of rainbow smelt, lake herring and chub varied over nearly 4 orders of magnitude between 1978 and 1999 with no obvious temporal pattern (Figure 5a). Individual species biomass ranged from 0.05 to 44 kg/ha, again with no obvious trend through time (Figure 5b). Our index of preferred prey biomass was slightly less variable, although it too ranged from 0.23 to 33 kg/ha without trend.

Estimated population size of parasitic phase sea lamprey in the US waters of Lake Superior varied between 621,096 in 1959 to 4,153 in 1993, although most estimates lie between 10,000 and 50,000 since 1960 and have shown a gradual decrease (Figure 6a). Scarring rates of lake trout has varied without trend since 1959, averaging near 1.7 / 100 fish for 432-508 mm (age 5) lake trout and 8.2 / 100 fish for 631-711 mm (age 9) lake trout (Fig 6b).

The degree day (temperature) indices have also been extremely variable during the past 40 years (Figure 7). The growing degree day index ( $5^{\circ}\text{C} < \text{DD} < 15^{\circ}\text{C}$ ) has ranged from 787 to 1331, showing a gradual decrease over the period from 1959-1999. Our two no growth indices ( $\text{DD} < 0^{\circ}\text{C}$  and  $\text{DD} > 20^{\circ}\text{C}$ ) have varied without trend, although the variability in both has increased in the past 15 years.

## Identifying Constraints to Growth of Lake Trout

Interannual variation in growth was assessed using the instantaneous growth coefficients (G) estimated for each progressive age from 5 to 9 for both wild and hatchery lake trout. Two parameters, lamprey abundance and hatchery CPUE were both significantly positively correlated with lake trout growth parameters, however, these correlations were deemed spurious as no mechanism could be ascertained to explain the positive relationship. We were unable to identify any other single (Pearson correlation coefficients) or multiple set of constraints (stepwise linear regression) that explained any significant amount of variation in interannual growth of lake trout.

We also examined years of strong contrast – good growth years (1985, 88, 90, 93) and poor growth years (1983, 86, 97) to see if general patterns could be identified. Once again, no obvious pattern was evident (Table 2). Prey abundance and biomass tended to be higher in good growth years and lower in poor growth years with the exception of 1986 (above average prey but very poor growth). CPUE and stocking rates ranged widely in both good and poor growth years suggesting little evidence of density dependent growth. Lamprey abundance and scarring rates were also variable within the two growth groups, and actually tended to be higher during good growth years. The absence of suitable temperature data in 1983 (a poor growth year) reduced the power for comparison of thermal indices, but again no pattern was evident between contrasting groups of growth.

Intrinsic changes in growth within cohorts of lake trout were assessed using the vonBertalanffy growth coefficients. We broke the analyses into two blocks to account for the fact that prey data were only available for cohorts post 1978. With no prey terms

in the model, we were able to explain 86 to 92% of the variation in L-infinity for both hatchery and wild fish with a combination of CPUE, stocking and thermal indices (Table 3). Adding prey terms substantially reduced the number of observations (from 24 to 11 for wild fish, and 23 to 10 for hatchery fish). In these cases, L-infinity for both stocks was explained by thermal indices (+) and smelt abundance (-) (Table 3). Using these factors to extrapolate growth forward, we would expect L-infinity to increase for the next few cohorts.

Variation in K, the growth coefficient, was explained by a wider range of parameters than L-infinity (Table 4) and generally had poorer fit for both hatchery and wild lake trout. Inclusion of prey parameters once again reduced the number of observations and actually weakened the overall regression. Smelt abundance was once again the only prey term to enter the model.

## Discussion

Overall we were able to explain very little variation in growth of hatchery and wild lake trout in Lake Superior. Size-at-age and L-infinity (more appropriately  $L_{10}$ ) declined significantly over the past 40 years. The growth coefficient K increased, as fish reached the asymptotic size more quickly. Instantaneous growth coefficients were more variable between years, although general patterns of better and poorer growth was evident across ages, within a year.

Irrespective of which growth metric was used, few of our hypotheses regarding constraints to growth were supported by the available data. Eby et al. (1995) found no relationship between lake trout growth rate and prey biomass (kg/ha) in Lakes Superior,

Michigan or Ontario. Growth rates were lowest in Lake Superior where prey biomass was lowest, but Eby et al. (1995) demonstrated that differences in prey taxa consumed (smelt vs alewife) explained this inter-lake difference, to the extent that consumption rates (g prey/ g lake trout / day) were invariant across a 100-fold difference in prey density across the three lakes. Using the general algorithms presented in Mason et al (1998) that linked a bioenergetic and foraging model, we estimated the prey biomass (kg/ha) needed to support lake trout growth in Lake Superior (Figure 8). These results suggest that required prey biomass would lie between 0.83 and 2.35 kg/ha for a 700mm lake trout (average  $L_{10}$  observed in our analyses). In only 2 years between 1978 and 1999 (1980 and 1996) was prey biomass lower than this, while 12 of 22 years had prey biomass well in excess of that needed for maximum growth. Our analyses do not account for spatial and temporal scales upon which the predator-prey interactions operate, but they do support Eby et al.'s (1995) conclusion that prey biomass may not be constraining growth rate potential of lake trout in Lake Superior and elsewhere in the Great Lakes system.

Ferreri and Taylor (1996) provided evidence of growth compensation for lake trout from the Michigan waters of Lake Superior which they classified as a density-dependent response related to prey density. Ferreri and Taylor did not present any data on prey, and as stated above we found no evidence to support this hypothesis. This apparent absence of prey resource limitation, also explained why we saw no relationship between lake trout growth rates and abundance of lake trout (CPUE or stocking rates) or other salmonids (chinook and coho salmon stocking rates).

Changes in the composition of the prey base may explain some of the changes in lake trout growth (Eby et al. 1995, Mason et al. 1998). The diet of lake trout has shifted from lake herring and chubs to smelt (Dryer et al 1965, Conner et al 1993) during the period of observation of this study, and differences in energetic quality, predator avoidance and escapement, spatial distribution, etc. could all affect the quality of the prey base. We attempted to address this question by considering the three dominant prey fishes both individually and in combination, as well as considering only prey that corresponded to the theoretical optimum size (10 to 50% of lake trout total length, with a maximum at 25%, Power 1987). Again, we were unable to find a significant relationship between any of these metrics of the prey fish community and lake trout growth.

We had also expected to find a negative relationship between lamprey abundance and lake trout growth, hypothesizing that energy lost to the attack by the parasitic lamprey would reduce the scope for growth for the lake trout. While scarring rates on lake trout were highly correlated with sea lamprey abundance, they too failed to be strongly correlated with lake trout growth. We did find a weak positive relationship between lamprey abundance (and scarring rates) and lake trout growth which Ferreri and Taylor (1996) and Pycha and King (1975) and others speculated would result from the density dependent response to lower lake trout survival, and therefore greater prey resources for growth. As stated above, we found no evidence to support a density dependent growth or resource limitation for lake trout.

Our final hypothesis was related to basic thermodynamics – interannual variation in temperature would provide a range of growth responses. Again, we found no strong support for the role of temperature in influencing lake trout growth in Lake Superior.

This absence of a relationship could be related to the extremely large thermal volume of Lake Superior and its persistent cold temperatures. Ebener (1995) used the computer animation and database developed by the Great Lakes Environmental Research Laboratory (Schneider et al. 1993; Assel et al. 1994) to predict long-term water temperatures for Lake Superior. These results suggest that the long-term average surface temperature does not exceed 15 C, and that optimal growth temperatures for lake trout (10 C, Wismer and Christie 1987) is only available in the upper 20m of the water column for approximately 2 months each year. With over 94% of the lake volume >20m, interannual changes in thermal conditions will not significantly alter the thermal habitat available to lake trout. The absence of long-term thermal profiles necessitated our use of air temperatures to generate the thermal indices, and may have also contributed to our inability to detect a relationship, although McCombie (1959) and Shuter et al. (1983) have found strong correlations between the patterns of air and surface water temperatures.

An additional limitation of our analyses can be attributed to the aging techniques employed. Scales are not suitable structures for aging lake trout, especially older individuals, because of the slow growth and unclear annuli which make aging very imprecise. Assignment of incorrect ages could have masked any pattern in growth. The coefficient of variation in length-at-age did decrease with time for some ages, but was less variable (10-20%) than we had expected. The earliest sample years were associated with the most precise ages, as all these fish were marked hatchery origin fish. However, few of these years and cohorts could be included in the analyses as only a few cohorts persisted across the sample years to generate the needed growth metrics.

Small sample sizes may have also contributed to imprecision in assignment of true size-at-age. We attempted to minimise this effect by using only ages where at least 5 individuals had been sampled, and weighting all models and regressions by the sample size. We also did not attempt to discriminate between males and females, in part because this information was not always recorded, but also because that would have further reduced our sample size. Where gender information was available, size-at-age were not significantly different. Our decision to use only fish age 10 or less likely buffered us from detecting the expected differential growth rates between males and females.

While marked fish would provide the most precise ages for analyses such as this, it is obviously impossible to mark sufficient numbers of wild fish with hopes of recapturing them in a large system like Lake Superior. Otoliths (used on larger fish since 1986) are a more precise alternative to scales, although they too become less precise with very old fish. However, the extensive otolith archive which was the basis for the recent data used in these analyses could be used to generate growth chronologies for individual fish. These back-calculated size-at-ages would be devoid of any inter-individual variability, and therefore provide more precise estimators of growth upon which to evaluate the constraints.

While the growth chronologies would improve our estimates of size-at-age and growth, we will continue to be challenged in identifying constraints to growth on long-lived species like lake trout because of the relatively short time period that the species, and the constraints have been sampled. While some time-series like stocking rates, CPUE and lamprey have been sampled for nearly 50 years, the prey parameters have been sampled for only 21 (still an impressive time series). However, a cohort based

growth analyses quickly reduces the time series, by whatever the maximum age is that is used in the growth calculation (i.e. we truncated our analysis at age 10, which meant the 10 most recent years of size-at-age data could not be used because not all ages were yet recruited to describe these cohorts).

Describing and understanding changes in growth can have important implications to the management of the species. More rapidly growing fish reach sexual maturity sooner, and larger fish for a given age have higher fecundity and therefore potential to produce new recruits. More rapid growth will affect size selective interactions such as vulnerability to predators (including a fishery), and sea lamprey parasitism. Fish that are larger for a given age will consume more prey than smaller individuals and also consume different prey taxa and sizes (Mason et al. 1998). Analyses such as this one will continue to add to our understanding of the complex interactions that ultimately govern the productive capacity of the Great Lakes ecosystem.

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**Table 1a.- Length-based instantaneous growth coefficients for wild and hatchery lake trout between 1959 and 1998 in Lake Superior management unit WI-2.**

Year	Hatchery					Wild				
	age 5	age 6	age 7	age 8	age 9	age 5	age 6	age 7	age 8	age 9
1959	0.08									
1960		0.02								
1961			0.13							
1962				0.05						
1963	0.09									
1964	0.06	0.06								
1965	0.07	0.07	0.07							
1966	0.10	0.07	0.04	0.06						
1967	0.05	0.08	0.05	0.07	0.01					
1968										
1969										
1970										
1971	0.43				-0.02	0.07				
1972										
1973										
1974										
1975	0.07	0.06	0.07	0.08	0.05	0.09	0.17	0.08	0.08	0.11
1976	0.06	0.04	0.04	0.10	0.17	0.14	0.17	0.09	0.15	0.10
1977	0.04	0.02	0.06	0.13	0.04	0.12	0.01	0.01	0.08	0.04
1978	0.05	0.03	0.08	0.09	0.05	0.15	0.08	0.16	0.15	0.05
1979	0.07	0.04	0.10	0.08	0.05	0.05	-0.02	0.16	0.13	0.03
1980	0.02	0.03	0.04	0.06	0.08	0.08	0.13	0.08	-0.01	-0.07
1981						0.12	0.06	0.00	0.03	0.01
1982						0.07	0.06	0.09	0.10	0.13
1983	0.08	0.06	0.03	0.03	0.00	0.04	0.03	0.04	0.07	0.06
1984	0.05	0.05	0.07	0.09	0.04	0.09	0.09	0.09	0.09	0.04
1985	0.06	0.08	0.06	0.04	0.01	0.09	0.14	0.11	0.08	0.12
1986	0.04	0.06	0.03	0.01	0.04	0.04	0.03	-0.01	-0.03	-0.03
1987	0.05	0.05	0.04	0.04	0.08	0.06	0.08	0.11	0.11	0.08
1988	0.11	0.07	0.08	0.06	0.06	0.12	0.09	0.08	0.05	0.02
1989	0.04	-0.01	0.04	0.06	0.02	-0.02	-0.01	0.02	0.05	0.05
1990	0.11	0.09	0.01	0.10	0.04	0.14	0.12	0.15	0.11	0.06
1991	0.11	0.05	0.04	0.13	-0.01	0.22	0.10	0.07	0.03	0.03
1992	0.07	0.06	0.05	0.04	0.12	0.08	0.03	0.10	0.07	0.05
1993	0.07	0.03	0.06	0.06	-0.01	0.13	0.10	0.07	0.01	0.04
1994	0.16	0.09	0.09	0.04	0.05	0.32	0.11	0.06	0.06	0.03
1995										
1996										
1997	0.07	0.06	0.00		0.04	0.19	0.08	0.03	0.02	0.05
1998	0.08	0.02	-0.01	0.10		0.22	0.10	0.06	0.08	0.06
Mean	0.08	0.05	0.05	0.07	0.04	0.11	0.08	0.08	0.07	0.05
Std. Dev.	0.07	0.02	0.03	0.03	0.04	0.07	0.05	0.05	0.05	0.05

**Table 1b.- Weight-based instantaneous growth coefficients for wild and hatchery lake trout between 1983 and 1998 in Lake Superior management unit WI-2.**

Year	Hatchery					Wild				
	age 5	age 6	age 7	age 8	age 9	age 5	age 6	age 7	age 8	age 9
1983		0.12	-0.08	-0.06	0.24		0.44	0.40		0.29
1984	-0.01	0.09	0.13	0.27	0.07	0.31	0.22	0.17	0.14	0.19
1985	0.27	0.35	0.23	0.07	-0.05	0.34	0.44	0.27	0.16	0.04
1986	0.16	0.13	0.08	-0.03	0.14	0.16	0.08	0.03	-0.01	-0.05
1987	0.17	0.09	0.16	0.11	0.12	0.22	0.25	0.35	0.30	0.26
1988	0.35	0.19	0.28	0.13	0.23	0.25	0.28	0.19	0.12	0.00
1989	0.22	-0.01	0.11	0.21	0.09			0.12	0.14	0.23
1990	0.35	-0.07		0.25	-0.10				0.18	0.07
1991	0.63	0.11	0.26		-0.19		0.42	0.07	-0.01	0.12
1992	0.29		0.20	0.07	0.32	0.72		0.09	0.04	0.11
1993	0.39	0.22	0.65	0.33	0.08	0.76	0.42	0.34	0.13	0.18
1994	0.11	0.19	0.06	-0.05	-0.02		0.24	0.14	0.17	-0.01
1995										
1996										
1997	-0.08	0.00	-0.18		-0.17	0.47	0.17	-0.09	-0.05	0.07
1998	0.27	0.29	0.06	0.29		0.63	0.17	0.11	0.26	0.19
Mean	0.24	0.13	0.15	0.13	0.06	0.43	0.28	0.17	0.12	0.12
Std. Dev.	0.18	0.12	0.20	0.14	0.16	0.23	0.13	0.14	0.10	0.11

Table 2.- Means and standard deviations of constraints to growth of lake trout in Lake Superior management unit WI-2, and values for good (mean+1 SD) and poor (mean-1 SD) years of growth.

	time series		poor growth			good growth			
	mean	stdev	1983	1986	1997	1985	1988	1990	1993
wild lake trout CPUE	12.19	6.69	5.26	19.91	21.52	8.49	13.13	18.31	19.01
hatchery lake trout CPUE*	2.75	0.73	2.44	3	1.8	2.68	2.42	2.44	1.81
total lake trout CPUE	32.28	14.96	16.76	40.02	27.59	23.14	24.43	29.81	25.09
lake trout stocked	2356.41	696.99	2966.09	3371.73	1222.68	3930.64	2640.41	2612.72	1883.13
salmon stocked	964.76	561.11	1178	1597.54	1262.94	1028.08	1715.07	2062.7	1395.9
all salmonids stocked	3321.18	982.3	4144.09	4969.26	2485.61	4958.72	4355.48	4675.42	3279.04
lamprey abundance	25815.48	15138.35	10749.04	12742.44	9981.08	27417.68	22998.12	6550.72	4153.44
lamprey scar 1*	0.12	0.63	-0.36	0.18	-1.2	1.41	0.1	0.64	0
lamprey scar 3	6.28	3.64	1.7	6.2	4.8	4.2	12.9	10.1	5.8
degree days<0 C	963.66	213.36	.	-826.29	-928.61	-1250.48	-1047.71	-692.1	-943.61
5<degree days<15	1073.42	139.57	.	1063.35	933.33	1251.53	843.61	1001.9	960.56
degree days>20C	525.19	285.33	.	523.33	634.72	147.78	1159.44	649.17	505.56
number of days<0 C	123	13.97	.	128	137	139	122	111	120
5<number of days<15	105.89	13.01	.	105	92	115	76	104	98
number of days>20C	23.83	12.62	.	24	29	7	49	30	23
herring density*	2.41	2.43	0.06	6.12	1.91	6.08	0.95	6.46	3
smelt density*	5.15	0.64	4.47	5.57	5.27	5.46	5.7	5.7	5.79
chub density*	1.66	1.01	1.58	3.13	0.69	3.56	0.3	1.39	0.42
all prey density*	5.45	0.8	4.53	6.6	5.32	6.56	5.71	6.85	5.86
herring biomass**	1.93	1.25	-0.57	3.78	2.87	3.73	2.84	3.31	2.03
smelt biomass*	0.12	0.87	0.03	1.85	-0.74	0.37	0.8	0.48	-0.38
chub biomass*	1.03	0.98	0.2	1.07	1.91	0.15	2.16	0.04	1.38
all prey biomass**	2.62	0.88	1.04	3.98	3.21	3.79	3.33	3.4	2.51

\* log transformed values

\*\* log (x+1) transformed values

**Table 3.- Results of the multiple regression of constraints to asymptotic size (L10) for wild and hatchery lake trout in Lake Superior management unit WI-2, for the 1959-1999 cohorts.**

Wild lake trout, no prey terms in model (N=24, R<sup>2</sup>=0.86, F=30.36, P=0.00)

Regression variable	Coefficient	Standard Error	Standardized coefficient	t	P
intercept	533.67	106.18	0.00	5.03	0.00
DD<5 <sub>lag3</sub>	0.32	0.09	0.49	3.57	0.00
wild CPUE <sub>lag10</sub>	-45.52	6.78	-2.86	-6.71	0.00
hatchery CPUE <sub>lag3</sub>	1.53	0.48	0.34	3.21	0.00
salmon stocked <sub>lag5</sub>	0.39	0.07	2.59	5.26	0.00

Wild lake trout, prey terms included in model (N=11, R<sup>2</sup>=0.98, F=62.34, P=0.00)

Regression variable	Coefficient	Standard Error	Standardized coefficient	t	P
intercept	909.99	32.29	0.00	28.18	0.00
DD<0 <sub>lag3</sub>	0.06	0.03	0.16	1.91	0.11
DD>20 <sub>lag5</sub>	0.19	0.03	0.75	6.09	0.00
smelt density <sub>lag3</sub>	-0.14	0.07	-0.27	-1.88	0.11
smelt density <sub>lag5</sub>	-1.02	0.13	-1.30	-7.87	0.00

Hatchery lake trout, no prey terms in model (N=23, R<sup>2</sup>=0.92, F=72.49, P=0.00)

Regression variable	Coefficient	Standard Error	Standardized coefficient	t	P
intercept	693.30	23.33	0.00	29.72	0.00
wild CPUE <sub>lag10</sub>	-12.00	0.99	-0.86	-12.00	0.00
hatchery CPUE <sub>lag3</sub>	1.30	0.26	0.34	5.02	0.00
lake trout stocked <sub>lag3</sub>	0.05	0.01	0.39	5.63	0.00

Hatchery lake trout, prey terms included in model (N=10, R<sup>2</sup>=0.82, F=16.09, P<0.01)

Regression variable	Coefficient	Standard Error	Standardized coefficient	t	P
intercept	550.54	111.87	0.00	4.92	0.00
5<DD<15 <sub>lag3</sub>	0.15	0.09	0.40	1.67	0.14
smelt density <sub>lag3</sub>	-0.23	0.10	-0.57	-2.37	0.05

**Table 4- Results of the multiple regression of constraints on the growth coefficient (K) for wild and hatchery lake trout in Lake Superior management unit WI-2, for the 1959-1999 cohorts.**

Wild lake trout, no prey terms in model (N=24, R<sup>2</sup>=0.86, F=30.36, P=0.00)

Regression variable	Coefficient	Standard Error	Standardized coefficient	t	P
intercept	0.32	0.02	0.00	15.90	0.00
DD>20 <sub>lag3</sub>	-0.00014	0.00002	-0.96	-6.55	0.00
DD>20 <sub>lag5</sub>	-0.00009	0.00003	-0.47	-3.06	0.01
hatchery CPUE <sub>lag3</sub>	-0.00218	0.00033	-1.07	-6.64	0.00
salmon stocked <sub>lag5</sub>	0.00008	0.00003	1.22	2.69	0.02
salmon stocked <sub>lag10</sub>	-0.00017	0.00003	-2.19	-4.92	0.00
lamprey scar 1 <sub>lag5</sub>	0.03508	0.00788	0.70	4.45	0.00
lamprey scar 3 <sub>lag5</sub>	0.01881	0.00346	1.39	5.43	0.00

Wild lake trout, prey terms included in model (N=11, R<sup>2</sup>=0.99, F=68.93, P=0.00)

Regression variable	Coefficient	Standard Error	Standardized coefficient	t	P
intercept	-1.07164	0.28044	0.00	-3.82	0.01
DD<0 <sub>lag3</sub>	-0.00008	0.00002	-0.44	-5.09	0.00
5<DD<15 <sub>lag10</sub>	0.00089	0.00020	1.42	4.38	0.01
DD>20 <sub>lag5</sub>	-0.00017	0.00002	-1.32	-10.9	0.00
DD>20 <sub>lag10</sub>	0.00039	0.00011	1.09	3.42	0.02
smelt density <sub>lag5</sub>	0.00090	0.00006	2.22	14.91	0.00

Hatchery lake trout, no prey terms in model (N=23, R<sup>2</sup>=0.68, F=13.33, P=0.00)

Regression variable	Coefficient	Standard Error	Standardized coefficient	t	P
intercept	0.54144	0.10538	0.00	5.14	0.00
5<DD<15 <sub>lag5</sub>	0.00020	0.00013	0.34	1.51	0.15
5<DD<15 <sub>lag10</sub>	-0.00051	0.00013	-0.86	-3.87	0.00
wild CPUE <sub>lag3</sub>	0.00349	0.00136	0.38	2.56	0.02

Hatchery lake trout, prey terms included in model (N=10, R<sup>2</sup>=0.40, F=5.34, P<0.05)

Regression variable	Coefficient	Standard Error	Standardized coefficient	t	P
intercept	0.22111	0.02637	0.00	8.38	0.00
smelt density <sub>lag3</sub>	0.00027	0.00012	0.63	2.31	0.05

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Figure 7.- Thermal indices based on air temperatures recorded at Madeline Island between 1960 and 1999. A) Degree days less than  $0^{\circ}\text{C}$ , B) degree days  $> 5^{\circ}\text{C}$  but  $< 15^{\circ}\text{C}$ , and C) degree days  $> 20^{\circ}\text{C}$ .

Figure 8.- Predicted prey biomass ( $\text{kg}/ha$ ) needed to satisfy maintenance demand and maximum growth rate of lake trout in Lake Superior.

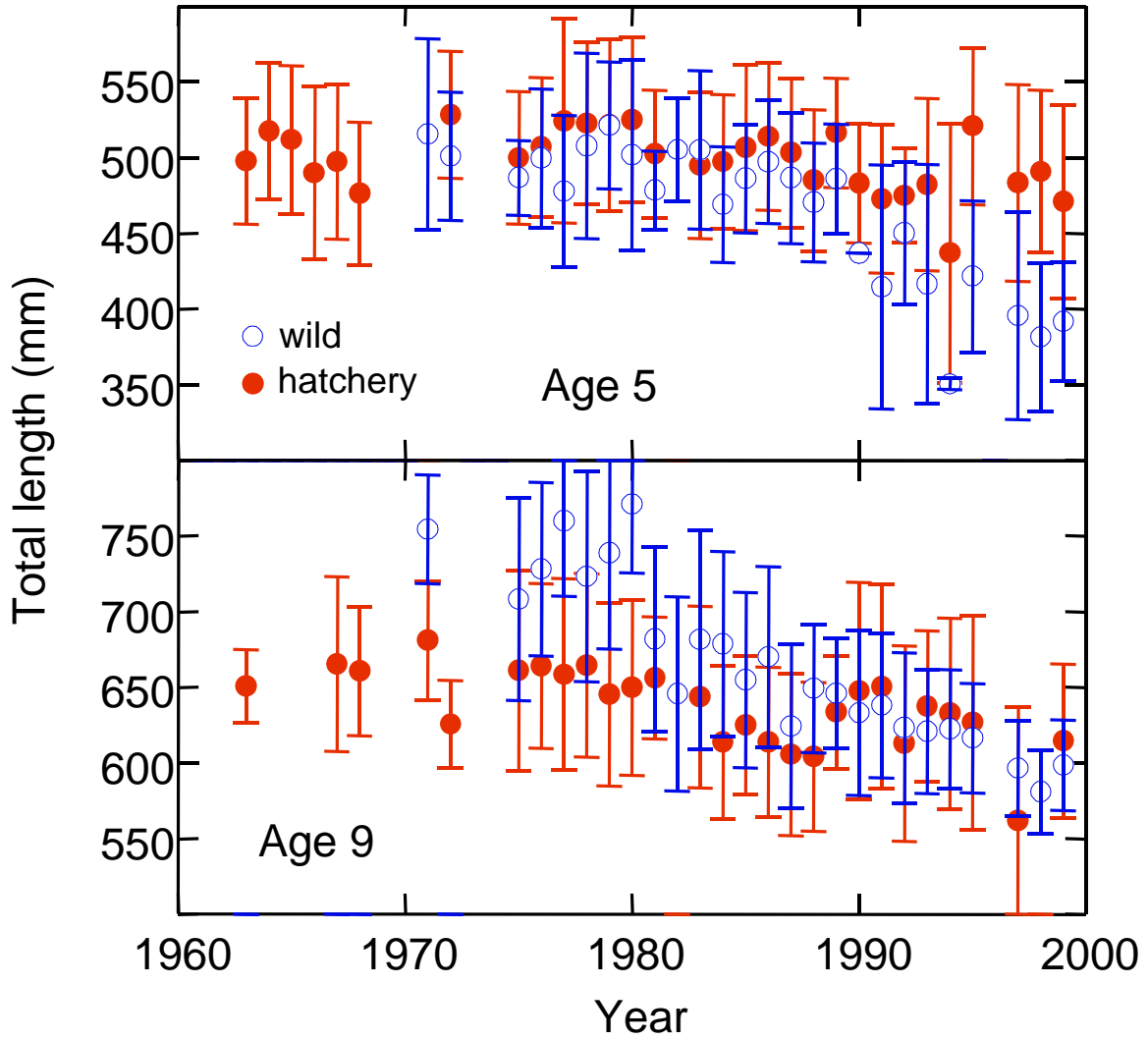


Figure 1  
Johnson et al.

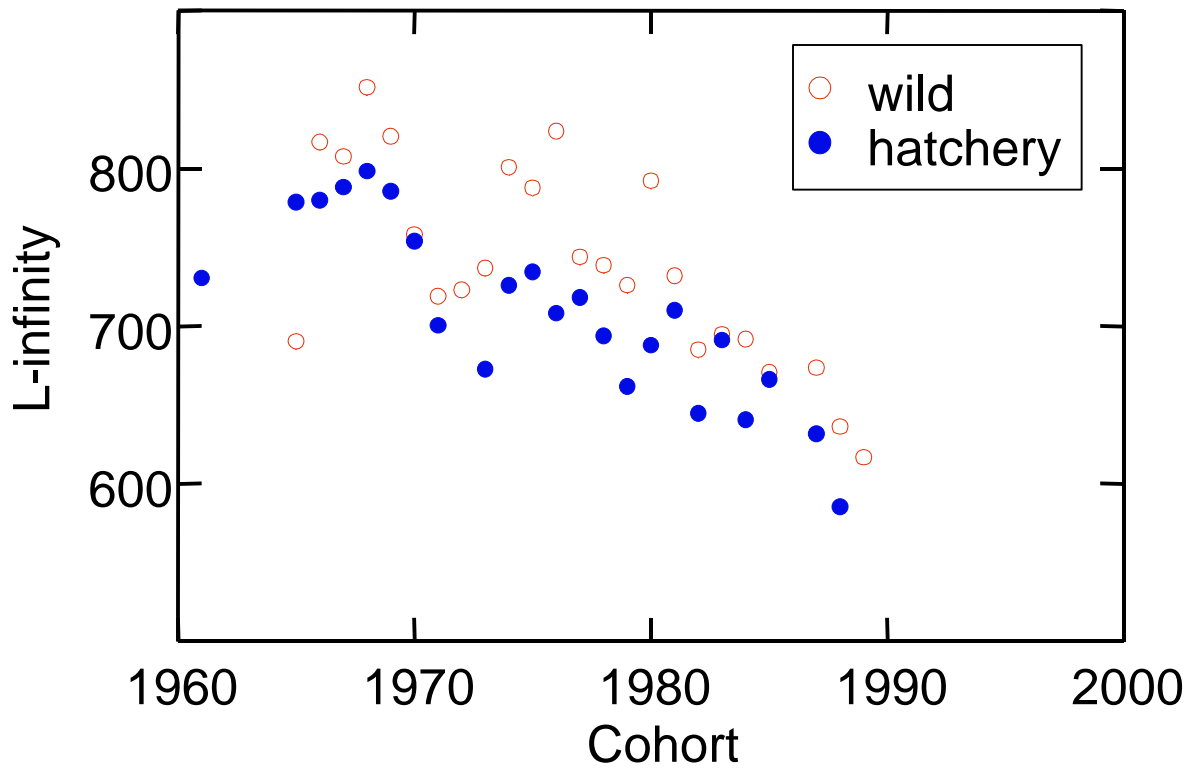


Figure 2  
Johnson et al.

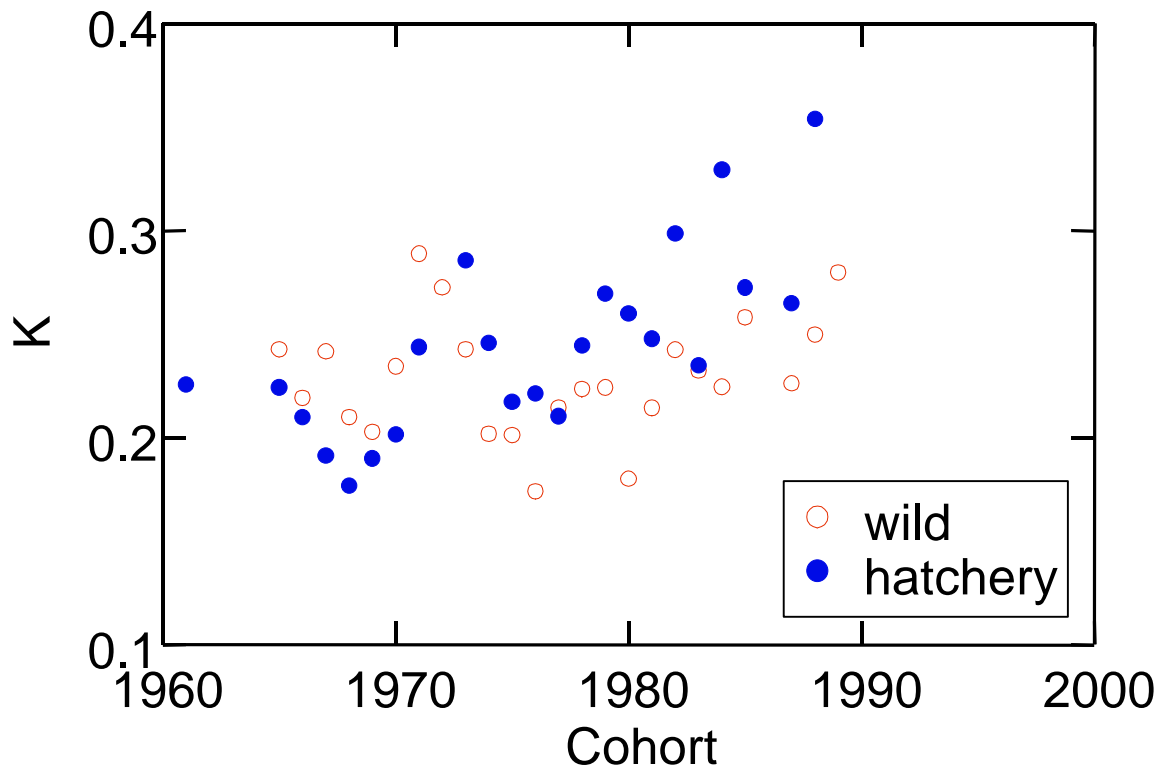


Figure 3  
Johnson et al.

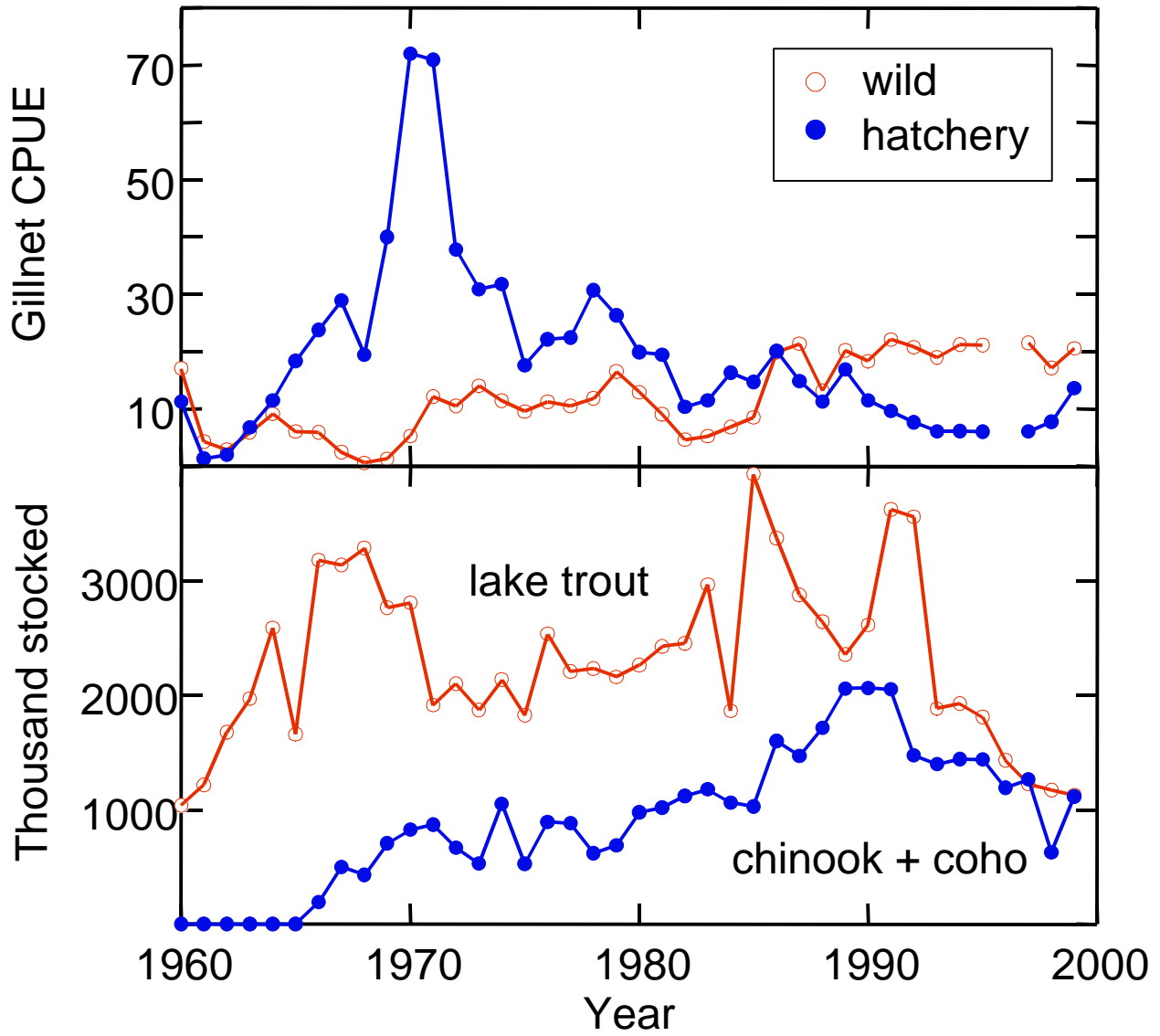


Figure 4  
Johnson et al.

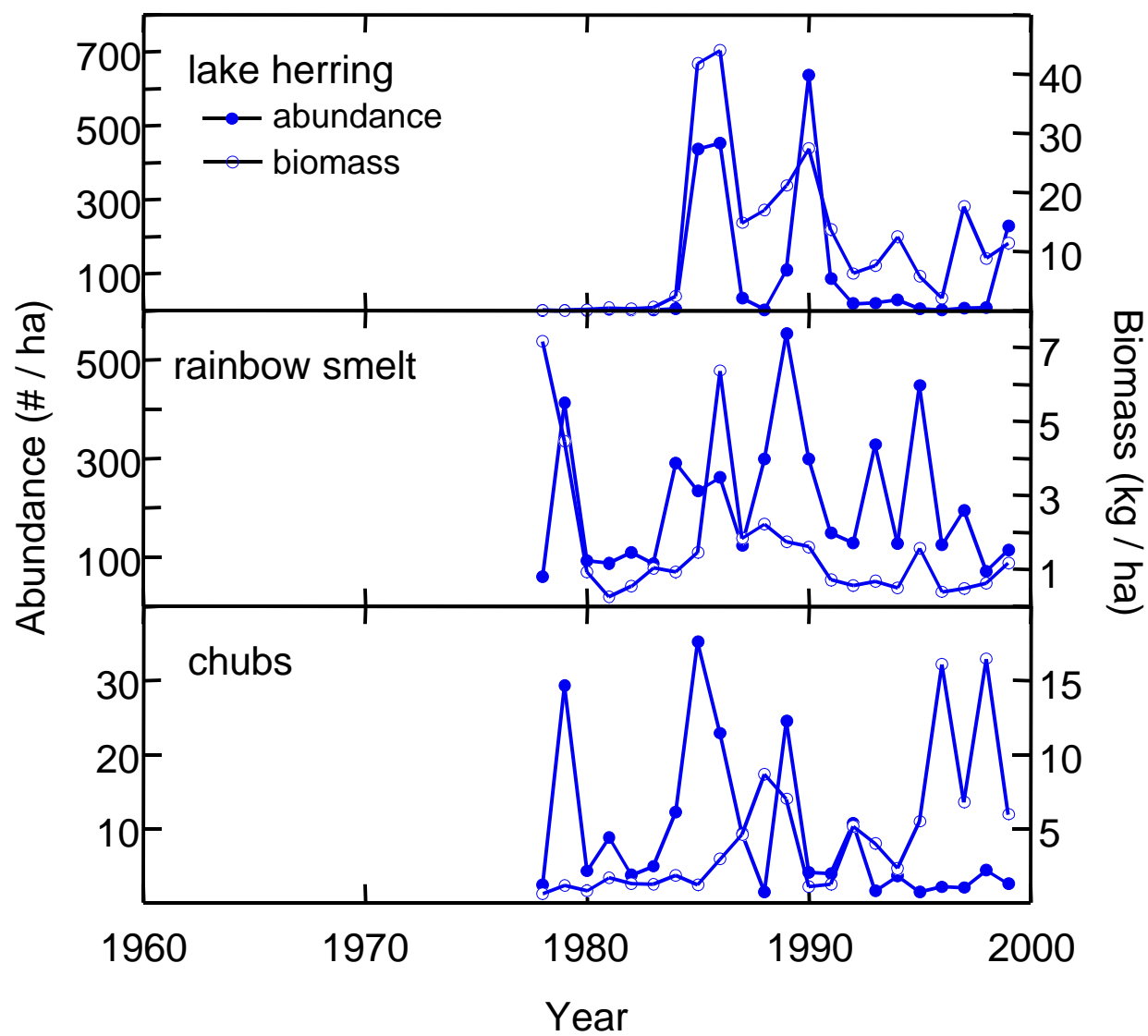


Figure 5  
Johnson et al.

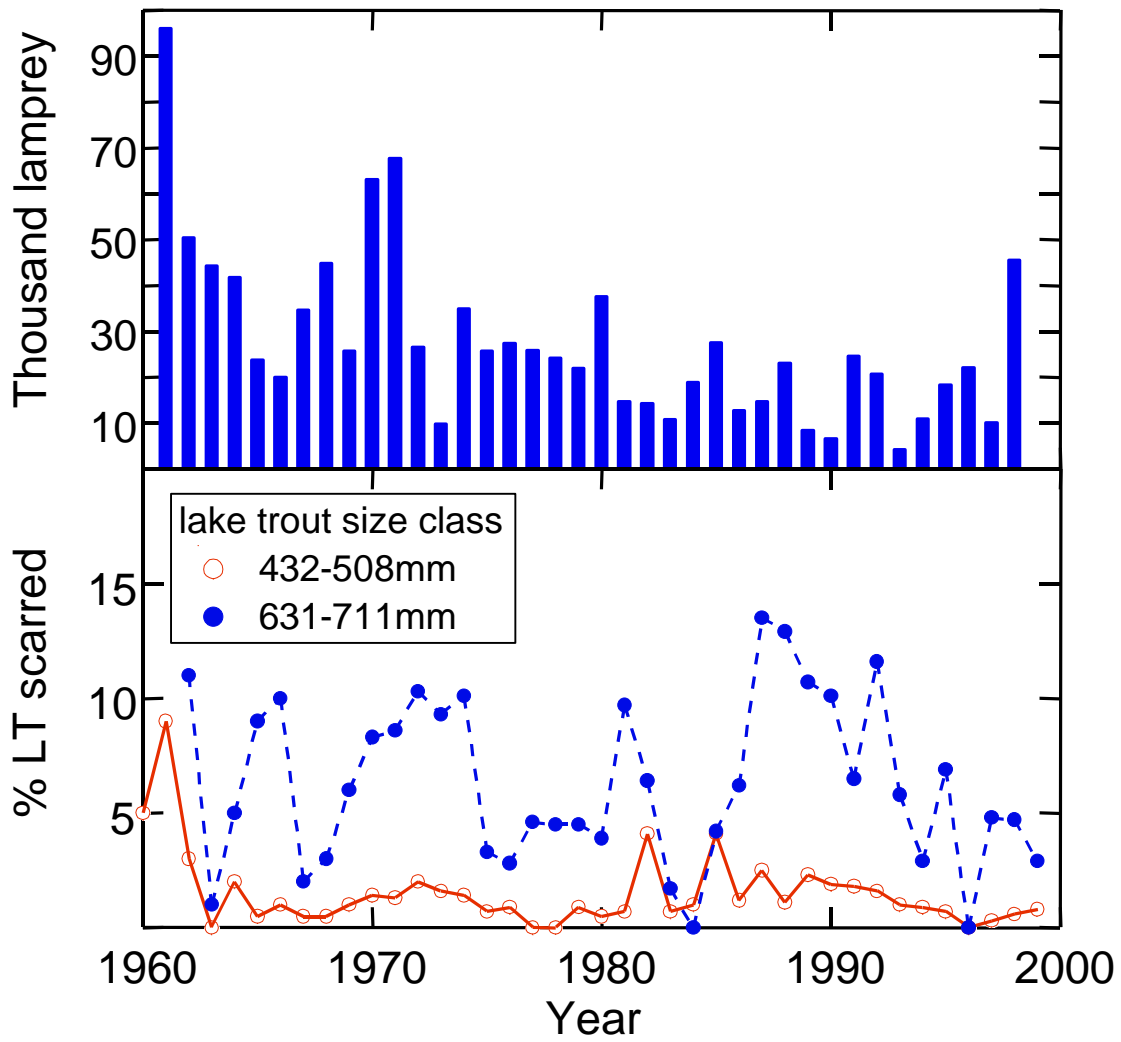


Figure 6  
Johnson et al.

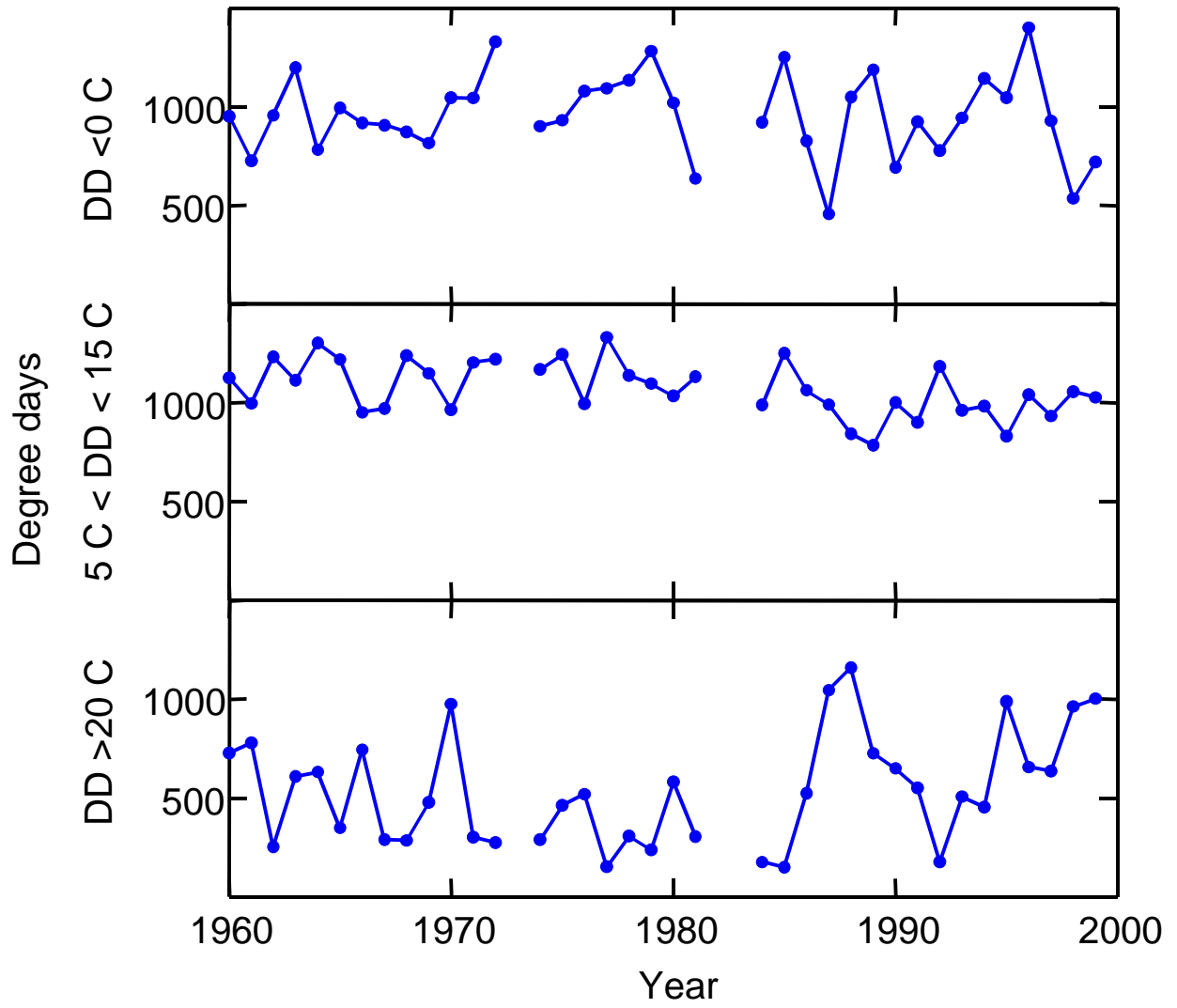


Figure7  
Johnson et al.

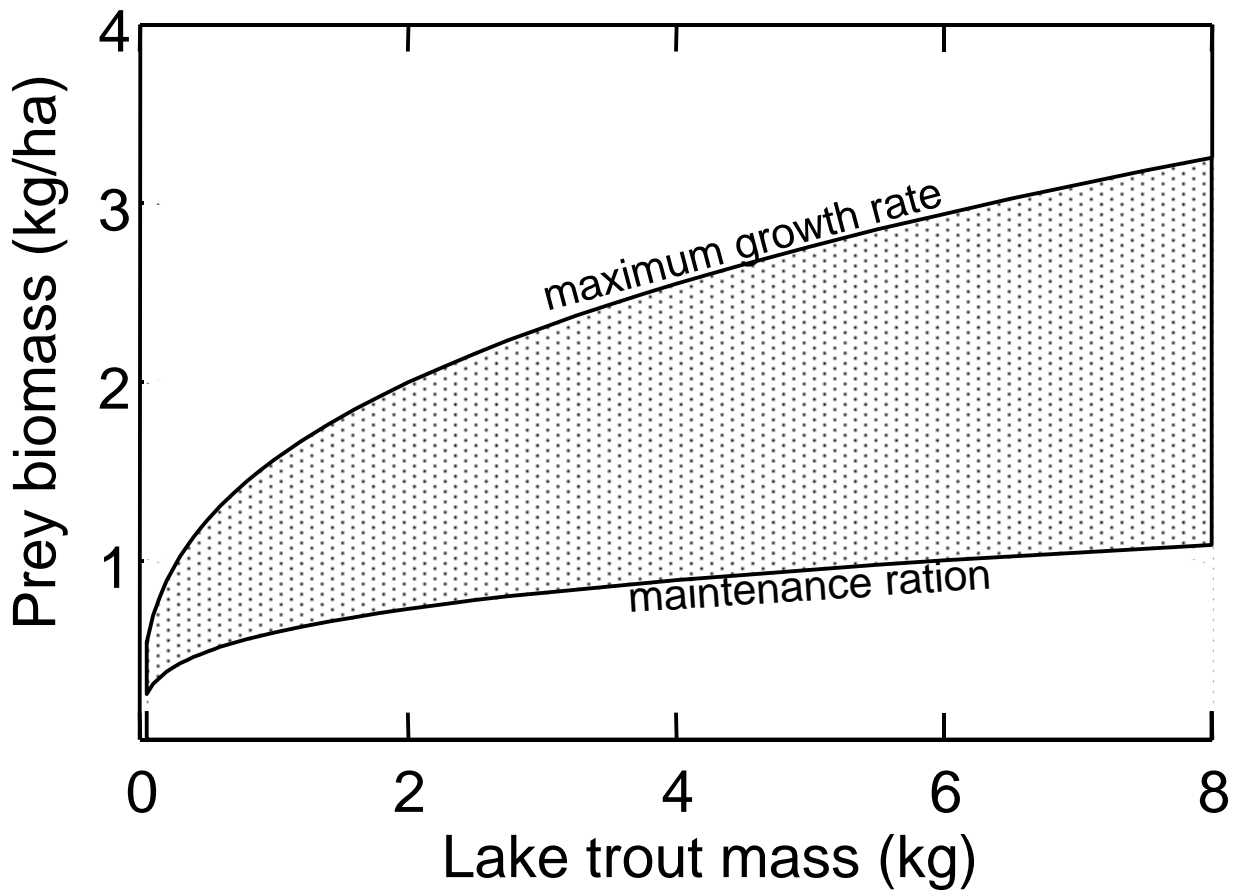


Figure 8  
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