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Estimating Differences in Growth and Metabolism in Two Spatially Segregated Groups of Columbia River White Sturgeon Using a Field-Based Bioenergetics Model

Brett T. van Poorten* and Steven O. McAdam

Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver, B.C., Canada, V6T 1Z4

British Columbia Ministry of Environment, 2202 Main Mall, Vancouver, B.C., Canada, V6T 1Z4

Abstract: Recovery of white sturgeon in the Upper Columbia River continues to be limited by our understanding of the species' biology, including factors which influence growth, habitat selection and their interaction. Sampling challenges in large rivers coupled with limitations to invasive research on endangered species also create specific challenges to the detailed understanding of growth and metabolism. A new bioenergetics modelling approach which estimates basic parameters from field data, specifically length-increment and length-at-age data was therefore applied in order to provide novel insights into white sturgeon growth and metabolism. A large existing capture database was used to examine two groups of white sturgeon which preferentially occupy habitats in the transboundary section of the Upper Columbia River downstream of Keenleyside Dam (HLK group) or further downstream near Waneta (WAN group). Successful application of the model showed differences in both growth and metabolism. Mean annual food intake appears similar for the two groups; however growth was more rapid for the HLK group. This resulted from a higher metabolic rate for the WAN group coupled with contrasts in seasonal food intake. Growth differences between groups lead to slower growth and later maturity for the WAN group. In aggregate, results suggest that the WAN group may be food limited and ultimately may have lower lifetime fecundity due its apparently later maturity and the possibility that lower energy intake might increase the interspawning interval. Finally, the functional structure of the model leads to concerns that both groups are approaching the thermal maxima for consumption, which may lead to reductions in body growth if increases in water temperature continue. Overall, application of this bioenergetics model identified new avenues for study which should assist conservation efforts in this species.

Keywords: Bioenergetics, metabolism, white sturgeon, group-level difference.

INTRODUCTION

White sturgeon (*Acipenser transmontanus*) is a long-lived species from an ancient lineage and is a significant conservation concern throughout most of its range. Historic harvest led to severe population declines in the Sacramento, Columbia, and Fraser [1-4] rivers, the three main rivers where reproductive populations occur. Contemporary impacts are primarily dominated by the effects of hydroelectric development and flow regulation in all three river basins [5], with the notable exclusion of the mainstream Fraser where dams are absent. The continued decline of white sturgeon in several spatially isolated populations within these watersheds has led to the species being listed as endangered in Canada [6, 7] and the Kootenai River within the Columbia drainage in the United States [8].

White Sturgeon are distributed through much of the Columbia River watershed and are believed to have historically ranged from the Pacific Ocean upstream into the headwaters of the Columbia and Kootenay (Kootenai in the United States) rivers [2]. Subsequently, the distribution of white sturgeon in the Columbia River watershed has been repeatedly subdivided due to the construction of numerous dams since 1897 [2]. While conservation concerns have been expressed for this species for some time [9] successful management actions that could lead to population recovery continues to be limited by our basic biological understanding of the species [2]. For example, changes in the white sturgeon prey base within the river have been indicated as a potential conservation concern [10, 11], yet this concern is based on a fairly limited understanding of adult diet composition. Variation in relative weight across the species' range [12] indicates variation in growth potential, with such variation being the combined effect of variability in food, environmental conditions (*i.e.* water temperature) and the intrinsic population characteristics. Ultimately all of these factors also affect fecundity and population viability, making their evaluating causes of variation of particular interest to this species. Past identification of growth differences in the Snake River [13], and particularly Beamesderfer's [12] comparison of relative weight, suggests that potentially informative differences between populations should be identifiable.

Bioenergetics models provide useful tools for the analysis of growth patterns, and particularly determining differences in growth and attributing these differences to the combined effects of consumption and metabolism. Unfortunately, most bioenergetics models require the use of extensive laboratory studies across a range of body sizes and wa-

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*Address correspondence to this author at the Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver, B.C., Canada, V6T 1Z4, Canada; Tel: 604-822-0046; Fax: 604-822-8934;
E-mail: b.vanpoorten@fisheries.ubc.ca

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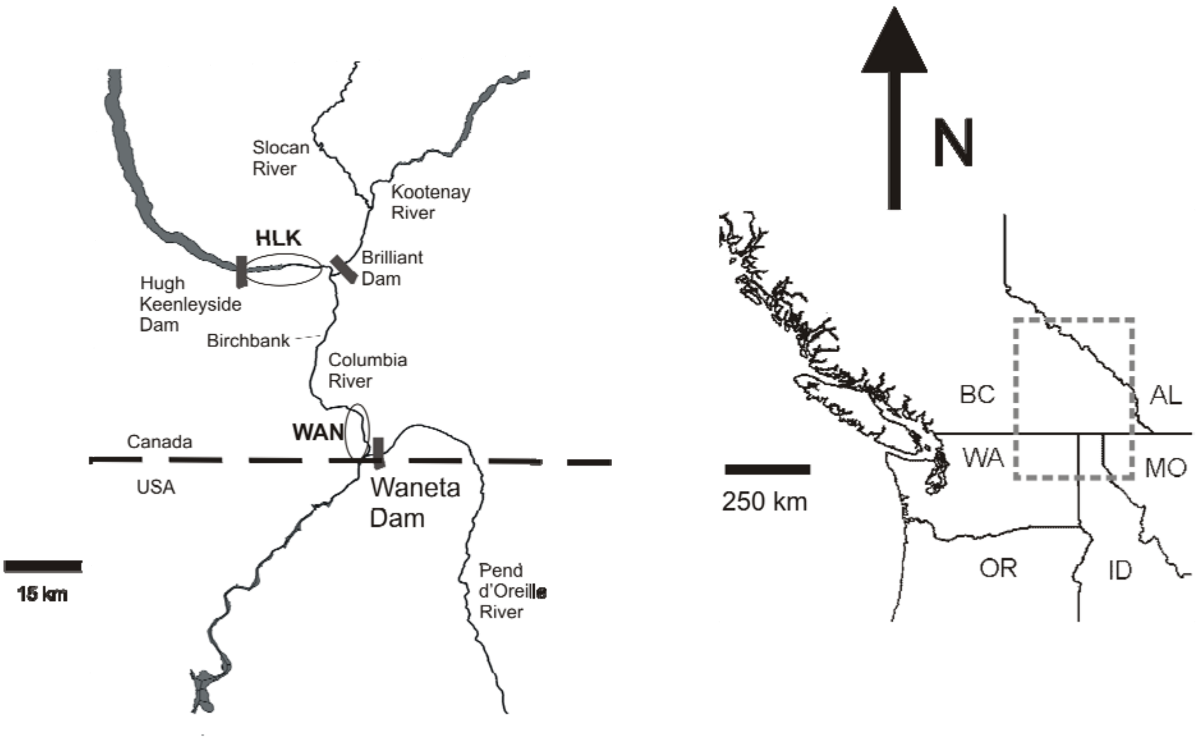

Fig. (1). Map of the transboundary reach of the upper Columbia River (left) showing its position within Western North America (right). While white sturgeon occur throughout the transboundary reach this analysis focused on fish which preferentially occupied the two areas indicated by HLK and WAN. Only principal dams adjacent to this river reach are indicated. Temperature records were from the HLK area and Birchbank.

ter temperatures. When studying endangered species with low population abundance levels, such methods may be practically impossible. The recent formulation of a field-based bioenergetics model by Walters and Essington [14] informed by commonly collected field data provides a useful alternative for research in situations where population-level laboratory studies are prohibitive. This model uses information commonly collected in field-based mark-recapture studies; namely length-increment and length-at-age data. Using these data means that a wide range of sizes and ages of fish can be sampled across the full spectrum of temperatures experienced by fish in the wild.

White sturgeon in the transboundary reach of the Upper Columbia River (UCR) have been monitored extensively since the early 1990's, and therefore provide the long term resampling dataset required for such a modelling exercise. Historically white sturgeon in this area would have had access to marine derived nutrients from anadromous Pacific salmon, however, anadromous salmon have been absent from the upper basin since the completion of Grand Coulee Dam in 1942. Additionally nutrient trapping by upstream reservoirs may also limit productivity [15, 16], though contemporary fertilization in the reservoirs [16, 17] may replace some of this productivity. As a result of these various past impacts, factors affecting growth have been considered a potential contributor to recruitment failure in this population [10] and are similarly a concern for other populations [11].

An additional interesting feature of the UCR white sturgeon is the recent identification of genetic differences [18] amongst spatially segregated groups of fish within this larger unbroken habitat area. The tendency to occupy different habitats [7] means that growth modelling offers the opportunity to examine the presence of differences between identified groups, as well as a means to develop hypotheses regarding the contribution of environmental and genetic factors, which can both affect growth patterns [19]. Environmental influences, particularly temperature can affect both metabolic rates (metabolism typically increases with temperature; [20]), as well as consumption and food availability (both predator and prey organisms increase foraging time to meet their respective rising metabolic rates). Since metabolic rates are primarily genetically determined [18], which can lead to growth differences between groups [19], evaluation of the different components within a growth model provides the basis for understanding the contribution of both extrinsic and intrinsic factors. In the present case, evaluating the sources of any differences may help identify important variation in either the habitat conditions or intrinsic group-specific characteristics. We apply the bioenergetics model described in Walters and Essington [14] to length-increment and length-at-age data available for two groups of white sturgeon in the transboundary reach of the UCR. One group, which we refer to as the Keenleyside group, or HLK, resides within 6.5 km downstream of the Hugh L. Keenleyside Dam (Fig. **1**). The second group, which we refer to as the Waneta group or WAN, resides from Fort Shepard (river km 52) to Waneta (river km 57), upstream of the US Border and adjacent to the Waneta dam (Fig. **1**). The identification of relatively high fidelity to capture areas or a particular river section [2, 7], suggests that any differences between groups may reflect both genetic and/or small-scale environmental differ-

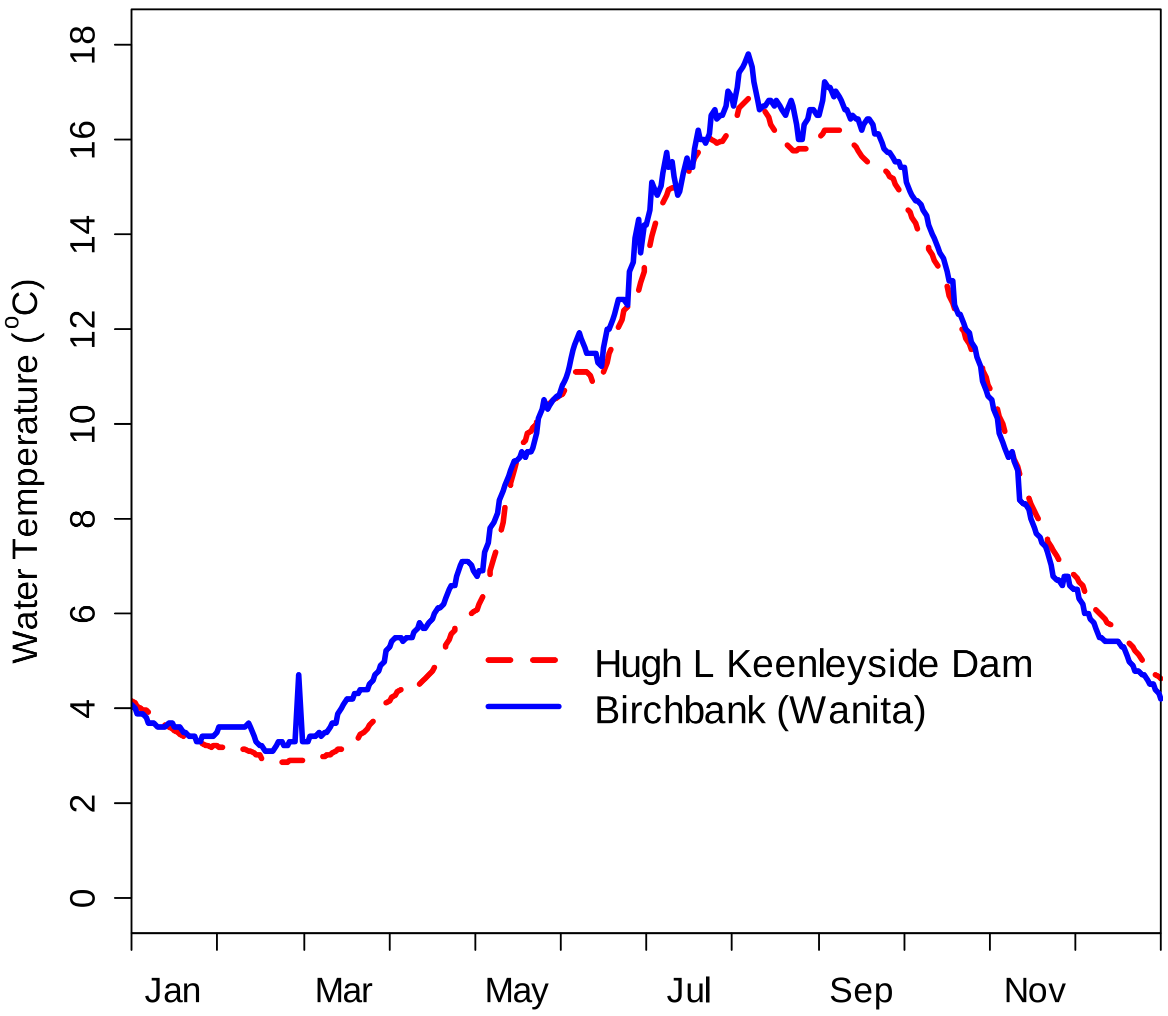

Fig. (2). Five-year mean daily temperatures measured from 1990 to 1995 immediately downstream of the Hugh L. Keenleyside Dam in the natal waters of the Keenleyside white sturgeon group and at Birchbank, immediately upstream of the natal waters of the Waneta white sturgeon group.

ences. Fitting this model to the available data provides estimates of mass- and temperature-specific energy intake and metabolism rates for each group. Evaluation of potential causes of variation should provide population specific insights which may contribute the conservation of this species.

METHODS

Length-at-age and length-increment data has been collected from setline sampling conducted in the Canadian portion of the Upper Columbia River (UCR) at different sites primarily since 1990. All fish captured have been spaghetti- or PIT-tagged and released after measurements of lengths and weights were collected. Some of these same individuals also had fin-rays sampled for later age analysis. A subset of fish also had reproductive status evaluated.

Fish used in this study included those caught two or more times since records started. While recapture records indicate a variety of locations where fish have been repeatedly caught, sufficient data was only available for the areas occupied by the HLK and WAN groups, therefore fish residing in other areas of the transboundary reach were not included in this analysis. Individual fish were assigned to either group based on the river section where captures occurred most often, with individuals caught an equal number of times in different areas removed from the dataset.

Two types of data were available for the analysis: growth-increment data of fish for which no age information is available; and growth-increment data of fish that had been aged. For fish that had been aged at least once, ages for capture events without an age were assigned an age by simply adding or subtracting the inter-sampling interval from the sample date for which estimated age is available. In cases where more than one age was available, mean age was interpolated.

Within the model [14], temperature acts both on consumption and metabolic rates in individuals. Temperatures used in the model are daily five-year mean temperatures from 1990 to 1995 (Fig. **2**). Temperatures used for the HLK group were recorded immediately downstream of the Keenleyside dam and temperatures used for the WAN group, which include inputs from the Kootenay River, are from a hydrology monitoring station at Birchbank, upstream of the Pend d'Oreille confluence (Fig. **1**). While the Pend d'Oreille River can affect temperatures in a portion of habitat used by the WAN group via entrainment into the upstream Waneta Eddy, we assume this effect is null. Keenleyside water temperatures peak at 16.8°C and have a mean annual temperature of 9.1°C. Birchbank water temperatures, assumed to represent temperatures experienced by the WAN group of white sturgeon, peak at 17.8°C and have a mean annual temperature of 9.4°C.

Data for fish maturity were based on the classifications system of Conte *et al.* [21], which describes seven progressive stages of maturity for each sex, from immature to mature and spent. These classifications were converted into only two categories, immature or maturing/mature (0 or 1). Weight-at-50%-maturity was then designated by ranking fish by weight, and identifying the weight at which the cumulative mean maturity index was half of the asymptotic value. Weight-at-maturity was assessed separately for males and females (43.2 kg and 24.1 kg, respectively) and then an average value across sexes (33.7 kg) was used as the rule for size-at-first spawning.

MODEL DESCRIPTION

Growth and metabolism of both groups were assessed using the bioenergetics model described in Walters and Essington [14]. This model takes growth information from tag-recapture (length at tagging, length at recapture, time interval between events) and length-at-age data to estimate various bioenergetics parameters for that group. The basic bioenergetics model takes the form [14]

$$\frac{dW}{dt} = HW^{d} f_c\left(T\left(t\right)\right) - mW^{n} f_m\left(T\left(t\right)\right) \tag{1}$$

where the first and second terms are energy intake and metabolism, respectively. H is a mass normalized rate of mass acquisition, W is whole-body mass, d is a scalar relating energy intake to mass, m is a mass normalized rate of mass loss and n is a scalar relating metabolism to mass. The two terms f_c and f_m are functions relating energy intake and metabolism to temperature at time t ($T(t)$). They take the form [14]

$$f_c\left(T\right) = Q_c^{\,T-\bar{T}/_{10}} \frac{e^{-g\left(T-T_m\right)}}{1+e^{-g\left(T-T_m\right)}} \tag{2}$$

$$f_m\left(T\right) = Q_m^{\,T-\bar{T}/_{10}}\,. \tag{3}$$

Equation 2 describes energy intake initially increasing at a rate Q_c, but begins to decline at higher temperatures to a point (T_m) where it is half that predicted from Q_c and continues to decline at a rate g. We assume g=0.39 and T_m=22, which is identical to the function derived in Bevelhimer [13], and implies a maximum consumption at 20°C and a maximum feeding temperature of 28°C which is similar to other sturgeon species [22]. Equation 3 describes metabolism increasing exponentially at a rate of Q_m for every 10° increase above the mean annual temperature, $\bar{T}$.

Walters and Essington [14] further define their Seasonal Reproduction, Skeletal Allocation (SRSA) model by assuming that mass is allocated separately to skeletal (W_s) and metabolizeable mass (W-W_s; see equations 16-19 in Walters and Essington [14]). The SRSA model assumes that a proportion (f_s) of ingested mass is allocated to structural growth when $W_s/W=f_s$, but as much as twice the proportion of consumed weight will be diverted to metabolizeable mass when W_s/W is low. The rate at which allocation to metabolizeable structure increases in times of metabolic stress increases is defined by θ [14]. This rate was set at 0.2, which is similar to that found in Jones *et al.* [23].

Within each group, differences in consumption between individuals will result in deviations from the mean group growth trajectory. This departure (R_i) for each i individual is [14]:

$$R_i\left(a_i\right) = \frac{\bar{L}\left(a_{c,i}\right)L_{c,i} + \bar{L}\left(a_{c,i}+\Delta t\right)L_{r,i} + \sigma_m^2/\sigma_R^2}{\bar{L}\left(a_{c,i}\right)^2 + \bar{L}\left(a_{c,i}+\Delta t\right)^2 + \sigma_m^2/\sigma_R^2} \tag{4}$$

where $L_{c,i}$ and $L_{r,i}$ are observed length at capture and recapture for individual i and $\bar{L}\left(a_{c,i}\right)$ and $\bar{L}\left(a_{c,i}+\Delta t\right)$ are model estimated lengths at capture and recapture for the same individual. The departures estimated in equation 4 can be calculated for each data type (tagged fish with and without age information). For tagged fish without age information, the maximum likelihood estimate for the age of individual i at tagging is found by searching over discrete ages $a_{c,i}$. For tagged fish for which age information exists, $a_{c,i}$ is simply the age at tagging. These departures are then used in equation 21 in Walters and Essington [14] to calculate the log-likelihood of the model fit to the data. Measurement error variance (σ^2_m) was assessed using fish captured and recaptured within seven days and calculating the root mean square difference between the two measurements. Coefficient of variation in asymptotic size, which is used to calculate the deviance variance (σ^2_R) was set at 0.09. All model parameters are shown in Table **1**.

The model estimates growth in length and weight by estimating the four main bioenergetics parameters (H, m, d, n: equation 1) as well as the two Q_{10} parameters (Q_m and Q_c: equations 2-3). Prior probability distributions for each parameter were added to the log-likelihood of the data to estimate the posterior probability distribution function for each parameter. Uniform prior distributions were used for H, m, d and Q_c. Walters and Essington [14] caution that it may not always be possible to estimate both d and n simultaneously nor Q_m and Q_c. This is indeed so with white sturgeon in the Columbia River. Therefore, normal prior distributions were used for n and Q_m. The value used for n was based on that used in Bevelhimer [13] (Table **1**). Uncertainty in n was not given in Bevelhimer, so the standard deviation was arbitrarily set at 0.01. Walters and Essington [14] suggest that Q_c should ordinarily be approximately 2.0 and so we used a normal prior probability distribution with mean of 2.0 and standard deviation of 0.1.

Model progression proceeds as follows. Individuals in each group are assumed to spawn July 1 and eggs take two weeks to hatch. Larvae are born at a length of 18 mm [2]. They are further assumed to grow with a 'normal' length-

Table 1. Parameters Used in the General Bioenergetics Model. Median Posterior Values of the Estimated Parameters are Shown with Prior Distributions Indicated Below

Parameter	Description	Keenleyside	Waneta	Units
		Value (Prior Bounds)	Value (Prior Bounds)	
a	Intercept coefficient of length-weight relationship	5.08 e^{-6}	5.08 e^{-6}	g mm^{-b}
b	Power coefficient of length-weight relationship	3.07	3.07	–
H	Net food consumption rate per W^{-d}	7.48 $U(0,20)$	8.36 $U(0,20)$	g g^{-1} yr^{-1}
m	Standard metabolic rate per W^{-n}	1.50 e^{-4} $U(0,4)$	0.07 $U(0,4)$	g g^{-1} yr^{-1}
d	Food consumption power parameter	0.55 $U(0.5,1)$	0.51 $U(0.5,1)$	–
n	Metabolism power parameter	0.78 $N(0.78,0.01)$	0.76 $N(0.78,0.01)$	–
Q_c	Proportional increase in feeding rate per 10ºC temperature increase	2.30 $U(0,10)$	4.41 $U(0,10)$	–
Q_m	Proportional increase in metabolism per 10ºC temperature increase	1.99 $N(2,0.1)$	1.91 $N(2,0.1)$	–
θ	Slope parameter for decreasing allocation to structural tissue as W_s/W varies around f^*_s	0.2	0.2	–
g	Steepness parameter for decrease in feeding at high temperatures	0.39	0.39	ºC^{-1}
T_m	Water temperature at which feeding drops by half	22	22	ºC
W_{ma}	Weight-at-maturity	32	32	kg
p_{gonad}	Proportion of body weight lost to spawning	0.14	0.14	–
Sp_{int}	Spawning interval	5	5	yr
CV_L	Coefficient of variation of individual maximum body lengths	0.09	0.09	mm^2
σ^2_m	Measurement variance for L_1 and L_2	112.0	112.0	mm^2

weight relationship assumed as $W = 5.08 \times 10^{-5} L^{3.0726}$ based on field observations [24] where W is weight in grams and L is fork length in mm. This relationship is deviated from in times of metabolic stress, outlined above. When fish exceed 33.7 kg, they are assumed to be mature. Interspawning interval was set at 5 years, which is greater than the 4 years reported in Welch and Beamesderfer [20], as suggested in the basin specific recovery plan [14]. Spawning coincides with a 14% decrease in body mass, consistent with an observed GSI of 0.14 [13]. Length- and weight-at-age are evaluated on a two-week time interval.

RESULTS

A total of 442 individual fish were identified as belonging to either the HLK or the WAN group of white sturgeon based on our assignment criteria. Of fish associated with the HLK group, 80% were captured in that area every time, and all were captured in that location in at least two-thirds of the total number of captures. Of fish associated with the WAN group, 87% were captured in that area every time and 98% were captured in that location in at least two-thirds of the total number of captures. Forty-one fish from the HLK group were aged and 176 fish from the WAN group were aged. In the HLK group, 200 instances of fish being tagged and recaptured were recorded and 117 of these involved aged individuals. Fish from the WAN group had 1581 instances of fish being tagged and recaptured and 871 of these involved aged individuals. Most time intervals between tagging and recapture were greater than one year: 20 and 235 observations occurred within the same year in the HLK and WAN groups, respectively. Only one fish was removed because it was captured an equal number of times in each area.

Estimated parameters describing consumption and metabolism offer interesting insights into the similarities and differences between the two groups (Fig. **3**; Table **1**). H represents the mean mass-specific mass acquisition and was

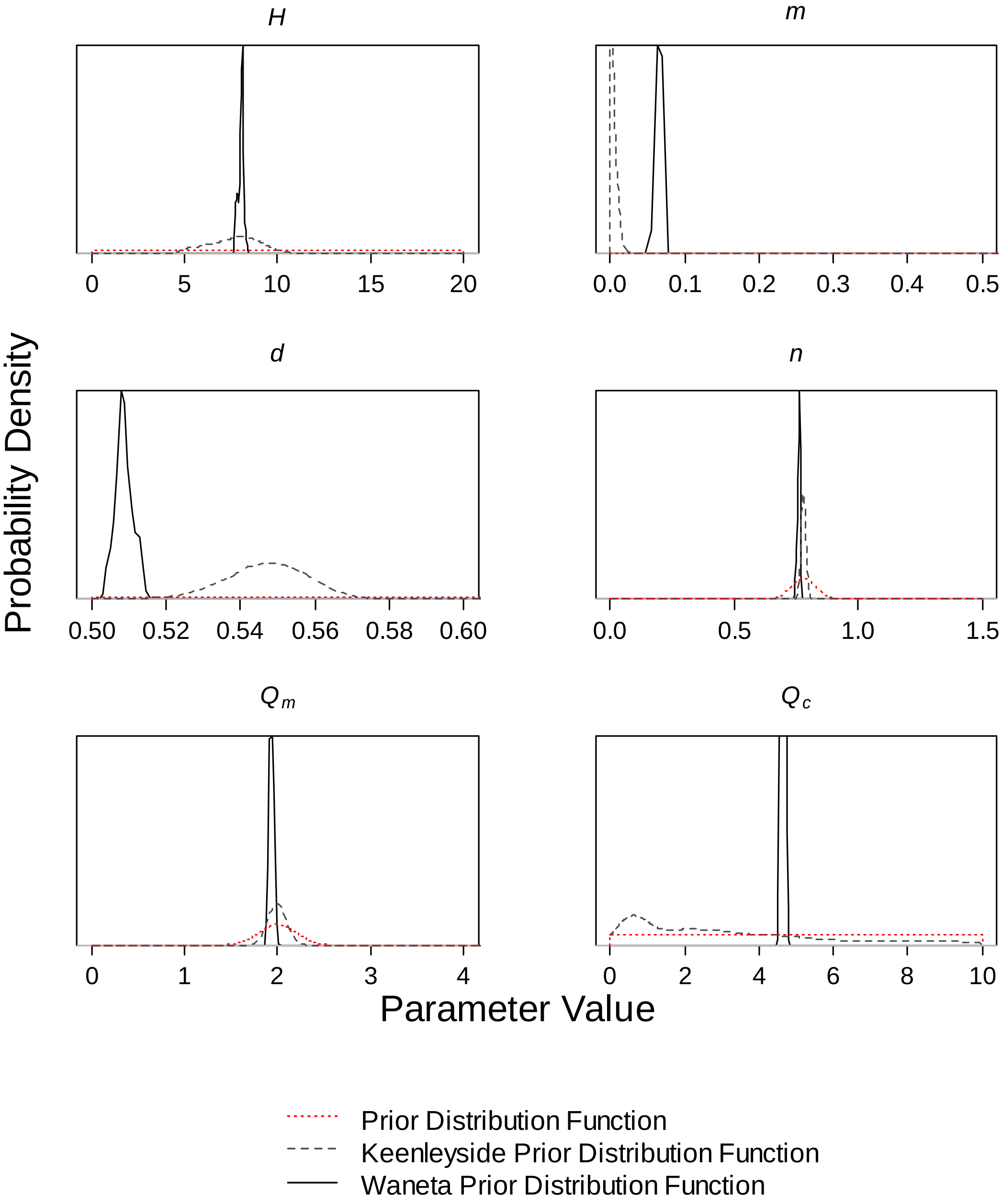

Fig. (3). Prior and posterior probability densities for the four general bioenergetics parameters (*H*, *m*, *d* and *n*) relating to consumption and metabolism, and the two Q_{10} parameters (Q_m and Q_c) which scale consumption and metabolism as a function of temperature. Densities are Gaussian smoothed approximations. The range of possible parameter values of *m*, *d* and Q_m have been truncated for better viewing of posterior distribution functions.

very similar for each of the two groups, indicating similar levels of energy intake at mean water temperatures. We find that *m*, the mass-specific rate of metabolism is lower in the HLK group. Both *d* and *n*, which are scalars relating energy intake and metabolism to mass, respectively are quite similar across groups. There was some information in the data to define the posterior distributions of *n* for each group, which were similar and had lower variance than the prior distribution. Q_m, which is the Q_{10} parameter relating metabolism to temperature is poorly defined by the data for the HLK group, but better defined for the WAN group and is approximately 2.0 for each. Finally, Q_c, which is the Q_{10} parameter relating consumption to temperature, was quite different between the groups. The low but highly variable Q_c in the HLK group indicated that most consumption occurs at low water temperature, whereas the much higher Q_c in the WAN group indicates that consumption increases with water temperatures (Fig. **3**; Table **1**).

Estimated growth is generally similar between the two white sturgeon groups, but some key differences do occur (Fig. **4**). Both groups show von Bertalanffy-like growth until maturing. Thereafter, the loss in mass following spawning

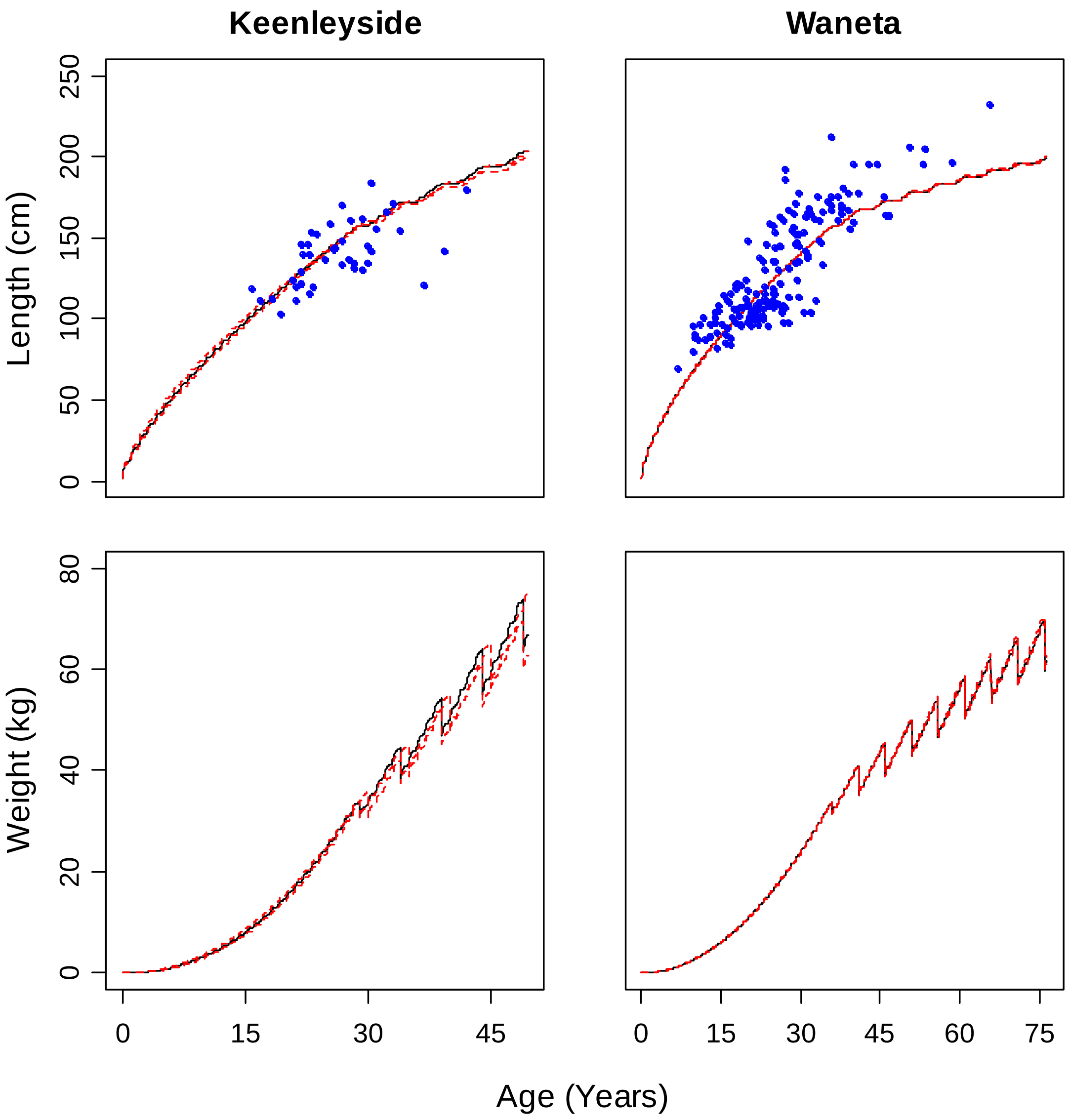

Fig. (4). Observed length-at-age (points; top panels) of white sturgeon from the Keenleyside (left) and Waneta (right) groups in the upper Columbia River. Mean and 95% credible intervals of lifetime growth are shown as solid black lines and dashed red lines, respectively. Note that the two x-axes have been truncated to cover the range of observed ages in each group.

takes at least two years to regain before growth in length can resume. This results in an estimated decline in the rate of length growth in both groups. Interestingly, most growth for the HLK group occurs in the winter, whereas growth in WAN sturgeon primarily occurs in the summer. HLK white sturgeon also achieve a higher growth rate than WAN sturgeon. Age at maturity is estimated at age 29 in HLK sturgeon as opposed to 36 in WAN sturgeon. Although WAN sturgeon do achieve a larger body size, they are also older.

DISCUSSION

Identification of differences between these two groups of white sturgeon emphasize the utility of this approach to growth modelling, not just because of the success at developing the parameter estimates from resampling data, but due to identification of differences between adjacent groups of fish in a relatively limited section of river. Identified differences generally appear to reflect spatial and temporal variation in factors such as food supply, but an intrinsic (i.e. genetic) difference between groups may also exist. Surprisingly, *H*, which relates to consumption rate, displays a substantial overlap in the posterior distributions for each group. This indicates that across seasons, individuals of both groups have similar rates of energy acquisition across years. This similarity in energy intake is offset by a distinct metabolic rate between groups. Such differences in the metabolism could result from either differences in basal metabolic rate, or may reflect a higher activity seen in the WAN group. While data to evaluate between these alternatives is not available, increased activity for the WAN group is plausible if these fish were to spend significant amounts of time in the river mainstem (rather than Fort Shepard and Waneta eddies), since water velocities are much higher in this area relative to the area occupied by the HLK group due to a greater water volume and more constricted channel. Inter-group differences in metabolism have been seen in other species [25] and can either result from or cause differences in activity and consumption [26]. Other instances of closely related groups having differences in metabolic rates are often due to adaptation to different historical environmental drivers [27], which is likely not the case here (Fig. **2**).

The consumption Q_{10} parameter (Q_c) was very different between the groups. The large variation in Q_c of the HLK group is likely due to a combination of low within-year observations and a growth temporal response to some unmeasured correlate, with food availability a likely candidate. While potential food organisms in this river reach are described in a number of monitoring studies (e.g. [28]), the specific diets of white sturgeon is not nearly so well understood, and the possibility of spatial variation in food resulting in growth differences is novel. Prior to the loss of anadromous salmonids both groups of fish were likely influenced by this same dominant seasonal food increase. However, loss of salmon as a large external input may have resulted in growth reflecting more localized variation in food availability. Given that fish in this analysis are almost exclusively older adults a high level of piscivory can be assumed, and the forage base for these two areas show clear dichotomies. White sturgeon in the vicinity of HLK should have access to food resources including fish entrained through Keenleyside Dam, as well as the more highly seasonal food sources such as spawning Kokanee (fall) and mountain whitefish (fall/winter) [28]. In contrast, feeding opportunities associated with large spawning aggregations are not readily available in areas primarily occupied by the WAN group. However, predation on seasonally abundant migrants (e.g. walleye show summer migrants into the Canadian section of this reach) might provide some seasonally abundant food [28]. Apparent differences in the seasonal variation in food supply agree quite well with the variation in Q_c, as well as the differences in growth seasonality. Given that studying the diets of white sturgeon in this river reach is challenging due to the very limited ability to harm fish protected by species at risk legislation, these results provide very interesting insights into both the presence of growth variation between groups of fish and their potential links to food availability.

In presenting these results it is important also to consider potential sources of error or variation, and it must be acknowledged that aging error presents some concerns in this species. A wide range of calcified structures have been evaluated to determine which is best for assigning ages to white sturgeon [29]. Of these, pectoral fin rays have been shown to provide the most accurate age, but significant errors can still exist in age-assignment. These errors have been shown to increase with fish age and growth rates [30], however in contrast to the large errors estimated by Paragamian and Beamesderfer [31] a recent study of lake sturgeon suggests that ages derived from fin rays may be small and predictable [32]. Additionally, our method incorporates information from age estimates from both pectoral fin rays and length-increment. The net effect of this dual approach should make growth estimated in the present study relatively free of error and should minimize mean ageing error by concurrent use of length-increment information

While most parameters in our model were freely estimated, informative prior probability distributions were used for some parameters (*i.e.* n and Q_m). Several authors have cautioned against 'borrowing' parameters from other population or species [33-35] because of the possibility of model sensitivity to some parameters [36, 37] and because of some parameters showing variation across species or populations [38]. However, sensitivity analysis on analogues of n and Q_m in other bioenergetics models have shown model outputs are quite insensitive to these parameters [36, 39].

The only bioenergetics evaluation of white sturgeon growth to date has been by Bevelhimer [13] who examined white sturgeon in the Snake River watershed. Bevelhimer's model, although quite innovative, assumes constant metabolic rates among populations and attributes expected growth differences to different temperature regimes of each population. The model used here uses observed growth and temperature for each population and uses these to estimate energy intake and metabolism [14]. Use of more common bioenergetics models such as the 'Wisconsin' model [40] would have proven difficult for such applications, because laboratory studies would need to be conducted to ascertain the metabolic parameters of these two groups. In fact, few bioenergetics studies published actually estimate these rates *a priori* because of logistical difficulty or expense [40, 41]. The bioenergetics model proposed by Walters and Essington [14] therefore provides a useful means of estimating these rates for situations where appropriate laboratory studies have not been, and possibly cannot be, conducted.

Findings of this study also provide a means to evaluate potential implications of perturbations such past or future changes to water temperature. Temperatures in the UCR have already increased over pre-impoundment levels [42], and can be expected to increase further due to climate change. The effects of climate change are manifold [43, 44], but two likely impacts will influence both metabolic and consumption rates as well as prey availability. Our parameterization of the model, based on the function provided by Bevelhimer [13], indicates that sturgeon in this section of the river are close to the temperature at which peak consumption occurs. This means that further warming of the river could result in decreased growth as consumption declines while metabolism continues to increase. Further, since the effects of increased water temperatures and general climate instability will influence other species in the system, including prey species (see [42]), this may also influence the timing and magnitude of energy acquisition in each group. Our findings indicate that growth in these groups can be highly influenced by seasonal availability of prey resources and further disruption to this pattern may reduce overall growth in one or more groups of white sturgeon. Although only considering temperature effects Bevelhimer [20] suggested limited spawning in the Brownlee Reservoir was the results of its elevated thermal regime. While the results here draw no specific conclusions about how future scenarios of climate change or other impacts may impact these groups, they do provide useful hypotheses that might not otherwise be considered.

Differences in growth and metabolic rates across these two groups of white sturgeon may have important implications for their conservation. First, in addition to prior genetic analysis [15], these differences provide a further indication of the lack of random mixing between fish in this river reach, since the present results could not have occurred in the presence of random mixing. Secondly they suggest that growth in the WAN group in particular may be limited by food supply or metabolic demands. The greater age at maturity for this group is an apparent consequence of this. Assuming longevity is similar between groups, lower energy intake and slower growth could increase inter-spawning interval or decrease batch fecundity. Both effects would decrease lifetime fecundity which could affect population recovery potential. While recruitment failure is acknowledged as the primary factor limiting white sturgeon populations in the UCR [2,7,14], the present identification of growth differences provide a further factor that warrants consideration.

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