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Anticipating climate change impacts on Mongolian salmonids: bioenergetics models for lenok and Baikal grayling

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Abstract – The Eg–Uur River ecosystem in north-central Mongolia provides an opportunity to study salmonid species in a system that has already experienced significant climate change. These species are currently imperilled in Mongolian waters, with Baikal grayling (*Thymallus arcticus baicalensis*) listed as near-threatened and lenok (*Brachymystax lenok*) listed as vulnerable on the Mongolian red list. Air temperature records demonstrate that in the last 40 years Northern Mongolia's rate of warming has been three times greater than the northern hemisphere average. Despite alarming trends in air temperatures, little is known of the thermal ecology of these species. Due to the threat of climate change to these species, the objective of our study was to quantify metabolic costs for these species from streamside routine metabolic measures and derive bioenergetics models that we used to assess potential climate change response. Streamside measurements of metabolism were remarkably consistent with expectations from measures of other salmonids gathered under more closely controlled laboratory conditions. Metabolism increased exponentially with temperature for both species. The resulting preliminary bioenergetics models suggest these species are already experiencing temperatures near their upper levels for growth during summer and conditions are expected to deteriorate with warming. Even a modest 2 °C increase in water temperatures during ice out would result in a 59% reduction in growth of lenok, and an inability of Baikal grayling to grow (if food levels remained unchanged) or a 14–23% increase in consumption in order to maintain current growth rates.

Key words: climate change; lenok; Baikal grayling; bioenergetics; growth

Introduction

Salmonids in the cold water guild (Meisner 1990) are among those fishes likely to be most vulnerable to climate change, including rising water temperatures and changes to flow regimes (Wenger et al. 2011). Changes in habitat availability (Isaak et al. 2010) and biogeographic (Keleher & Rahel 1996) distribution of North American salmonids are predicted consequences of climate change. Similarly, studies on European salmonids predict changes in habitat from altered hydrology (Junker et al. 2015) and entire fish assemblages are likely to change in many European rivers (Pletterbauer et al. 2015).

However, little is known about the impacts of climate change on Asian salmonids, and many basic aspects of their biology remain unknown. This knowledge gap is particularly pressing as climate change has proceeded rapidly in northern Asia (Cruz et al. 2007).

The Eg–Uur River ecosystem in north-central Mongolia provides an opportunity to study salmonid species: lenok (*Brachymystax lenok*), Baikal grayling (*Thymallus baicalensis*) and taimen (*Hucho taimen*) in a system relatively undisturbed by human influences other than climate change (see Appendix Fig. A1). These species are currently imperilled in Mongolian waters, with Baikal grayling listed as near-threatened,

lenok listed as vulnerable and taimen listed as endangered on the Mongolian red list (Ocock et al. 2006).

Air temperature records demonstrate that northern Mongolia is experiencing not only warmer temperatures, but longer heat wave duration (Batima et al. 2005; Nandintsetseg et al. 2007; Sharkhuu et al. 2007; Dagvadorj et al. 2009). Air temperatures have increased by more than 2 °C since the 1940s (Nandintsetseg et al. 2007) with temperature anomalies of 1.5 °C since 1980 (through 2000; Batima et al. 2005). Heat wave duration as defined by daytime high temperatures of 25–30 °C, increased by 8–18 days since ~1960 (Batima et al. 2005). Despite alarming trends in air temperatures in Mongolia, little is known of the thermal ecology of these species.

Bioenergetics models have emerged as an important tool in predicting climate change impacts to fishes (Hill & Magnuson 1990; Petersen & Kitchell 2001; Kao et al. 2015a). Such models directly integrate changes in thermal regime to energy costs and production of fishes making them ideal for studying climate change impacts on individuals and populations (Griffiths & Schindler 2012; Hardiman & Mesa 2014; Holt & Jorgensen 2014) and communities (Cline et al. 2013; Kao et al. 2015a,b). Bioenergetics can be incorporated into models that consider other biotic and abiotic factors affected by a changing climate (Megrey et al. 2007; Okunishi et al. 2009).

Due to the threat of climate change to these species, the objective of our study was to quantify metabolic costs of grayling, lenok and taimen, and develop bioenergetics models of fish growth that could in turn be used to assess possible impacts of climate change on these species. We then used bioenergetics models to evaluate effects of increased water temperature on salmonid growth and consumption rates. However, due to low catches of taimen, we could only proceed with bioenergetics models for lenok and Baikal grayling.

Study area

Our study area was the Eg and Uur Rivers (referred to here as the Eg–Uur River) within 10 km of their confluence. The Eg River is the outflow from Lake Hovsgol, Mongolia's largest lake by volume and connects Lake Hovsgol to the Selenge River. The Uur is considered a tributary of the Eg, although at their confluence, the discharge of the Uur is frequently greater (Jensen unpublished data). Both rivers are typically ice covered from November through May, and they reach their peak discharge during the wetter summer months (June and July). The fish community of the Eg–Uur River near their confluence consists of 12 species, including three salmonids: taimen, lenok and Baikal grayling (Mercado-Silva et al. 2008). Fishing pressure in this remote area is low and consists mainly of recreational fishing for lenok and grayling, which are often retained, and taimen, which must be released (Jensen et al. 2009).

Materials and methods

Construction of bioenergetics models for Mongolian fishes is limited by a lack of development and infrastructure including electricity in the countryside. Traditionally bioenergetics models are developed from laboratory measures on fish under carefully controlled thermal and photoperiod conditions (Brett & Groves 1979; Hartman & Brandt 1995a). Most attention is paid to how fish size and temperature affect metabolism and *ad libitum* feeding rate, whereas other energetic components are frequently borrowed from other species (Hanson et al. 1997; Chipps & Wahl 2008). This is particularly true for rare and endangered species (Petersen et al. 2008). In developing bioenergetics models for lenok and Baikal grayling, we chose to measure routine metabolism directly, derived consumption functions from functions reported for other salmonids and borrowed parameters for other cost and waste terms from the literature.

Bioenergetics models

Bioenergetics models are based upon the balanced energy equation (Winberg 1956).

$$C = G + (M + \text{SDA}) + F + U,$$

where C is consumption, M is metabolism, SDA is heat lost in transforming food into utilisable energy, F is egestion, and U is excretion. Knowledge of five of these values allows solution for the sixth. Most commonly, the bioenergetics models are used to estimate consumption from measures of growth.

Such models have been increasingly popularised by the advent of software that enabled greater ease of use of the models (Hanson et al. 1997; Hartman & Kitchell 2008). Due to this popularity and the upcoming advent of a Fish Bioenergetics Model 4.0 software which will run in the statistical computing environment, R, the parameters for our bioenergetics models for lenok and Baikal grayling follow the naming and parameter convention used in the Fish Bioenergetics 3.0 software (Hanson et al. 1997).

The Fish Bioenergetics 3.0 software uses one of several submodels to estimate the various cost and

loss terms and to establish a limit (C_{max}) on consumption rates for fish (Hanson et al. 1997). The maximum consumption function is modelled as a product of both an allometric function and a temperature dependence function.

$$C_{max} = CA \cdot W^{CB} \cdot f(T).$$

Where CA is the intercept of the allometric function, W is fish mass (g), CB is the slope of the allometric mass function, and $f(T)$ is the temperature dependence function. The temperature dependence of salmonids has generally been modelled using the Thornton & Lessem (1978) algorithm

$$f(T) = K_A \cdot K_B,$$

where K_A and K_B describe C_{max} as it increased and decreases with increasing temperature respectively:

$$K_A = \frac{CK1 \cdot L1}{1 + CK1 \cdot (L1 - 1)},$$

$$L1 = e^{(G1 \cdot (T - CQ))},$$

$$G1 = \frac{1}{CTO - CQ} \cdot \ln \frac{0.98 \cdot (1 - CK1)}{CK1 \cdot 0.02},$$

$$KB = \frac{CK4 \cdot L2}{1 + CK4 \cdot (L2 - 1)},$$

$$L2 = e^{(G2 \cdot (CTL - T))},$$

$$G2 = \frac{1}{CTL - CTM} \cdot \ln \frac{0.98 \cdot (1 - CK4)}{CK4 \cdot 0.02}.$$

Here, CQ and CTL are the lower and upper water temperature, respectively, where the temperature dependence is a small proportion (CK1 and CK4 respectively) of C_{max}. The CTO is the water temperature corresponding to 0.98 of C_{max}. More details on these submodels and other models used to describe fish energetics can be found at: http://aqua.wisc.edu/publications/PDFs/FishBioenergetics3-Manual.pdf (Hanson et al. 1997).

Metabolism (M) of fish was modelled as a function of fish mass (W, g) and temperature (T):

$$M = RA \cdot W^{RB} \cdot f(T) \cdot ACT,$$

where M is a specific rate of metabolism ($g \cdot g^{-1} \cdot d^{-1}$), RA is the intercept of the allometric mass function, RB is the slope of the allometric mass function; $f(T)$ is the temperature dependence function, and ACT is

an activity multiplier to account for a fish's normal daily activities. The temperature dependence of metabolism was modelled as an exponential function (equation 1 in Hanson et al. 1997):

$$F(T) = e^{(RQ \times T)} ACT,$$

where RQ describes how metabolism changes with temperature and ACT is a constant.

In developing bioenergetics models for lenok and grayling, we relied on our streamside measures of metabolism to define metabolic costs for the species. Metabolism is the major 'cost' term and varies from species to species (Winberg 1956; Hanson et al. 1997). However, parameters to describe SDA, F, U and C are still needed and unlikely capable of streamside measurement in the field. Fortunately, bioenergetic models already exist for a suite of salmonid species: Lake Champlain morphotype lake trout *Salvelinus namaycush* (little difference between the morphotypes tested in: Kepler et al. 2014); steelhead trout *Onchorynchus mykiss* (Rand et al. 1993); brown trout *Salmo trutta* (Elliott 1976a,b); bull trout *Salvelinus confluentus* (Mesa et al. 2013); sockeye salmon *Oncorhynchus nerka* (Beauchamp et al. 1989); Chinook salmon *Onchorynchus tshawytscha* (Stewart & Ibarra 1991); and brook trout *Salvelinus fontinalis* (Hartman & Cox 2008); and these can be used to guide parameterisation of the Mongolian salmonid models. Energetic parameters for SDA, F and U are a small component of the total energy budget, vary little from species to species (Winberg 1956), and are well-described for salmonids, largely based on measures by Elliott (1976a,b) for brown trout and Brett (1976) for sockeye salmon. We borrowed the parameters for SDA, F and U from the Chinook salmon model (Stewart & Ibarra 1991) (Table 1). We considered lenok and Baikal grayling to be moderately active fish and used a constant ACT of 1.5 to account for active metabolism of fish in the bioenergetics model. Active metabolism has commonly been found to be about twice the resting rates for a wide range of species including brown bullhead *Ameiurus nebulosus*, goldfish *Carassius auratus* and brook trout among others (Winberg 1956; Boisclair and Sirois 1993).

Metabolism measures

We measured metabolic rates of fish streamside during three field seasons on 19–27 September 2012, 9–13 July 2013 and 3–9 October 2015. Fish were collected by seining (fish < 120 mm TL) or by angling (fish > 120 mm TL). Once collected, fish were maintained in river water streamside until used in metabolism measurements, within 48 h of collection.

Table 1. The models and parameter values used in the bioenergetics model for Baikal grayling and lenok in Mongolia.Consumption and respiration model parameters were derived from this study, and egestion, excretion and SDA models were borrowed from Stewart & Ibarra (1991) for Chinook salmon. Respiration is converted from g O_2 to units of energy (J) using an oxycalorific value of 13,562 $J \cdot g^{-1}$ O_2 (Elliott & Davidson 1975) within the Fish Bioenergetics Model software (Hanson et al. 1997).

Model parameter	Baikal grayling Value	Lenok Value
Consumption model equation	3	3
CA	0.303	0.303
CB	−0.275	−0.275
CQ	5	5
CTO	15	15
CTM	19	19
CTL	24	24
CK1	0.5	0.5
CK4	0.1	0.1
Respiration model equation	1	1
RA	0.00145	0.00249
RB	−0.173	−0.178
RQ	0.115	0.0848
RTO	0.69311	0.69311
RTM	0	0
RTL	0	0
RK1	1	1
RK4	0	0
ACT	1	1
BACT	0	0
SDA*	0.172	0.172
Egestion†/Excretion‡ model equation	2	2
FA	0.212	0.212
FB	−0.222	−0.222
FG	0.631	0.631
UA	0.0314	0.0314
UB	0.58	0.58
UG	−0.299	−0.299
Predator energy density ($J \cdot g^{-1}$)	5500	5500
Prey energy density ($J \cdot g^{-1}$)	5500	5500

*Specific dynamic action (S) is modelled as: $S = \text{SDA} \cdot (C - F)$, where C is amount consumed and F is the egestion rate all in units of $g \cdot g^{-1} \cdot day^{-1}$.

†Egestion (F) is modelled as: $F = \text{FA} \cdot T^{\text{FB}} \cdot e^{(\text{FG} \times p)} C$. In units of $g \cdot g^{-1} \cdot day^{-1}$ where C is consumption, T is temperature, and p is the proportion of maximum consumption.

‡$U = \text{UA} \cdot T^{\text{UB}} \cdot e^{(\text{UG} \times p)} (C - F)$. In units of $g \cdot g^{-1} \cdot day^{-1}$ where C is consumption, T is temperature, F is egestion, and p is the proportion of maximum consumption.

Routine metabolism was measured using established procedures (Hartman & Brandt 1995a). Individual fish were placed into a metabolism chamber appropriate for the size of fish such that internal dimensions allowed fish to perform routine functions. Fish less than 100 mm TL were placed in 2.2 L chambers. Fish > 100 mm but less than 250 mm TL were measured in 12.6 L chambers. Fish > 249 mm but less than 500 mm TL were placed in 135 l, and fish > 500 mm TL were measured in 310 l metabolism chambers. Changes in dissolved oxygen levels over time were made using a Pro ODO metre (Yellow Springs International). In preliminary measurements, fish metabolic rates declined to a baseline

level 17–20 h after being placed in the chambers. Therefore, fish were allowed to acclimate to these chambers for a period of 24 h prior to beginning recorded measurements.

The metabolism chambers were maintained in a bath of river water or in a portable swimming pool to minimise the rate of temperature change experienced by fish within the chambers during an observation. This was necessary as it was not uncommon for air temperatures to vary by 20 °C within a 24-h period. When taking an observation, the water temperature and D.O. levels were measured and recorded at the time the metabolism chamber was closed and again once D.O. levels were depleted by approximately 1.0 $mg \cdot l^{-1}$. The temperature for an observation was the mean of the initial and final temperatures taken along with dissolved oxygen using a YSI Pro ODO optical D.O. meter (www.ysi.com/proODO). The temperature range during observations was 1.1 ± 0.2 °C. Thereafter, observations for which initial and final temperatures differed by more than 2 °C were excluded from analysis resulting in a mean temperature range of 0.75 °C during observations. Between metabolism observations, water was provided to each chamber via a pump that circulated fresh water through each tank. Metabolism measures were taken multiple times on each fish over the next 24 h as the river water temperature or pool water temperature changed throughout the period, often affording us the opportunity to measure metabolism at multiple temperatures for each fish. Ambient temperatures during these experiments in July and September spanned much of the nonwinter environmental temperatures occupied by these species. Ambient temperatures in October 2015 provided low temperature observations reflective of transitional periods in early spring and late fall. Metabolism was expressed in units of mg $O_2 \cdot g$ $fish^{-1} \cdot h^{-1}$ and converted to g $O_2 \cdot day^{-1}$ for the development of statistical models describing metabolism as a function of temperature and fish size for each species.

Because individual fish frequently were used for multiple metabolism observations, we used a mixed model with fish number as the random effect to describe metabolism. Generalised linear mixed-effect models within the R software package LME (R Development Core Team; www.r-project.org) were used to establish relationships between metabolism (g $O_2 \cdot day^{-1}$) and fish weight and temperature.

Consumption models

Bioenergetics models are bounded by the use of a maximum consumption (C_{max}) function that limits the feeding rate to the maximum levels observed in

laboratory under *ad libitum* feeding. The C_{max} function is of the form:

$$C_{max}(\text{g food} \cdot \text{g fish}^{-1} \cdot \text{day}^{-1}) = CA \cdot W^{CB} \cdot f(T),$$

where CA is the intercept, and CB is the slope of the size-dependent function, and $f(T)$ is the temperature dependence function. For salmonids, the temperature function [$f(T)$] has been described by the Thornton & Lessem (1978) algorithm that fits one curve to the increasing and one curve to the decreasing portion of the relationship. Experiments to determine C_{max} in fish typically require days to weeks to complete with careful control of water temperatures and weeks of acclimation. The fish culture facilities necessary for such experiments do not currently exist in Mongolia. Therefore, we used existing models of salmonid C_{max} and knowledge of the thermograph in the Eg–Uur River to derive a likely C_{max} function for lenok and grayling.

The C_{max} functions for six salmonids adjusted to the weight of a common size for lenok and grayling (250 g) show very similar peaks in consumption rates, with differences in how quickly and at what temperatures consumption declines as temperatures move away from the optimum (Fig. 1). Water temperature data from 8 July 2011 (Julian day 189) to 2 July 2012 (Julian day 184) on the Uur River show the annual thermal cycle lenok and grayling may experience (Fig. 2). The temperature logger was placed on an anchor 20 cm above the bottom in a 3-m-deep pool approximately 12 km above the confluence with the Eg River.

Nearly half the year is under ice cover and most of the open water period is characterised by daily mean water temperatures under 15 °C (Fig. 2). A limited
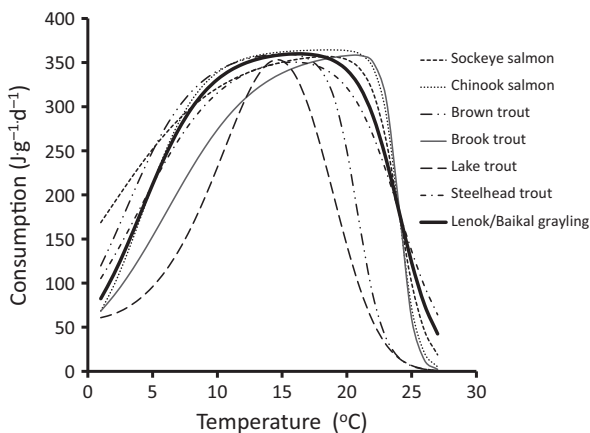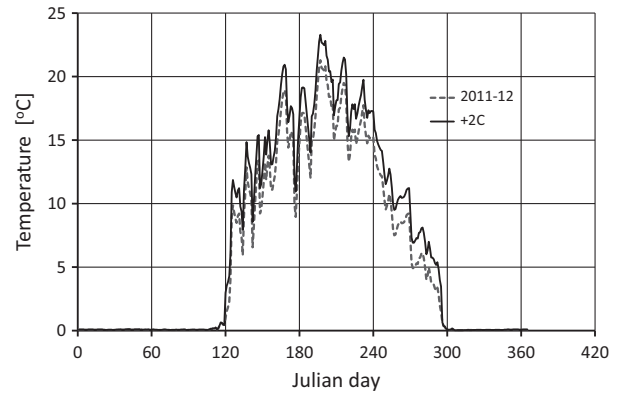

Fig. 2. Daily mean water temperatures from the Uur River, Mongolia during 8 July 2011 to 2 July 2012 (dashed line) and temperatures used to simulate a modest climate change of 2 °C during the ice-off period from Julian Day 120–296 (solid line).

growing season and low water temperatures suggest that these fish should have the capacity to feed at high levels when food is available implying the lake trout curve is too restrictive. The other salmonid species C_{max} curves showed similar magnitudes and inflection points. Therefore, we parameterised a C_{max} function for lenok and Baikal grayling that closely followed the central tendency of the other five species (Fig. 1; Table 1).

Scope for growth

Scope for growth is a measure of the potential performance of a fish at a range of environmental temperatures (Brett & Groves 1979). The typical scope for growth considers the amount of growth possible if a fish of a given size were feeding at the maximum ration (C_{max}). However, in general when reviewing studies that estimated consumption rates from field measures of growth, the typical fish is only feeding at 40–60% of C_{max} (Hartman & Margraf 1992; Hartman & Brandt 1995b; Petersen & Paukert 2005; Hartman & Cox 2008). Our assessments of scope for growth for lenok and grayling were made using both C_{max} and 50% of C_{max}. The latter to provide a realistic picture of field performance of these species. We developed the scope for growth for three typical-sized grayling (5, 100 and 250 g) and three typical-sized lenok (5, 100, 1000 g) based upon our observations of ranges of fish sizes collected during our fieldwork in Mongolia.

Model simulation

To evaluate the impact of climate change upon lenok and grayling, we conducted bioenergetics model simulations using daily mean temperature data collected between 8 July 2011 and 2 July 2012 from a temper-

Fig. 1. Comparison of the maximum consumption (C_{max}) functions for six species of salmonids standardised to a fish size of 250 g – a common size lenok or Baikal grayling in the Eg–Uur River. The thicker black line represents a generalised salmonid C_{max} function that we considered appropriate for Baikal grayling and lenok.

Table 2. Size at age of Baikal grayling and lenok as derived from Von Bertalanffy growth equations using otoliths (Tsogtsaikhan et al. In review). Length at age (total length – TL, mm) was converted to weight (WW, g) for use in the bioenergetics models using the equations: $BG = 0.000006 \cdot TL^{3.0862}$ and $LK = 0.00000070 \cdot TL^{3.0328}$, where BG and LK are weight of Baikal grayling and lenok respectively.

	Baikal grayling		Lenok	
	TL	WW	TL	WW
Age-1	154	25.3	111	12.1
Age-2	225	82.5	206	79.4
Age-3	258	126.2	286	217.7
Age-4	273	150.9	355	419.5
Age-5	280	163.4	413	668.3
Age-6	283	169.4	463	946.0
Age-7	285	172.2	506	1236.6
Age-8			542	1526.7
Age-9			573	1807.6
Age-10			599	2072.8

ature logger (TidbiT v2; Onset Computer Corporation, Bourne, MA, USA) deployed in a large pool on the Uur River. Bioenergetics models also require information on the energy content of the fish and its prey, and growth of the fish. We assumed that the energy content of grayling, lenok and their diet was 5500 $J \cdot g^{-1}$, a value within the ranges reported for carnivorous fish of similar sizes (Hartman & Brandt 1995b; Hanson et al. 1997). Growth data were obtained from otolith-aged fish from the study site collected during 2009–2013 (Tsogtsaikhan et al. In review). Total lengths at age were converted to weights (as needed by the bioenergetics model) by species-specific length mass equations generated from our collections. Weight at age used to model baseline consumption levels is included in Table 2. We assumed growth was negligible during the portion of the year when temperatures were less than 1 °C and therefore modelled only between Julian day 120 and 295.

Most climate models predict a minimum of a further 2 °C increase in temperature for Asia by 2100 (Batima et al. 2008; Pachauri et al. 2014) with some predicting as high as 5.1 °C (Sokolov et al. 2009). Our baseline temperatures indicated ice covered the river for about 6 months and that the onset of ice cover and ice break up was rapid (Fig. 2). Lacking data on changes in ice cover dates related to climate change on the river we used a conservative simplifying assumption that the date of ice cover and ice break up would remain unchanged from our baseline. We simulated a modest climate change of 2 °C by increasing our baseline temperature by 2 °C between Julian day 120 and day 295 (Fig. 2).

Two simulations evaluated climate change impacts to fish energetics. One scenario assumed fish could increase their consumption to achieve the same growth rates under the climate change

scenario as during baseline. Here, initial and final weights of an individual were maintained as in baseline and simulations rerun under the +2C thermal regime. The other evaluation assumed no compensation in prey abundance and examined the final weight of fish under +2C thermal regime when constrained by the total consumption level estimated in baseline runs.

Results

Metabolism

We measured the routine metabolism of 15 Baikal grayling and 14 lenok. Grayling ranged in size from 5 to 350 g wet weight over temperatures ranging from 2.1 to 18.9 °C. Measures were taken on lenok from 5 to 1199 g over a range of temperatures from 7.5 to 25.2 °C. A total of 54 and 73 observations (weight/temperature combination) of metabolism were included for Baikal grayling and lenok respectively.

The generalised linear mixed-effect model found both fish weight and temperature to be significantly related to routine metabolic rates of Baikal grayling and lenok (Table 3). Using the size-dependent exponent derived from regression (Table 3), we adjusted the metabolism measures to that of the average sized fish for each species. Lenok and Baikal grayling metabolism appeared to be an exponential function of water temperature (Fig. 3).

The metabolism data were analysed using the mixed-effect linear model to estimate the parameters RA, RB and RQ. We followed the $\log_e$ transformations and conversions of metabolism data from g $O_2 \cdot day^{-1}$ to $g \cdot g^{-1} \cdot day^{-1}$ using the ratio of Elliott & Davidson's (1975) oxycalorific equivalent (13,560 $J \cdot g^{-1}$ O_2) and energy density of these salmonids (5500 $J \cdot g^{-1}$). The solution to the models for

Table 3. Generalised linear mixed-effect model predicting metabolism (M) of Baikal grayling and lenok (g $O_2 \cdot g^{-1} \cdot day^{-1}$) as a function of fish weight (W) and temperature (T). Model is of the form: $M = RA \cdot W^{RB} \cdot e^{RQ \times T}$. The approximate 95% confidence intervals about each variable are shown in parentheses below each value. Oxygen is converted into units of energy in the fish bioenergetics model (Hanson et al. 1997) using the oxycalorific equivalent 13,560 $J \cdot g^{-1}$ (Elliott & Davidson 1975).

Species	Value	t-Value	$Pr(>|t|)$
Baikal grayling			
RA	0.00145 (0.0009, 0.0024)	−25.35	<0.0001
RB	−0.173 (−0.069, −0.275)	16.87	<0.0001
RQ	0.115 (0.098, 0.131)	13.87	<0.0001
Lenok			
RA	0.00249 (0.0019, 0.0025)	−43.58	<0.0001
RB	0.175 (−0.132, −0.218)	37.46	<0.0001
RQ	0.0848 (0.0715, 0.0981)	12.51	<0.0001

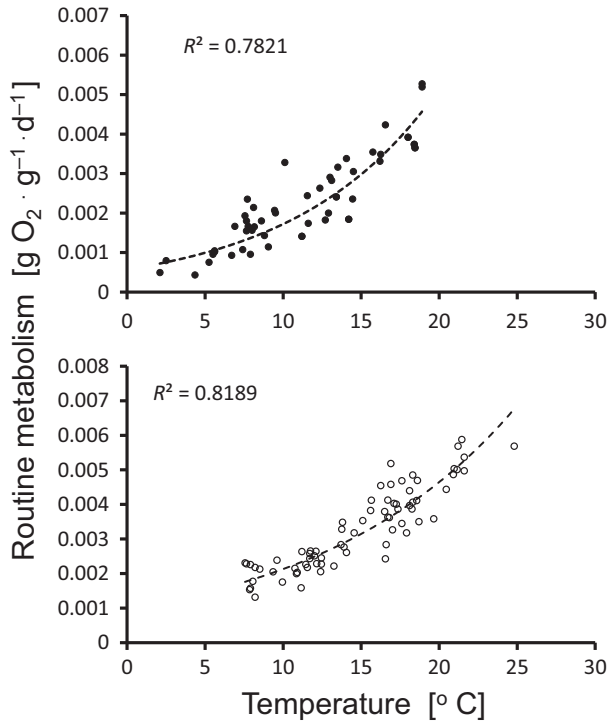*Fig. 3.* Routine metabolism rates (g $O_2 \cdot g^{-1} \cdot day^{-1}$) as a function of temperature for Baikal grayling and lenok adjusted to a common size of 250 g using the size dependence function we derived for this data reported in Table 3. Measures are on individual fish measured under natural conditions riverside in Mongolia.

Baikal grayling and lenok is:

$$M_{grayling} = 0.00145 \cdot W^{-0.173} \cdot e^{(0.115 \times T)},$$

$$M_{lenok} = 0.00225 \cdot W^{-0.178} \cdot e^{(0.0848 \times T)}.$$

Scope for growth

The scope for growth for Baikal grayling and lenok suggests the theoretical upper limits of temperature at which growth can occur are similar (Figs 4 and 5). Under *ad libitum* feeding (100% of C_{max}), all sizes of both species can achieve positive growth at temperatures up to about 23 °C. However, under more realistic feeding conditions of 50% of C_{max} differences emerge between the species and across sizes within a species.

In the scopes for growth, metabolism costs increase exponentially with temperature while other cost or loss terms (Egestion, Excretion and Specific Dynamic Action) follow the relationship between consumption and temperature. As a result, the growth curves reach zero prior to consumption doing so. This point where growth is zero is a break-even temperature where fish can expect to potentially subsist given continued food

supplies. For grayling feeding at the 50% C_{max} level, the break-even temperature is 1–3 °C lower than when feeding at C_{max} (Fig. 4). The trend is more pronounced moving from smaller to larger sized fish, particularly for lenok where the difference in break-even temperatures is as large as 4 °C for a 1000 g individual (Fig. 5).

Bioenergetics simulations

Consumption
Baseline simulations showed that Baikal grayling and lenok required increasing levels of consumption across age classes to grow as described in Table 2. Grayling required 330 g of food to grow from 25.3 to 82.5 g as age-1 fish, and this level increased to 643 g to grow from 169.4 to 172.2 g as age-6 fish (Fig. 6). Lenok required 354 g of food to grow from 12.1 to 79.4 g as age-1 fish. Consumption increased for lenok with age, peaking at age-9 with 6384 g of food (Fig. 6).

Under the climate change scenario of increased water temperature by 2 °C, Baikal grayling and lenok would need to increase their consumption to grow at the same rates as in baseline conditions (Fig. 6). Age-1 grayling consumption would increase by 14.0% to 313 g per fish to attain the same final weight as under baseline. Age-6 grayling consumption would increase by 23.4% under the climate change scenario to match baseline growth (Fig. 6). Lenok were not as strongly affected by the effects of increased temperature with age-1 consumption increasing 7.6% and age-9 consumption increasing by 16.0% under the climate change scenario (Fig. 6).

The effects of climate change are more dramatic when considering the cumulative impacts of increased predator demand to achieve similar sizes at age to baseline. Growing from age-1 through age-6 requires 2777 g for grayling and growing from age-1 through age-9 requires 22,257 g for lenok. These values increase by 21.4% and 14.64% for grayling and lenok, respectively, to 3372 g and 25,506 g under the +2 °C climate change scenario. If we assume a typical prey item has a live weight of 0.1 g, then the 2 °C increase in temperature would increase the demand for prey by 5947 per Baikal grayling growing from age-1 through age-6 and lenok prey demand would increase by 32,489 to grow from age-1 through age-9.

Growth
Under the climate change scenario, growth was suppressed in lenok and negative in Baikal grayling when feeding levels were maintained at baseline levels (Fig. 6). Without increasing feeding levels, positive growth did not occur for age-2 and older
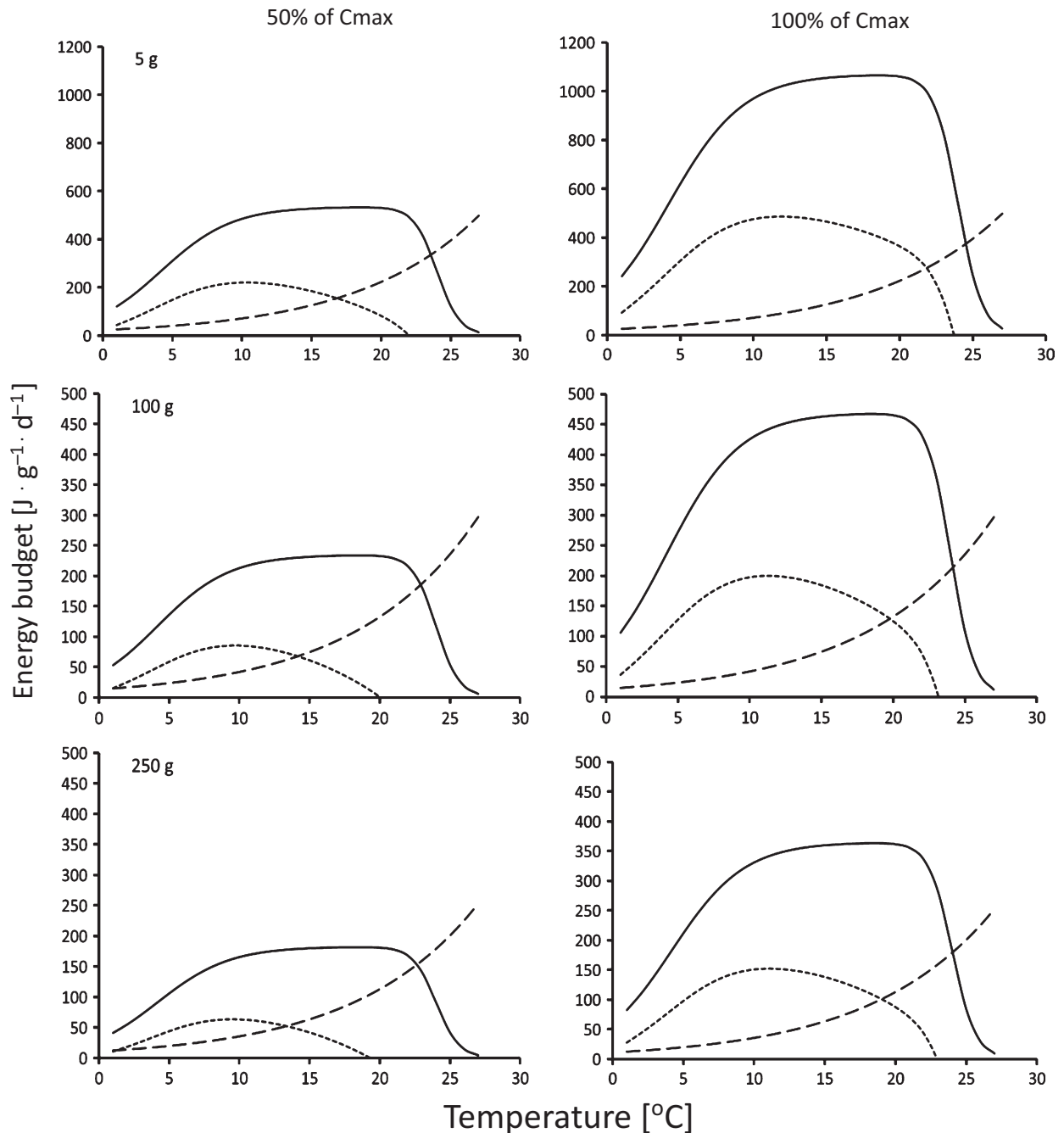
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Fig. 4. The scope for growth for three sizes of Baikal grayling: 5 g (top panels); 100 g (centre panels); and 250 g (bottom panels). For each size fish, the panels in the right hand column represent fish feeding at C_{max}, while the panels in the left hand column represent the scope for growth possible feeding at the more realistic 50% of *ad libitum* level. Here, the solid line represents consumption, long dashed line is metabolism, and the short dashed line is growth.

grayling. Lenok continued to grow under CC + 2 temperatures. Within a cohort, lenok weights were 20.7–51.5% lower under climate change temperatures (Fig. 6). When consumption was maintained at levels from baseline runs, the growth of grayling and lenok was reduced under the 2 °C climate change thermal conditions. Grayling reached a weight of 55.4 g by age-2 (compared with 82.5 g under baseline conditions) but weights declined for successive cohorts.

Lenok reached a weight of 1005 g by age-10 under climate change, but this was 1068 g less than under baseline.

Discussion

The metabolism measurements on lenok and Baikal grayling provide a first look at the species thermal ecology as well as a foundation for bioenergetics
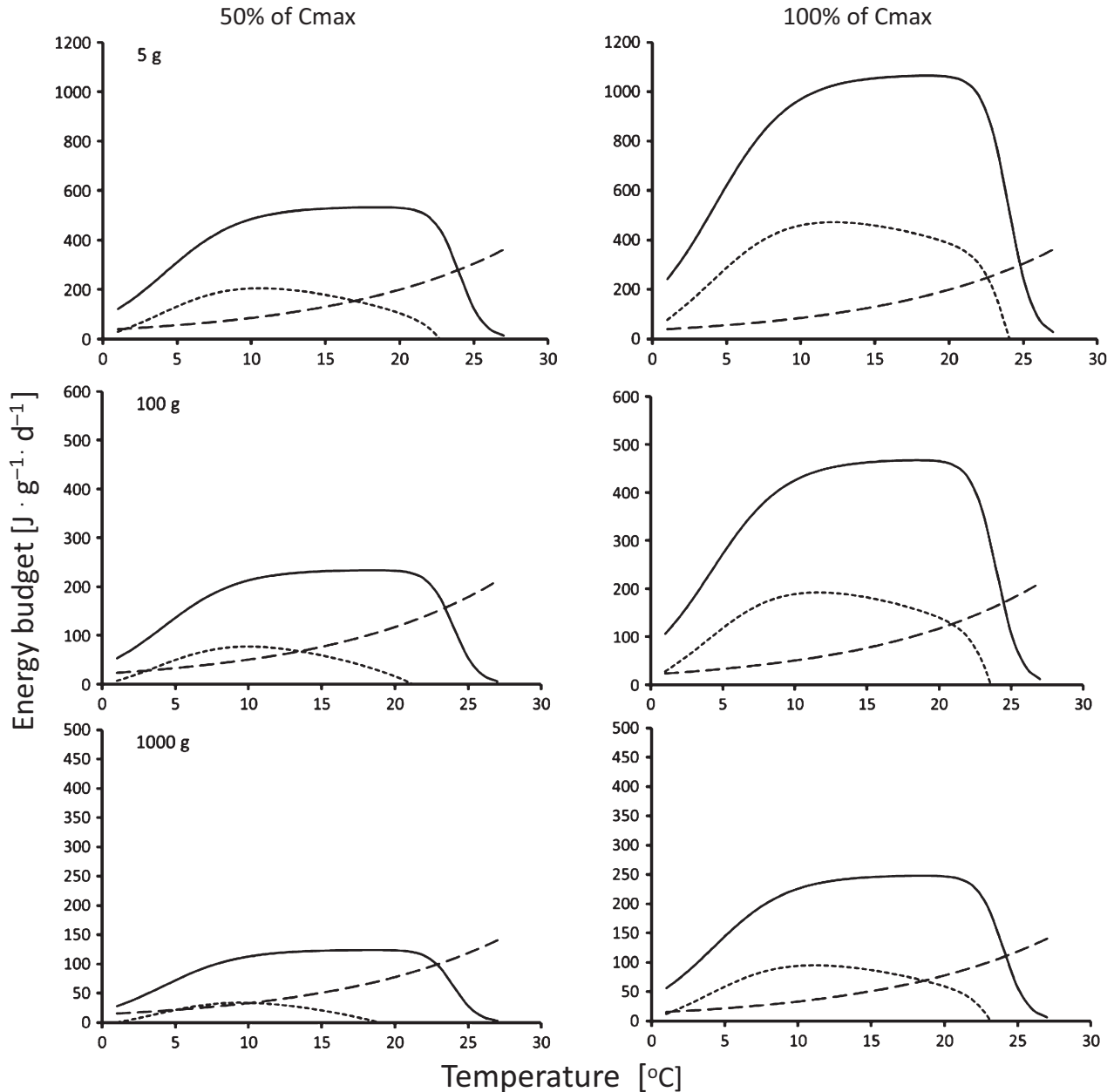
Fig. 5. The scope for growth for three sizes of lenok: 5 g (top panels); 100 g (second row of panels) and 1000 g (third row of panels). For each size fish, the panels on the right represent fish feeding at C_{max}, while those on the left represent fish feeding at the more realistic 50% of *ad libitum* level. Here, the solid line represents consumption, long dashed line is metabolism, and the short dashed line is growth.

models of these species. Both species metabolic rates increased exponentially with temperature as has been found with other salmonid species (Elliott 1976a; Stewart & Ibarra 1991; Rand et al. 1993; Hartman & Cox 2008; Kepler 2013). However, our stream-side metabolism measures on wild-caught fish that relied on environmental temperatures rather than strict laboratory control may be questioned. Metabolic measures on lenok are lacking in the literature. However, for Baikal grayling, two comparisons are available. Deegan et al. (2005) published several points on resting metabolic rates of the closely related North

American Arctic grayling *Thymallus arcticus* and Stolbov & Alikin (1978) presented data on the Baikal grayling that can be used for comparison with our stream-side measures.

The metabolic rates measured stream-side compared favourably with the available measures from other Baikal grayling and from North American Arctic grayling (Fig. 7), lending confidence that our measures under field conditions were accurate. North American Arctic grayling measures were higher than ours at 6° C and in line with ours at 12 and 20 °C. The Deegan et al. (2005) measures above 20 °C
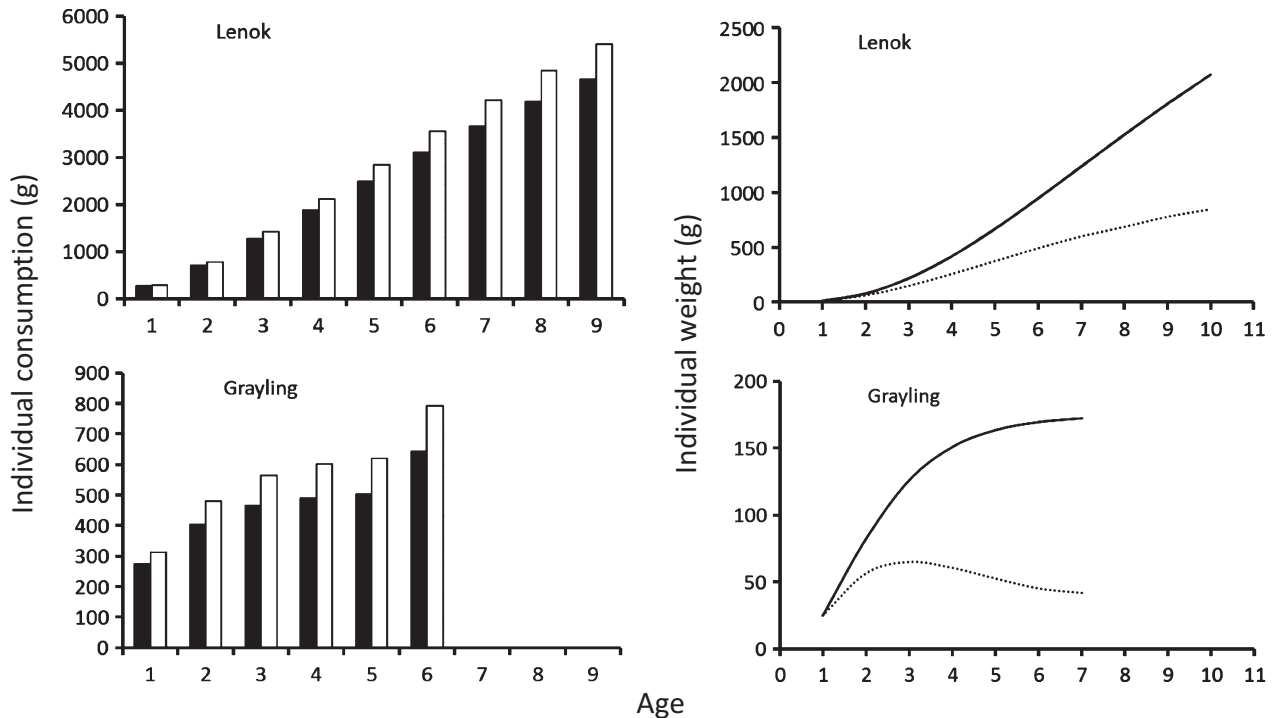
Fig. 6. Individual annual consumption (left panels) and growth (right panels) for lenok (top) and Baikal grayling (bottom) under baseline (2011–2012) water temperatures and under $a + 2\ °C$ climate change scenario. Consumption by an individual of each age class is shown for baseline (black bars) and +2 °C (open bars) under the assumption that growth remained unchanged and fish were able to feed at higher levels under +2 °C. The weight of individuals of each cohort is shown in the right hand column under baseline temperatures (solid line) and under +2 °C scenarios (dotted line) with consumption limited to baseline levels.

appear to level off and decline with increasing temperature, but these temperatures exceeded those at which we were able to measure grayling metabolism in the field so direct comparison is not possible. The Deegan et al. (2005) data were estimated from the intercept of the regression line on their Fig. 2 for a 1 g fish, then adjusted to 285 g using the size-dependence we derived for Baikal grayling. At low temperatures (6–12 °C), Deegan et al.'s (2005) Arctic grayling data lacked temperature dependence and greatly exceeded metabolism measures of other sources at 6 °C. Metabolism measures for Baikal grayling reported in Stolbov & Alikin (1978) fell in line with our least squares regression line for Eg–Uur River fish suggesting our measures were accurate. We assert that although there are no metabolic measures in the literature available for comparison with our field measures for lenok that they are also likely representative of measures taken under more controlled laboratory conditions as the methods we used for lenok were identical to those used for Baikal grayling.

Model behaviour at temperatures above 20 °C is important to understanding thermal limits of Baikal grayling and lenok. Our metabolism models continue to increase exponentially at high temperatures which may overestimate metabolic costs for Baikal grayling.
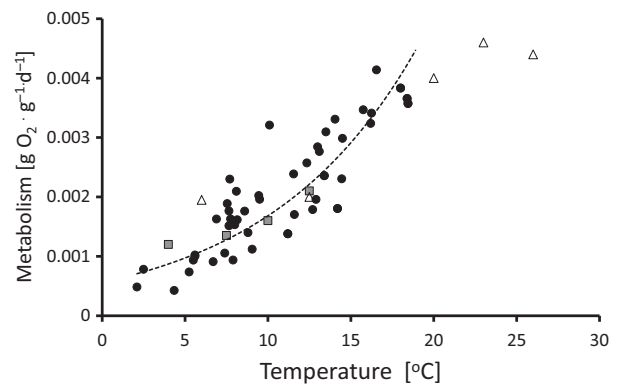

Fig. 7. Comparison of routine metabolism rates (g $O_2 \cdot g^{-1} \cdot day^{-1}$) found in this study (filled circles and least squares line), North American Arctic grayling (open triangles, Deegan et al. 2005) and Baikal grayling (filled squares, Stolbov & Alikin 1978). Data from this study and Deegan et al. (2005) were adjusted to that of a 285 g fish using the size-dependent exponent (-0.173 see Table 1) for comparison with Baikal grayling measurements that were taken on fish ranging from 270 to 300 mm.

However, given the declining maximum consumption function between 20 and 25 °C (Figs 4 and 5), the differences in temperatures that would support growth would be small (~1 °C). Our metabolism measures for lenok extend to 25 °C, so we are confident of an exponential function for that relationship. Although more work on the thermal ecology of these

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species is warranted, we believe our bioenergetics models for lenok and Baikal grayling are reasonable starting points for understanding energy budgets for these species and how they may respond to climate change.

In many systems, fish are able to behaviourally thermoregulate, seeking out optimum or less stressful temperatures. Often in lotic systems during warm summer months cooler temperatures may be found in deep pools which thermally stratify or at cooler groundwater seeps or tributaries (Nielsen et al. 1994; Petty et al. 2012). The thermal preference for Baikal grayling and lenok is currently unknown. However, the preferred temperature often falls near the optimum temperature for growth (Jobling 1981). Highest growth rates for these species vary somewhat depending on the size and feeding level, but were generally about 8–12 °C for grayling and lenok in our scopes for growth. This suggests during warmest summer temperatures that these species should seek out cooler water habitats. Field observations by the authors tend to bear this out with these species often found inside the mouths of tributaries during summer. The Eg–Uur River is well mixed with no evidence of thermal stratification during summer suggesting seeps and cooler tributaries are the only sources of thermal refugia available to these fishes.

The scope for growth of Baikal grayling and lenok depicts two species already living near their thermal limits in the Eg–Uur River. Under conditions of unlimited food, the bioenergetics models predict growth over a wide range of temperatures for all modelled fish sizes. However, even under *ad libitum* feeding, growth ceases above about 22–23 °C for larger individuals. At a more realistic feeding level of 50% of maximum ration, growth is possible only below 18–22.5 and 19–22 °C for lenok and Baikal grayling respectively. Our temperature logger data show that temperatures regularly exceeded the 18 °C threshold in summer likely impacting feeding and growth of all but the smallest fish. When feeding at 50% of C_{max}, the growth threshold is 20–21 °C for grayling and lenok. In 2011–2012, mean daily temperatures in the Uur River exceeded this limit on 6 days (all consecutive). Under the +2 °C scenario, the threshold for 100 g fish would be exceeded on 12–21 days – or up to 12% of the ice-free days available for growth. Diet overlap between lenok and Baikal grayling in the Eg–Uur River is high (Olson et al. *in press*), and if warming temperatures lead to higher consumption, competition for food resources between these species is likely to increase.

Conditions are less favourable for larger fish. Under baseline temperatures (2011–2012), a 1000 g lenok (at 50% C_{max}) would have found temperatures exceeded the break-even point for growth on

21 days. However, under the +2 °C climate change scenario small fish would experience zero or negative growth on 12 days (9 consecutive days) and a large lenok would not grow for 22% of the ice-free period (39 of 175 days). Field observations support these thermal limits. Catch rates of lenok and grayling on the Eg River during the hottest part of the summer are typically highest in or near springs where temperatures are colder than in the mainstem (Jensen, unpublished data). It is important to note although the smaller lenok and grayling experienced fewer days of zero or negative growth than the larger fish, those days may have a larger impact on the growth and survival of small fish due to their higher specific metabolic rates (Clarke & Johnston 1999) and lower energy reserves (Thompson et al. 1991; Post & Parkinson 2001; Heermann et al. 2009) relative to larger fish.

The implications of this study suggest further climate warming will likely result in declines in numbers and distribution of Baikal grayling and lenok. The prevailing predictions in the literature are for warm water species to potentially see increases in growth (Rypel 2009; Pease & Paukert 2014) and cold water species to see declines in growth (Keleher & Rahel 1996; Jonsson & Jonsson 2009; Isaak et al. 2010, 2012) as a result of climate warming. Although increased feeding levels can offset some of the growth reductions predicted by the bioenergetics models under $a + 2$ °C thermal regime, it is not realistic to expect fish that fed at 40–50% of maximum consumption under baseline conditions to achieve 100% of maximum consumption under climate warming. As mortality rates generally decline with increasing size in fish (Sogard 1997), reduced growth rates associated with warming temperatures may be expected to result in reduced population levels even if direct thermal mortality is not experienced.

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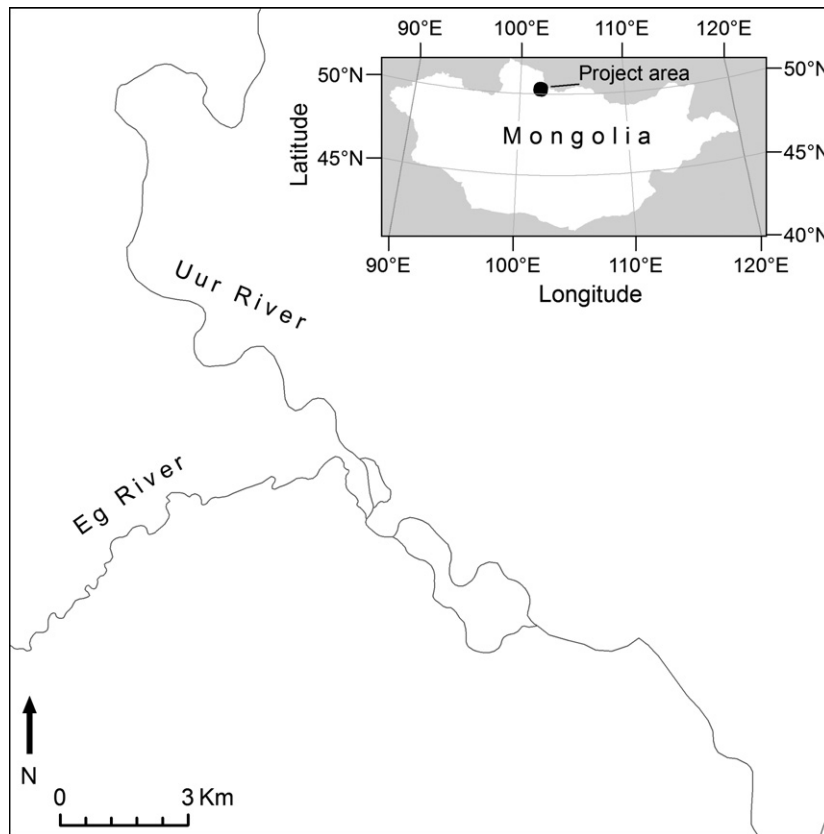
Appendix

Fig. A1. Study areas within 10 km of the confluence of the Eg and Uur Rivers in northern Mongolia (see inset) where stream side metabolism measures were made for Baikal grayling and Lenok.