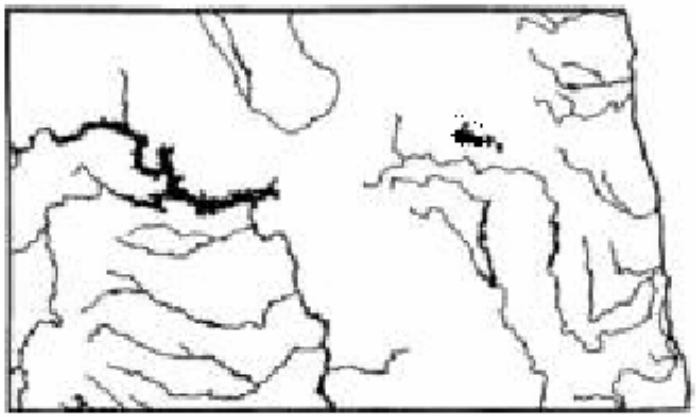

Technical Report No: ND07- 4

CLIMATE CHANGE AND EVOLUTION OF GROWTH IN NORTH AMERICAN HIODONTIDAE, ESOCIDAE, AND PERCIDAE

by

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Abstract

Relationships between temperature and von Bertalanffy growth characteristics (i.e., total length prior to sexual maturity, maximum total length, growth rate, and longevity) are examined for extinct and extant taxa of North American Hiodontidae, Esocidae, and Percidae. There are multiple relationships between growth characteristics and temperature of extant and extinct taxa with significant differences in size, growth rate, and life span of fossil hiodontids and esocoids. No comparisons of growth characteristics can be made between fossil percids and extant taxa from North America because of a short fossil record. Total length prior to sexual maturity was significantly and positively correlated with MAT for all taxa examined. There were multiple negatively correlated relationships between maximum total length (MTL) and MAT for all taxa examined. Growth rate was most often positively correlated with MAT in extant hiodontids and esocids. For the extant percids, 66% of the relationships between growth rate and MAT were significant and positively correlated. Life span was significantly greater in colder climates for extant and extinct Hiodontidae and Esocidae, but only half of the relationships examined for the percids were significant. In general, the species of Percidae examined have fewer relationships between growth characteristics and temperature. The only taxon that shows opposite responses to temperature compared to other species examined is *Esox niger*. Cretaceous hiodontids and esocoids were significantly smaller than those of the Cenozoic, but for the esocoids size changed around two major climatic events, the Cretaceous-Cenozoic and Pliocene-Pleistocene boundaries. Growth rates in Cenozoic esocids were significantly slower than extant taxa following the Pliocene-Pleistocene boundary. Growth rates for Eocene hiodontids were significantly slower compared to those of extant *Hiodon*. Prior to the Pliocene-Pleistocene boundary, only esocids showed significantly longer life spans at similar temperatures. The

latitudinal distribution of Cenozoic hiodontids, esocids, and percids is correlated with temperature with the exception for the esocoids at the EETM when a new subgenus appeared. Unlike Miocene and Pliocene Eurasian percids, esocids and hiodontids dispersed northward during warm episodes and southward during cool episodes. Given the many significant relationships between temperature and growth characteristics, it is plausible that times of major climate change were especially significant in the evolution of the Hiodontidae and Esocidae.

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Introduction and Background

Temperature and growth of fish

While studies of fish growth are commonplace in extant fisheries (Ricker 1975), there has been almost no comparable research of growth in fossil fish (Thompson and McCune 1984). However, fossils can provide information about growth, mortality, and other life history characteristics that are studied in contemporary systems (e.g., Beverton and Holt 1957; Ryder 1965; Ricker 1975; Forney 1976; Tyler et al. 1989). Fish lineages that extend back to the Mesozoic are particularly important to study because they have evolved in a changing climate.

From many studies of contemporary fish stocks, it is known that aspects of growth are generally regulated by temperature (e.g., Taylor 1958; Beverton and Holt 1959; Pauly 1979, 1980; Beamesderfer and North 1995). Beverton and Holt (1959) examined fish populations for relationships between maximum length, growth rate, age of maturity, and mortality. They found that asymptotic size and growth rate are inversely correlated, and that both are affected by temperature. Beamesderfer and North (1995) and Holmes (1990) found significant correlations between fish age and mean annual temperature; they reported that fish mature at earlier ages as temperature increases. Pauly (1979, 1980) examined the interrelationships between natural mortality, growth parameters, and temperature, and found correlations between mortality and

higher temperatures. Pauly (1980) examined many fish populations from polar to tropical regions and from fresh to salt water. He derived a mathematical relationship linking mortality, growth, and temperature, which provides a highly reliable estimate of mortality rate given the knowledge of weight, length and growth rate for over 80 species of fish. The relationship he described is based on the combined data from a wide variety of taxa and differing ecosystems.

Fish growth rate varies depending on aquatic and ambient mean annual temperatures (King et al. 1999; Gillooly et al. 2002). McCombie (1959) and Livingstone and Lotter (1998) investigated the strong relationships between air temperature and surface water temperature. Temperature has a strong influence on metabolic rate (i.e., Q_{10} relationship) and growth of ectothermic taxa; a temperature increase of 10°C increases the metabolic rate two- to three-fold and reaction rates increase 100-200% across most taxa (Cossins and Bowler 1987). Metabolic rates are higher in warmer water; for example, feeding rates of *Esox lucius* are positively correlated to temperature (Salam and Davies 1994). Both Guyette and Rabeni (1995) and Lebreton and Beamish (2000) examined fish and adjacent riparian trees for correlations in growth. Both studies addressed the importance of allochthonous carbon in aquatic systems and recognized the importance of climate as a control on growth of fish and trees. It is important to note that many other factors can affect growth of fish to a greater degree than temperature, including, but not limited to, density dependence, productivity, prey availability, fish community, seasonality, oxygen concentrations, and hydrology (e.g., Svärdson and Molin 1973; Diana 1983; Weatherley 1990; Lott et al. 1996; Quist et al. 2003).

Numerous studies have considered and modeled the effects of climate change on fish, but none have empirically described the effects of climate change on a lineage of fishes in the fossil record from the Mesozoic and Cenozoic. Shuter and Post (1990) examined *Perca flavescens*

along with two other fish species to model a hypothetical response to climate change. They found that an increase of 4°C would increase the northern distributional limit of yellow perch, and depending on lake morphometry and productivity, would also greatly influence survival, relative year class strength, and system carrying capacity. Hill and Magnuson (1990) modeled expected changes in bioenergetics caused by a hypothetical climate change in the Great Lakes region and found that yearling growth and prey consumption would be altered by climate warming, thereby greatly influencing food web dynamics. However, some longer-term studies also show significant population-level responses of fish to climate. Newbrey and Ashworth (2004) found that five populations of fish in a late Pleistocene lake fluctuated in abundance during approximately 1000 years, inferring a response to droughts during which nutrient levels were reduced and fish abundance declined. Furthermore, the fluctuations follow an overall trend of increased fish abundance during a time when lake-marginal vegetation changed from a spruce to a deciduous forest in response to climatic warming.

Potential links between evolution, growth, and temperature

Many factors may influence interactions between speciation, evolution in growth, and climate change including fish growth-related proteins, fecundity, year-class strength, and major climatic events. Growth is phenotypically plastic but genetically mediated within a growth envelope regulated by agents such as growth hormone, somatostatins (Ehrman et al. 2005), and heat-shock proteins (Morimoto et al. 1994). Somatostatins are growth-hormone inhibitors common to almost all vertebrate groups including fishes (Sheridan et al. 2000; Møller et al. 2003). Somatostatins are proteins that are expressed through a variety of alleles and even multiple genes (Sheridan et al. 2000). Since growth is mediated by heritable traits, natural

selection may also affect other growth-related, phenotypic characteristics such as maximum size, longevity, and growth rate.

Many aspects of fish biology are related to temperature; for example: spawning, migration, preferred water temperature, activity, optimal growth, upper and lower thermal limits, physiological maintenance, swimming speeds, and peak feeding (Scott and Crossman 1973; Becker 1983; Wismer and Cristie 1987; Jenkins and Burkhead 1994). Wismer and Cristie (1987) provided a review of the thermal characteristics of many species of fish including the Hiodontidae, Esocidae, and Percidae; they cited 52 studies with regard to the three families addressed here. Their report was not all inclusive and other reviews (e.g., Becker 1983) cite additional references.

Fecundity and offspring survivorship can be variable among adult females of different sizes and ages (Bohnsack 1990; Collins et al. 1998; Berkeley et al. 2004), but size and life span are generally correlated with temperature (Beverton and Holt 1959; Pauly 1980). Bohnsack (1990) reported that a single female of *Lutjanus campechanus*, 61 cm total length (TL), could produce as many eggs as 212 females that were 43 cm TL. Similarly, one female grouper, *Mycteroperca microlepis*, at age 8 produces as many eggs as 48 females at age 3 (Collins et al. 1998). Berkeley et al. (2004) found that eggs from older females of *Sebastes* produced larvae that grew faster and were more resistant to starvation than larvae from younger females; this was due to more maternal investment in their eggs. Pauly (1980) showed that maximum size is related to temperature and Beverton and Holt (1959) showed a positive relationship between life span and size.

Temperature has been shown to be correlated with relative year class strength. Svärdson and Molin (1973) found that first summer growth of *Sander lucioperca* increased during warmer

years and was important for survival during the first winter. Ultimately this was found to result in stronger year-class strength. They related first winter mortality to natural selection that shapes geographic distribution and abundance in different environments. In addition, Kipling and Frost (1970) found that dominant year classes of pike were correlated to first-year growth and number of degree days over 14°C.

There is some evidence to suggest that prominent climatic events in the geologic record (as shown by Zachos et al. 2001) are associated with speciation (Grande 1999). The first appearance of the genus *Esox* occurred after the Cretaceous-Cenozoic boundary when temperature dropped 10°C (Wilson 1980; Wilf et al. 2003). Also, the subgenus *Esox* (*Kenoza*) appeared in the fossil record at the time of the EETM (Grande 1999).

Growth model

The von Bertalanffy (1938) growth equation is typically used to describe fish growth. Inherent in the von Bertalanffy model are numerical parameters that describe the growth curve, including, maximum total length, growth rate, and longevity:

$$TL_t = L_\infty[1-e^{-K(t-t_0)}]$$

where the parameters: TL_t = total length, transverse radial distance, or centrum radial distance at t (age in years); L_∞ = theoretical maximum TL; K = the Brody growth coefficient; t = time (i.e., age in years); and t_0 = time at age zero (time at theoretical zero length). Maximum total length, size at an age prior to sexual maturity, growth rate, and longevity will be examined for relationships with temperature.

Reports of temperature in the published literature

Many studies in fish biology lack standardized data collection for describing the relationships between aspects of biology and temperature (Beitinger et al. 2000). Beitinger et al. (2000) defined standardized methods for examining the thermal lethal limits of fish (i.e., thermal maxima and minima). However, how thermal characteristics are reported in the published literature is highly variable (Becker 1983; Jenkins and Burkhead 1994). There are examples of single temperature values, ranges of values, and means being used. For example, Niemuth et al. (1959) found that *Sander vitreus* eggs hatch in 26 days at a water temperature of 4.4°C, in 21 days at temperatures from 10 – 12.8°C, and in 7 days at a mean temperature of 13.9°C. Spawning for *S. vitreus* occurs from 5.6 – 10°C (Niemuth et al. 1959) and for *E. lucius* starts at temperatures within the range of 4.4 – 11.1°C and peaks at a mean temperature of 9°C (Scott and Crossman 1973).

Mean annual temperature

I used mean annual temperature (MAT) to provide a standardized, independent variable from which to compare the various extant growth characteristics to those in the fossil record. Mean annual temperature provides the only consistent measure of temperature from the Cretaceous to the present. Paleotemperature estimations for specific fish localities are derived from methods using leaf margin analysis (e.g., Wilf et al. 2003) and oxygen isotopes (e.g., He et al. 2005).

The use of MAT has its limitations. A potential problem of using MAT is that it may not always adequately express the extreme threshold temperatures important in fish biology. For example, the experimentally-determined maximum thermal limits (i.e., CT_{maxima}°C) of Esocidae

is 36°C (Beitinger et al. 2000), however, the maximum MAT for the native range of *Esox lucius* is about 14°C (Lee et al. 1980). In addition, variability in temperature has been shown to be correlated with survivorship and relative year class strength. Hansen et al. (1998) and Beard et al. (2003) found that years with the highest recruitment of *S. vitreus* were not related to the mean spring time temperatures but rather to warm and stable water temperatures in May. Stability in May water temperatures was quantified by the coefficient of variation in spring temperatures.

Paleoclimate and global cooling since the Cretaceous

Since the Cretaceous there have been several major climatic events. A paleotemperature curve created by Zachos et al. (2001) indicates that temperatures were cold at the Cretaceous-Cenozoic (K-T) and the Pliocene-Pleistocene (Plio-Pleistocene) boundaries, and that the warmest temperatures of the Cenozoic occurred during the early Eocene (i.e., Early Eocene Thermal Maximum, EETM). Paleoclimatological research by Wilf et al. (2003) and Zachos et al. (2001) also suggests that there were marked temperature fluctuations around the K-T and Plio-Pleistocene boundaries. Wilf et al. (2003) report that changes in fossil plant assemblages in North Dakota occurred a million years before the K-T boundary, which suggests that a rapid drop of at least 10°C mean annual temperature (MAT) occurred. Zachos et al. (2001) reported marked variability in temperature at the Plio-Pleistocene boundary. These major climatic events may have also played a role in fish evolution.

Description of the Regional Water Problem

It is important to consider the implications of climatic change on surface water resources in light of potential consequences of global warming. Fossils can be used to examine the effects of climate change on fish because of the long-term nature of the data. North Dakota boasts some of the best long-term data sets in the form of a fossil record to measure the effects of climatic warming on fish populations. This dissertation research will provide insight for fishery biologists and wetland ecologists concerning the long-term response of contemporary fish growth and population trends in North Dakota given potential climatic changes.

Scope and Objectives

The research examined and described age and growth related characteristics of extant and extinct taxa of three North American families: Hiodontidae, Esocidae, and Percidae. The objectives of my research were to 1) examine the relationships between growth characteristics (i.e., size prior to sexual maturity, maximum total length, growth rate, and life span) and temperature, 2) determine if growth characteristics were different between extinct and extant taxa, and 3) determine if changes in growth characteristics were correlated with major climatic events.

Methods

Data collection

Criteria for identification of annuli. Annuli from both opercula and scales were used to estimate age of extant fish (i.e., Carlander 1969). I identified annuli on fossil and extant fish scales using one or more of the following characteristics: crowding of circuli, wide then narrow spacing of circuli at the anterolateral angle to identify seasonality, and an anastomosis of circuli on lateral fields (Carlander 1961, Casselman 1996). I attempted to exclude all false annuli (Casselman 1996 and references therein).

Annuli on extant centra were defined as having translucent bands (i.e., winter growth) preceded by opaque/raised circular ridges with finely papilose surfaces of summer growth, as seen in Hiodontidae and other taxa (Donald et al. 1992, Lee and Prince 1995, Newbrey and Wilson 2005, Newbrey et al. 2007). On fossil centra, ages were assigned based on criteria similar to those for extant centra, except it was observed that circular ridges were followed by dark gray or black bands, rather than translucent bands as in extant hiodontids. I assumed that the seasonal effects produced from variation in daylight and productivity affected annulus formation because the various fossil localities were located in higher paleolatitudes (see Newbrey and Wilson [2005] for a discussion of the topic). To highlight the relief of annular features such as ridges, light was angled at 45° across the surface (Newbrey and Wilson 2005). I counted annuli and then recorded the total annular marks to estimate the age of each individual.

Growth assessment. To assess growth on scales, the center of the focus was marked using an ocular grid and the transverse radial distance (TRD mm) to the nearest 0.01 mm was determined to each annulus using a digital micrometer under a binocular dissecting microscope

(Newbrey et al. 2007). The TRD is that distance from the focus to the margin along the dorsal-ventral axis of the scale that transects the focus (Daniels 1996).

To assess growth on centra, the center of the notochord foramen was marked using an ocular grid and the radial distance (RD mm) to each annular mark was measured toward the distal margin (Newbrey and Wilson 2005). Centrum growth was determined to the nearest 0.01 mm using a digital micrometer under a binocular dissecting microscope. Newbrey and Wilson (2005) determined the methodology has a mean measurement error of 0.06 ± 0.01 s.e. mm using centra of extant fish. No consistent orientation of the centra was used for measurements, as some Cretaceous centra were partially incomplete. All measurements were made by a single observer to standardize error.

Growth data from extant populations. Data on populations were examined from published literature for a comparative examination of growth. Population information that included both age and TL data were primarily used. Total length is the distance from the anterior-most tip of the head to the vertical plane of the posterior caudal fin tips (Hubbs and Lagler 1964). For some populations, fork length or standard length were converted to TL using conversion formulas provided by Carlander (1969).

Mean annual temperature. Mean annual temperature (MAT) was used to provide a standardized, independent variable from which to compare growth characteristics to those in the fossil record. Paleotemperatures derived from oxygen isotopes or leaf physiognomy are often provided in values of MAT rather than other measures of temperature (i.e., mean summer highs, mean July temperatures, length of the growing season, etc). Data for MAT were obtained by matching locations of each fish population to the nearest location listed in WorldClimate database (Hoare 2003); temperatures were rounded to the nearest 0.1°C.

Analysis of growth

Individual growth profiles from fossil centra and scales and centra of extant skeletons were described using a von Bertalanffy growth equation. All tests were performed with SYSTAT® version 10.0 (2002) and population parameters were assessed with 95% confidence limits. A von Bertalanffy growth curve (i.e., nonlinear regression) was used to estimate size at a given age using TL, scale TRD, or centrum RD:

$$TL_t = L_\infty[1-e^{-K(t-t_0)}]$$

where the parameters: TL_t = Total length (cm), TRD, or RD (mm) at t (age in years); L_∞ = theoretical MTL, TRD, or RD; K = the Brody growth coefficient; t = time (i.e., age in years); and t_0 = time at age zero (time at theoretical zero length).

As many published data sets have never been examined statistically for error, all extant populations that exhibited characteristics of systematic aging error were eliminated. I used the von Bertalanffy equation in SYSTAT® version 10.0 (2002) to examine the confidence limits associated with theoretical maximum size and growth parameters. Valid age assignments typically produce realistic and/or significant maximum size and K growth parameters at the 95% confidence interval (Burnham-Curtis and Bronte 1996, Newbrey and Bozek 2003, Newbrey and Wilson 2005). If L_∞ and K were significant, the data were used in the analysis. Population data were used if only L_∞ was significant if the regression line produced a good fit to the data and K had a realistic value. Datasets with separate male and female data were combined prior to analysis to keep error constant with that found in the fossil data.

Changes in size through time

Since complete fish are relatively rare, sizes of scales and centra were used as proxies for size when determining whether the relative size of fish has changed since the Campanian. A separate variance t-test was used to ascertain differences in TL at ages 4-8 years old among extinct individuals and also to compare mean TL for each age class for published populations of extant fish. Analysis of Covariance (ANCOVA) was used to ascertain if the slopes of centrum diameter (i.e., a secondary proxy for size) were different between extinct and extant taxa. Centrum diameter is the widest diameter between the lateral margins.

Population/fossil locality data and taxonomic responses

I examined the relationships between the extant fish growth response variables $TL_{Age\ 2}$, MTL, the growth coefficient, and longevity and the independent variable, MAT; alpha was set at 0.05 for all tests. The relationships between longevity and the growth coefficient and between longevity and MTL were examined. Using the age, size, and growth data, I also determined whether extinct fish were similar to those of extant fish. Shared characteristics between extant fish and those in the fossil record were compared using eight comparisons (i.e., scale $TRD_{Age\ 2}$, centrum $RD_{Age\ 2}$, $TL_{Age\ 2}$, MTL, the growth coefficient, and longevity to MAT, the relationship between longevity and growth, and the relationship between longevity and MTL).

Total lengths at age 2 were recorded for each extant population. Maximum TL was noted from the single largest individual from a population. The growth series from each individual in the fossil record was analyzed using a von Bertalanffy growth regression to calculate a growth coefficient expressed either as a value (i.e., for $n = 1$) or a mean (i.e., for $n > 1$) for each

population or taxon using individuals that were at least 5 years old. Longevity for each population was based on the age of the oldest individual.

I used regression analysis (i.e., least squares and exponential) to describe the relationships between MAT and $TL_{Age\ 2}$, MTL, K, and longevity. For extant fish, TL at age 2 was used because this age represents the earliest inflection in size of some extinct. At sexual maturity, growth of individuals tends to slow as energy is diverted from somatic to gonadal growth (Carlander 1969). The fossil material was analyzed in a similar manner to that for extant fish, except that the data sets for the fossil record were comprised of multiple taxa that extended through the fossil records. To test the hypothesis that extant and extinct fish had different relationships between MTL, longevity, and growth, I regressed these parameters for extant taxa and then plotted the fossil data for comparison. Studentized residuals, two sample t-tests, and an ANCOVA were used to compare the extant and fossil data sets. In cases of small and unequal sample sizes, a separate variance t-test with bootstrap resampling was used with total alpha adjusted to 0.025 (Manly 1997; Ruxton 2006).

Distributional/taxonomic response to temperature

The latitudinal distribution of Cretaceous to Pliocene hiodontids, esocids, and percids was examined to determine if the geographic distribution was correlated with paleotemperature. Because some fish show preferences for specific temperatures (Medvick et al. 1981), I hypothesized that geographic distribution might shift to maintain thermal constancy. During warm episodes, I predicted that fossils would be found in more northerly latitudes and at more southerly latitudes during colder episodes.

To ascertain whether hiodontids, esocids, and percids responded in latitudinal distribution to temperature, the paleolatitude of fossil localities for hiodontids was regressed against a proxy

for paleotemperature based on stable isotopes. Paleolatitude (°N) of all hiodontid fossil localities was calculated using the PLATES program (Ian Dalziel, University of Texas). The paleotemperature proxy was estimated from $\delta^{18}O$ from marine benthic foraminiferans for the period of 2 to 67 Ma (Zachos et al. 2001). The data were smoothed using a 5-point moving average and then further smoothed using a kernel weighted, 2-degree polynomial regression in SYSTAT® version 10.0 (2002).

Results and Discussion

There are several lines of evidence which suggest that temperature-influenced thermal life history characteristics and perhaps evolution of taxa occurred within two of the three families: 1) there are many relationships between temperature and growth characteristics in extant species from all three families; 2) there are significant relationships between temperature and growth characteristics for extinct taxa; 3) there are significant changes in life span and growth rate, but there is only data for esocids across the Plio-Pleistocene boundary; 4) there are changes in body size around the K-T and the Plio-Pleistocene boundaries for the esocoids and hiodontids, but the data resolution is too low to implicate a climatic event; 5) the appearance of higher taxa at climatic events is only apparent for the esocoids, but higher taxonomic diversity seems to be present for Hiodontidae at the EETM; and 6) the latitudinal distribution of Cenozoic hiodontids, esocids, and percids is correlated with temperature, except during the EETM when a new esocid subgenus was first documented.

Growth characteristics of extant fish

Relationships between four growth characteristics (i.e., maximum total length, total length prior to sexual maturity, growth rate, and longevity) and MAT were examined for the three fish families. For the hiodontids and esocids, there were 17 significant relationships with MAT out of 20 examined (see Newbrey 2007, Newbrey et al. 2007, Newbrey et al. *In press*). The number of significant correlations with MAT was proportionately lower for the percids with 15 significant relationships out of 24 examined (see Newbrey 2007).

There were seven significant relationships between maximum total length (MTL) and MAT out of 11 examined for the three families to suggest a mixed response in life history characteristics. For the hiodontids and esocids, all five relationships were significantly correlated with MAT. However, for the percids only two of the six relationships were significant suggesting that percid maximum length is not as strongly linked to temperature as the hiodontids and esocoids. Of the significant relationships between MTL and MAT for the hiodontids, esocids, and percids, all but one species had larger sizes in colder temperatures. Total length prior to sexual maturity was significantly and positively correlated with MAT in all cases examined.

Growth rate was also significantly correlated with MAT in all relationships examined for the hiodontids (Fig. 1A) and esocids (Fig. 2A) suggesting a strong linkage between growth and temperature. For the percids, four relationships were significant out of six examined which indicates a slightly weaker linkage between growth and MAT. Of the significant relationships between growth rate and MAT for the hiodontids, esocids, and percids, all but one species had faster growth rates at warmer temperatures.

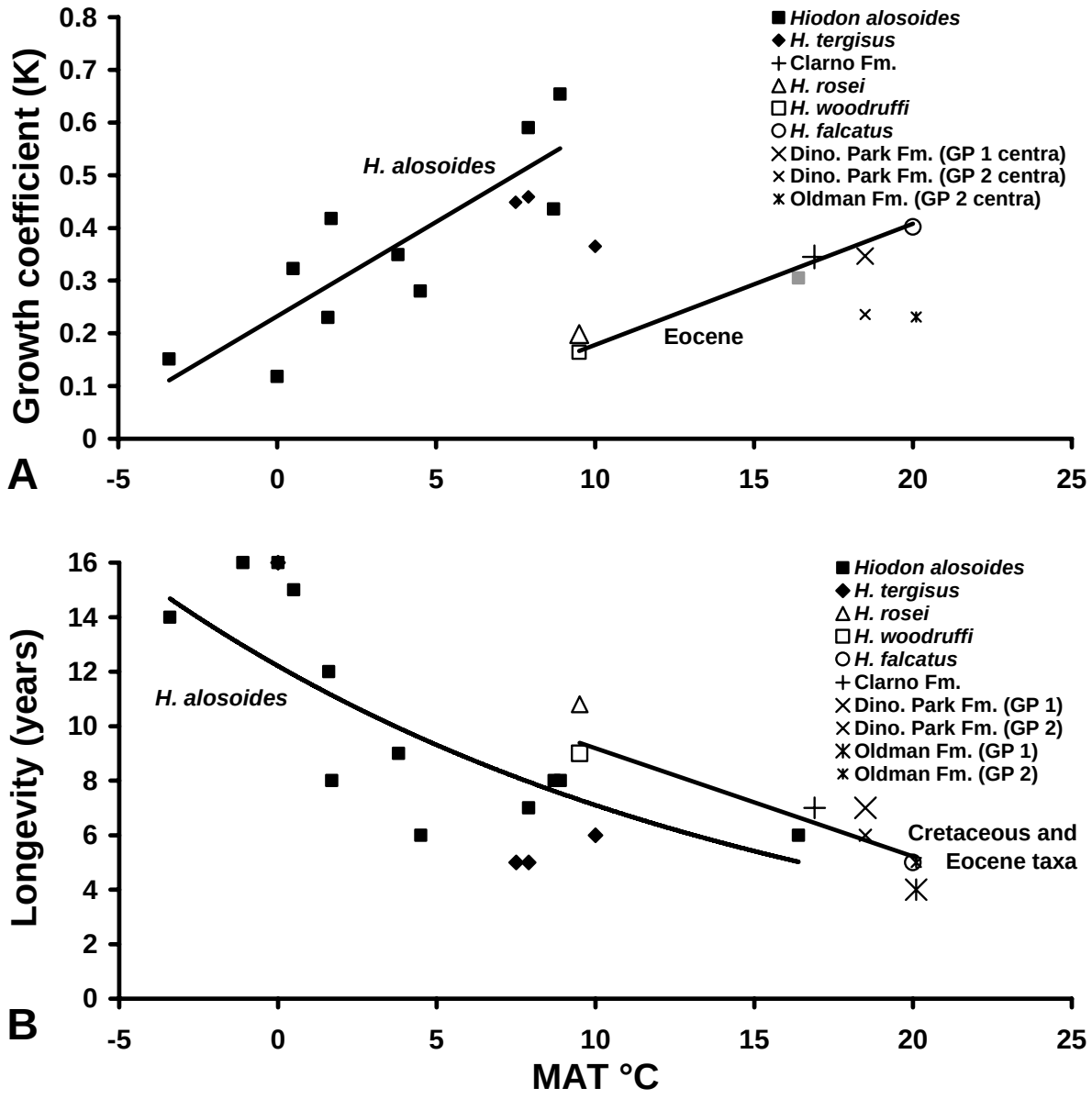

Figure 1. Hiodontid growth rate and lifespan compared to temperature (Newbrey 2007). The relationships between mean annual temperature (MAT°C) and **A**, the von Bertalanffy growth coefficient (K) as estimated from scales unless otherwise specified, a solid gray square indicates a single *Hiodon alosoides* population that was not included in the regression analysis because of data lacking between 10-15°C, the regression for Eocene taxa only includes scales; and **B**, life-span. Lines indicate significant relationships ($\propto = 0.05$). **Abbreviations: Dino.**, Dinosaur; **Fm.**, Formation; **GP**, growth profile.

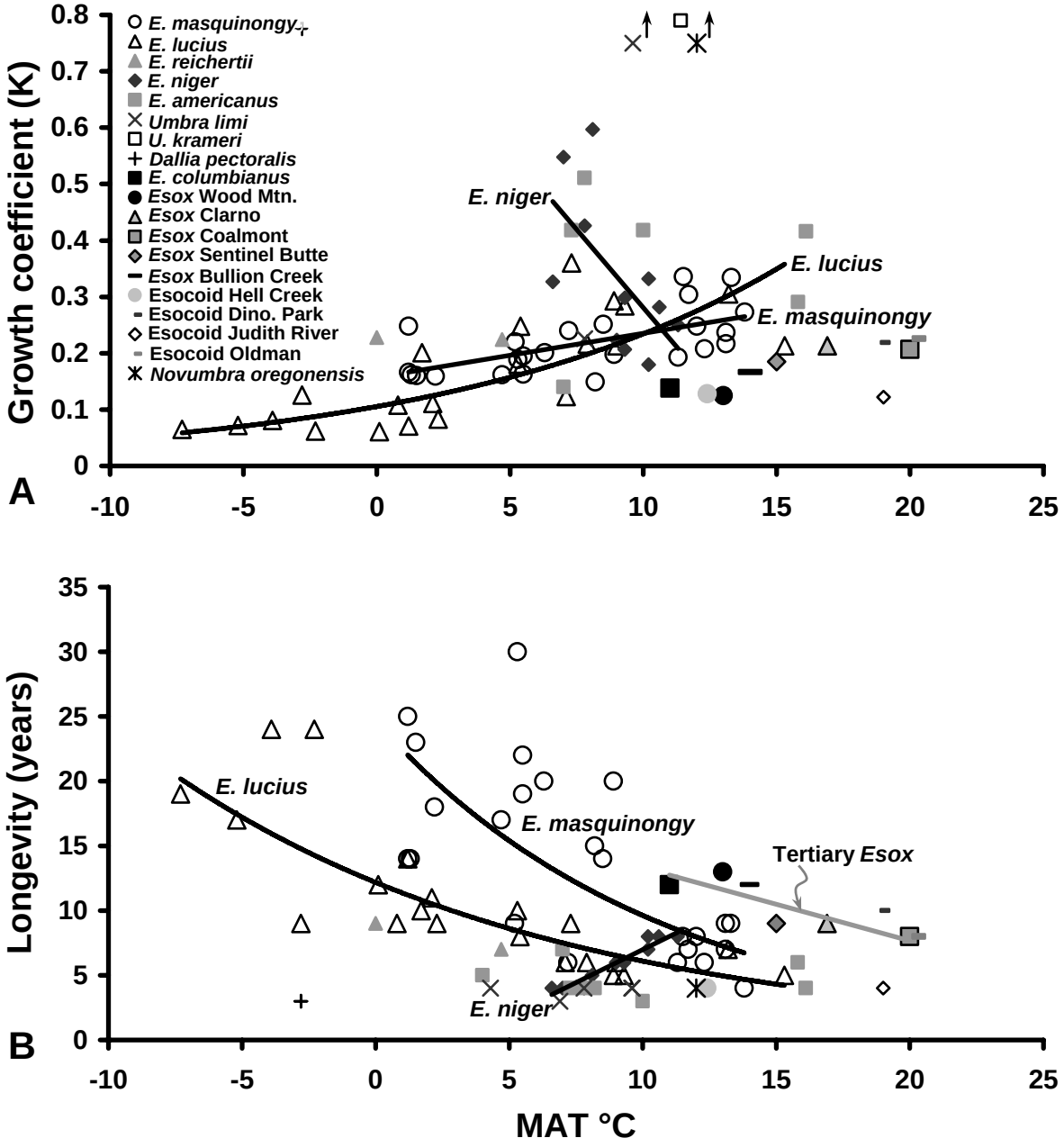

Figure 2. Esocoid growth rate and lifespan compared to temperature (see Newbrey et al. *In press*). The relationships between mean annual temperature (MAT) and **A**, the von Bertalanffy growth coefficient (K), the y-axis was truncated at 0.8, as a result data representing *Umbra limi* (K value of 1.05 at 9.6°C) and the Oligocene *Novumbra oregonensis* (K value of 2.15 at 12°C) were displaced but arrows show the direction of occurrence; and **B**, life-span. Taxa are listed by taxonomic group (i.e., extant *Esox*, extant umbrids, fossil esocoids) and then in stratigraphic order within groups. Lines indicate significant relationships (alpha = 0.05). **Abbreviations: Dino.**, Dinosaur; **Mtn.**, Mountain.

Life span was significantly greater in colder climates for four of the five species examined in Hiodontidae (Fig. 1B) and Esocidae (Fig. 2B) suggesting a strong linkage with temperature. However, only three of the six species of percids analyzed were significantly correlated with temperature. All but one species of fish within the three families had longer life spans at colder temperatures.

Growth characteristics of extinct fish

There were four relationships between MAT and growth characteristics out of six examined for Hiodontidae and Esocidae. Growth rate could only be examined for fossil hiodontids and was positively correlated with MAT (Fig. 1A). For both families, life span was negatively correlated with MAT in the fossil record as in extant families (Figs. 1B and 2B). Maximum total length and length prior to sexual maturity could not be examined for both families. However, proxies for size prior to sexual maturity were positively correlated with MAT in both fossil and extant hiodontids.

Changes in growth characteristics among extant and extinct fish

All growth characteristics examined for extinct taxa differed significantly from those of extant populations at similar temperatures. This suggests that growth characteristic change occurred in both the hiodontids and esocids. Life span was significantly longer in fossil esocids than extant species inhabiting similar temperatures following the Plio-Pleistocene boundary. Life spans were not significantly different for the hiodontids, but fossil individuals were older than extant individuals at similar temperatures. Longevities of extant taxa in cold environments

are longer than those in the fossil record, but cold environments were not common until the Pleistocene (Figs. 1B and 2B).

Growth rates in Cenozoic esocids and hiodontids were significantly slower than extant taxa at the same temperatures. Changes in esocid growth rates occurred following the Plio-Pleistocene boundary (Fig. 2A). Growth rates for Eocene hiodontids were significantly slower compared to those of extant *Hiodon*.

Sizes of Cenozoic hiodontids and esocids, prior to sexual maturity, were significantly smaller than those of extant species. Cretaceous hiodontids and esocoids were also significantly smaller than those of the Cenozoic. Specifically, Cretaceous hiodontid taxa are smaller than Eocene taxa at the same temperatures.

Hiodontid and esocid size remained unchanged during the later Cretaceous until just prior to the K-T boundary. At about the K-T boundary, MAT's declined 10°C with temperatures as low as 8°C (Wilf et al. 2003). The climatic change that occurred within the time of deposition of the Oldman and Dinosaur Park/Judith River formations amounted to a mean change of 2°C (Jenkyns et al. 2004) to perhaps 6°C (He et al. 2005); no detectable changes occurred in hiodontids during this time. Newbrey et al. (*In Press B*, Chapter 2) also reported that there was no change in size during the late Cretaceous in esocoids until after the K-T boundary significantly larger *Esox* appeared. Size of *Esox* did not change again until after the Plio-Pleistocene boundary. The largest shifts in hiodontid and esocid size also occurred around major climatic shifts, i.e., 1) from the K-T boundary to the EETM; 2) following the late Eocene to the Pliocene-Pleistocene (Plio-Pleistocene) boundary.

First appearances in the fossil record

The appearance of new esocid higher taxa and taxonomic diversity appear to be associated with major climatic events. A new genus of esocoid appeared following the K-T boundary (Wilson 1980) and a new esocoid subgenus appeared during the EETM (Grande 1999). However, hiodontid diversity was the greatest at the EETM (Hilton and Grande *In Press*). Esocid diversity at the EETM may have been higher due to a latitudinal anomaly in distribution in fossil localities at the EETM. There were no new higher taxa after the Plio-Pleistocene boundary. Changes in diversity at the Plio-Pleistocene boundary were not analyzed.

Geographic distribution and dispersal

The latitudinal distributions of Cenozoic hiodontids, esocids, and percids are correlated with temperature. The latitudinal distribution of Cenozoic esocids was positively correlated with temperature, except during the EETM when a new esocid subgenus was first documented. The distributions of the hiodontids and esocids were positively correlated with MAT which suggests that dispersal tracked with climate. However, percids apparently did not respond to temperature in a similar way as the other two families of fish; percids moved north during periods of cooling in the Miocene and Pliocene.

Influence of climate change on percid growth characteristics

Percids have differential responses to temperature that require more future examination. North American percids have a higher mean number of correlations with MAT but have less change in growth characteristics across their range compared to Eurasian taxa (Table 1). The data suggest that climate change influences the growth characteristics of some percid species

Table 1. Comparison of the percent change for four characteristics related to growth

	Perca		*Gymnocephalus*	*Sander*		
Characteristic	***P. fluviatilis***	***P. flavescens***	***G. cernuus***	***S. lucioperca***	***S. vitreus***	***S. canadense***
$TL_{Age\ 3}$ (% Δ/1°C)	4.8	3.2	3.8	7.8	3.5	2.6
MTL (% Δ/1°C)	2.8	---	---	---	1.1	---
K (% Δ/1°C)	---	3.8	---	10.8	3.8	3.7
Longevity (% Δ/1°C)	---	3.7	6.5	---	3.2	---
N correlelations with MAT	2	3	2	2	4	2
Mean (% Δ/1°C)	3.8	3.6	5.1	9.3	2.9	3.2

A comparison of the percent change for four characteristics related to growth for every 1°C change in mean annual temperature among six percids (Newbrey 2007). Of significant relationships, the mean percent change for North American species = 3.2% compared to that of Eurasian species, 6.1%. The North American species include *Perca flavescens*, *Sander vitreus*, and *S. canadense*. **Abbreviations: K**, von Bertalanffy growth coefficient; **MTL**, maximum TL; **RD**, centrum radial distance; **TL**, total length.

more than others. For example, more growth characteristics of *S. vitreus* are correlated with MAT than for any other percid examined. However, *S. vitreus* has generally a smaller percent change per unit increase in temperature (i.e., sensitivity) for each characteristic examined.

The growth characteristics of Eurasian taxa, that are also significantly correlated with MAT, are more sensitive (i.e., > %Δ/1°C) to temperature change than those of North American taxa; whether this makes them more or less adaptable to climate change is uncertain. The sensitivity to temperature is lower in percid species with fewer correlations with MAT. North American *Perca* and *Sander* have lower mean r^2 values of compared to Eurasian taxa that have fewer significant correlations. To interpret the significance, a comparison to *Esox* may be instructive. *Esox* has a higher mean r^2 value and number of significant relationships with MAT compared to those of percids (Table 2). *Esox* also has a longer fossil record than *Perca* or *Sander*. *Esox* has existed through more climatic events than either *Perca* or *Sander*, as *Esox* has remained relatively unchanged growth characteristics from the Paleocene to the Pliocene (Newbrey et al. *In press*). Initially, this suggests that Eurasian percids with a longer fossil record and generally higher r^2 values will be better adapted to climate change than North American species. However, this does not appear to be the case as Eurasian species have fewer correlations with MAT (i.e., less thermally influenced) unlike *Esox* and North American *Perca* and *Sander*.

Conclusion

Grande (1999) proposed that temperature could be an ecological mechanism to explain speciation in *Esox*. Grande based his idea on extant geographic and thermal distributions and temperature-affected variation in phenotypically plastic numbers of vertebrae. Grande

Table 2. Comparison of r^2 values for characteristics related to growth of percids

	Perca		***Gymnocephalus***	***Sander***			Percids	*Esox*
Characteristic	***P. fluviatilis***	***P. flavescens***	***G. cernuus***	***S. lucioperca***	***S. vitreus***	***S. canadense***	mean	mean
$TL_{Age\ 3}$ (r^2)	0.46	0.23	0.58	0.75	0.61	0.21	0.44	0.57
MTL (r^2)	0.18	---	---	---	0.07	---	0.13	0.45
K (r^2)	---	0.21	---	0.29	0.26	0.38	0.25	0.44
Longevity (r^2)	---	0.24	0.72	---	0.28	---	0.41	0.68
N correlelations with MAT	2	3	2	2	4	2	2.5	3.3
Mean (r^2)	0.32	0.23	0.65	0.52	0.31	0.30	0.31	0.54

A comparison of the coefficient of determination values (r^2) for characteristics related to growth of percids (Newbrey 2007). Data for *Esox* was provided for comparison from Newbrey et al. (*In press*). Of significant percid relationships, the mean r^2 for North American species is 0.28 compared to that of Eurasian species, 0.50. The North American species include *Perca flavescens*, *Sander vitreus*, and *S. canadense*. **Abbreviations: K**, von Bertalanffy growth coefficient; **MTL**, maximum TL; **RD**, centrum radial distance; **TL**, total length.

(1999) also documented the first appearance of the subgenus *E*. (*Kenoza*) at the EETM. From the dissertation research, the role of climate in natural selection of temperature-related phenotypic traits of hiodontids and esocids could be important given that: 1) extant and extinct taxa have phenotypically plastic growth characteristics in relation to temperature; 2) significant changes in growth characteristics were correlated with climatic events; and 3) new taxa appeared following major climatic events.

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