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ARTICLE

## A Field-based Bioenergetics Model for Estimating Time-Varying Food Consumption and Growth

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### Abstract

Bioenergetics models are often used to describe the implications of changes in growth and consumption of specific wild populations, and yet most parameters are derived from a variety of laboratory studies on other populations or species, leading to questions regarding the validity of predictions. A novel bioenergetics approach was recently developed where many parameters are estimated from the population being modeled, but growth and consumption are assumed invariant over time, which would not hold true when manipulations to the system are known or suspected. In the present paper, a bioenergetics model with many key parameters estimated from field data are presented where temporal deviations in growth rates were directly estimated. A series of rainbow trout *Oncorhynchus mykiss* and northern pikeminnow *Ptychocheilus oregonensis* populations, which have undergone various population manipulations, were used to evaluate the model. Further, the model was fit to a series of rainbow trout size-classes stocked into each of the study lakes to compare with their wild counterparts and evaluate intercohort differences in growth and consumption. We found the model with time-varying consumption was more parsimonious compared with models where growth and consumption were assumed to be constant over time. Our field data demonstrated how the model can detect different patterns in growth and consumption across populations and species. The model detected highly variable growth and consumption in rainbow trout over time and between populations but did not seem to be particularly influenced by past population manipulations. By contrast, northern pikeminnow demonstrated differences between lakes, but showed little temporal variation in growth and consumption. Stocked rainbow trout demonstrated similar growth rates to their wild counterparts, helping to validate growth estimates. Our bioenergetics model moves beyond existing ones by allowing measurement and process errors to be explicitly represented, while also permitting growth and consumption to vary over time.

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Growth in poikilothermic animals can be quite plastic, depending both on biotic factors, such as the quality and quantity of food organisms available, and abiotic factors, such as temperatures experienced, which influence production of food organisms as well as the consumption and metabolic rates of the consumer (Jobling 1994). While changes in growth are partially limited by the metabolic rate of an organism, it is net consumption rate that is likely to be the most variable over time and depends on the assimilation efficiency and the relative quantity

and quality of different prey items consumed. Changes in net consumption rates of a predator may have far-reaching implications for other organisms living in the system, through predation or competitive interactions.

The use of bioenergetics models for estimating growth and consumption in fish has grown rapidly over the last several decades (Hartman and Kitchell 2008). Bioenergetics models are essentially mass-balance models that partition consumed energy into growth and metabolism, or alternatively, attribute growth

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to the difference between consumed energy and metabolic costs (Brandt and Hartman 1993; Ney 1993; Walters and Essington 2010). These models typically include environmental covariates, most commonly water temperature, to predict seasonal variation in growth and consumption patterns. Direct estimates of consumption and metabolic rates from bioenergetics models can be incorporated into trophic interaction models where consumption by one group is a direct component of mortality for its prey group (Irwin et al. 2003; Rose et al. 2008; Tuomikoski et al. 2008; Myers et al. 2009). Similarly, consumption by predators can be predicted by abundance and availability of its prey (Hayes et al. 2000; Beauchamp et al. 2004; Johnson et al. 2006). The obvious utility of bioenergetics models has led to their use in studies for predicting or explaining changes in growth or consumption following various natural or anthropogenic disturbances (Hansen et al. 1993; Jobling 1994; Hanson et al. 1997; Chipps and Wahl 2008; Hartman and Kitchell 2008).

By far the most commonly used bioenergetics model for fish is the Fish Bioenergetics software (Hanson et al. 1997), more commonly known as the “Wisconsin” model (Ney 1990; Hanson et al. 1997). This model uses laboratory or in situ estimates of various metabolic and physiological rates and functions to parameterize anabolism and catabolism. Based on the parameter values provided and physiological functions chosen, the model calculates the maximum consumption an individual is capable of obtaining at a given temperature. The model estimates consumption rates at a given time interval by calculating the proportion of maximum consumption ( $P$ ) necessary to account for observed growth between two points in time (Hanson et al. 1997). There is considerable flexibility in this model, particularly because the growth trajectory can be broken up into multiple stanzas, each with an independent  $P$ , whose endpoints are defined as the age at which size or consumption estimates are provided.

An alternate bioenergetics model was recently developed by Walters and Essington (2010) and is referred to as a general bioenergetics model. This general bioenergetics model uses length-increment and length-at-age data commonly collected in field studies to directly estimate many of the parameters necessary to predict growth and consumption. By directly estimating parameters of the population of interest, and by summarizing the bioenergetics rates in terms of aggregate parameters, at least some of the parameters to be estimated do not need to be borrowed from other populations or similar species, as can be common with the Wisconsin model (Ney 1990, 1993; Petersen et al. 2008). Additionally, by estimating parameters using likelihood or Bayesian estimation techniques, uncertainty in parameter estimates and predicted growth and consumption are also estimated (van Poorten and Walters 2010). This represents an improvement over the Wisconsin model, which does not admit uncertainty either in the parameters used in the model, or in the predicted growth and consumption. A preliminary evaluation of the general bioenergetics model

suggests that it predicts growth and consumption at least as well as the Wisconsin model (van Poorten and Walters 2010).

One drawback of the general bioenergetics model presented by Walters and Essington (2010) is that growth is based on a single average lifetime trajectory with individual variation around this trajectory, which assumes the parameters being estimated are stationary over time. In situations where data are collected over several months or years and known manipulations to the system have taken place, this is unlikely (Matuszek et al. 1990; Jobling and Baardvik 1994). Indeed, one of the key uses of bioenergetics models is estimating how growth or consumption varies over time or space through changes in consumption. In the Wisconsin model, this is achieved by estimating a separate  $P$  for each size and time interval of interest (Hanson et al. 1997). While the general bioenergetics model accounts for seasonal changes in consumption, metabolism, and prey availability through their dependence with water temperatures, this probably underestimates variation owing to other sources, such as changes in inter- and intraspecific competition through changes in the predator or prey communities (Fraser and Gilliam 1992). To take advantage of the benefits of a field-based bioenergetics model, it would be beneficial to be able to detect differences in growth over time.

As an example, eight lakes in south-central British Columbia (Figure 1) were manipulated to reduce abundance of either rainbow trout *Oncorhynchus mykiss* (hereafter referred to simply as trout) or northern pikeminnow *Ptychocheilus oregonensis* (hereafter referred to as pikeminnow) with the express purpose of investigating interspecific competition and the influence of competition on recruitment. Depletion netting near the start of the study reduced adult densities of one species or the other in some lakes by between 60% and 90% (Taylor 2006; O'Brien 2009), which would be expected to result in changes in competition within and among populations for food, leading to changes in consumption and growth across lakes and over time after removals. In a scenario like this, the assumption of constant consumption over time would almost certainly be violated. Therefore, a new method of estimating time-varying consumption and growth using the general bioenergetics model is certainly warranted.

To account for changes in consumption that may occur owing to changes in community structure over time, we introduce a variation on the Walters and Essington (2010) general bioenergetics model where population- and year-specific changes in consumption and growth are directly estimated. If known perturbations occur over time or space, the model should be able to estimate their effects on growth and consumption. We evaluate the model using data from the populations in Bonaparte Plateau lakes (referred to here as the Bonaparte lakes). These lakes experience similar environmental conditions, but have varying productivity, prey, and competitor densities and have experienced changes to the fish community over the course of data collection (Taylor 2006; O'Brien 2009). We additionally fit the model to a series of differentially sized cohorts of trout stocked

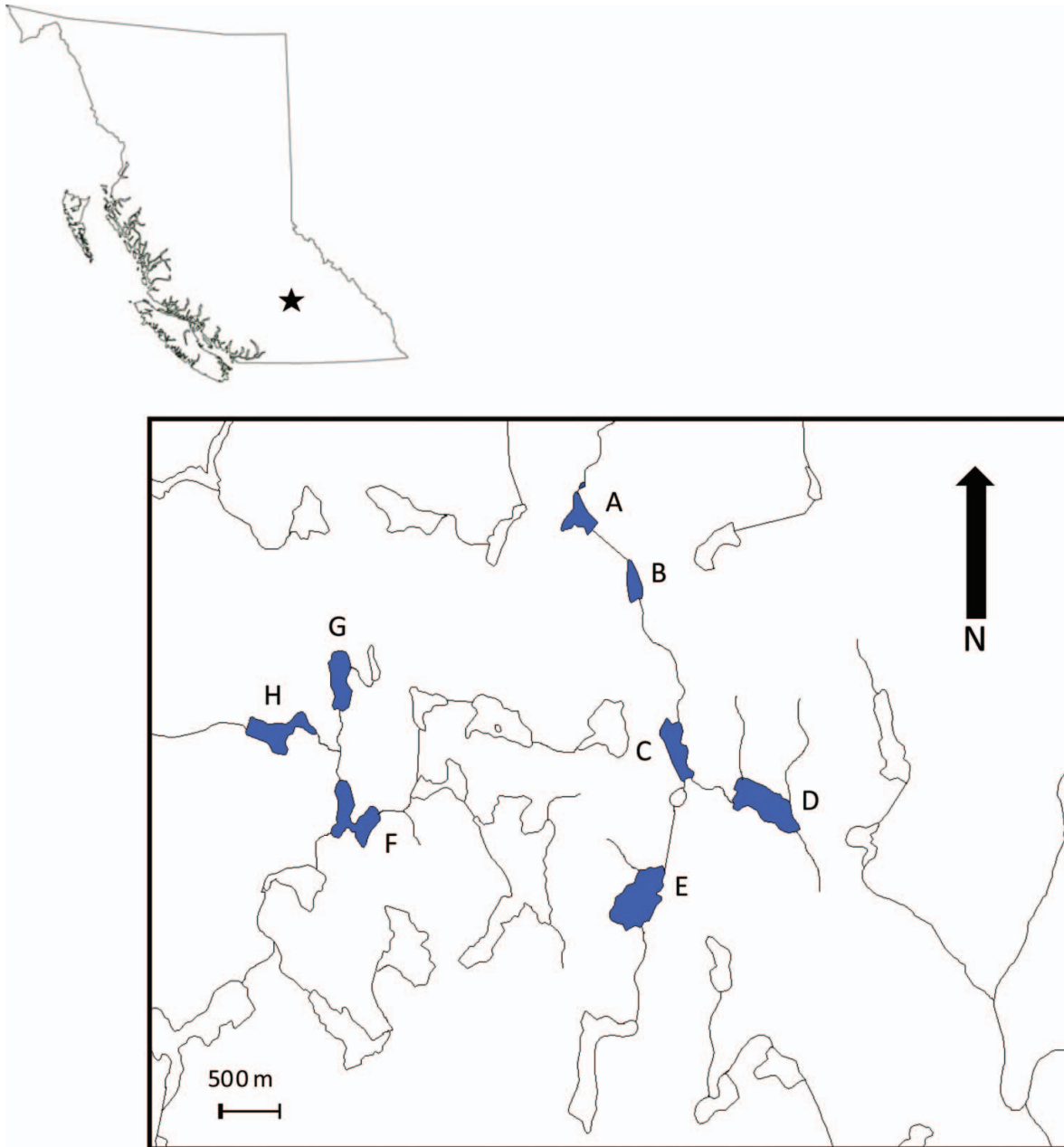


FIGURE 1. Study area in the Bonaparte Plateau (bottom panel) and the study area position within British Columbia (top). Lakes used in the current study are filled and labeled as A: Meghan Lake; B: Cath Lake; C: Moose Pasture Lake; D: Wilderness Lake; E: Cheryl Lake; F: Dads Lake; G: Moms Lake; H: Nestor Lake. [Figure available online in color.]

into all of the study lakes over several years to validate findings from the wild population and examine intercohort differences in growth and consumption.

**MODEL DEVELOPMENT**

Below, we briefly describe the general bioenergetics model of Walters and Essington (2010). For further details of model structure, refer to the original article. The general bioenergetics model as introduced by Walters and Essington (2010) assumed

growth can be modeled as

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

where the first and second terms are anabolism and catabolism, respectively;  $H$  is a mass normalized net (of assimilation and specific dynamic action losses) rate of mass acquisition through feeding,  $W$  is whole-body mass,  $d$  is a scalar relating anabolism

to mass,  $m$  is a mass-normalized rate of mass loss through catabolic processes, and  $n$  is a scalar relating catabolism to mass. The two terms  $f_c$  and  $f_m$  were functions relating anabolism and catabolism to temperature ( $T$ ). They take the forms

$$f_c(T) = Q_c^{T-\bar{T}/10} \frac{e^{-g(T-T_m)}}{(1 + e^{-g(T-T_m)})}$$

and

$$f_m(T) = Q_m^{T-\bar{T}/10},$$

where  $f_c(T)$  depicts consumption increasing exponentially at a rate of  $Q_c$  for every 10°C increase above the mean annual temperature,  $\bar{T}$ , to a maximum and then declines to half the maximum at a rate of  $g$  when temperature reaches  $T_m$ . The term  $f_m(T)$  simply results in metabolism increasing at a rate  $Q_m$  for every 10°C.

Walters and Essington (2010) introduced equation (1) to describe a seasonal model for growth that accounted for declines in growth, metabolism, and consumption with cooler water temperatures, as usually occurs in temperate climates. Walters and Essington (2010) termed this model the Continuous Allocation model, with the assumption that there is a constant length-weight relationship over the life of a fish (i.e.,  $W = aL^b$ ), which is unlikely. To describe a more realistic interpretation of lifetime growth, they further developed the model to describe what they term a Seasonal Reproduction, Skeletal Allocation (SRSA) model, which accounted for complex length-weight dynamics owing to annual loss in mass to gonad development and variable allocation of consumed mass to skeletal and metabolizable mass in times of metabolic stress (e.g., overwinter or after reproduction). The SRSA model used the information on variable length-weight dynamics to predict the sequence of mean length at age over a lifetime. Details of this model can be found in Walters and Essington (2010).

We evaluated a new parameterization of the general bioenergetics model, which included the possibility of consumption varying over time and across populations. We constructed the model to be able to estimate parameters from multiple, similar populations simultaneously, but this is not necessary. In our parameterization, we assumed that net consumption rate varied both across populations and over time within each population, while all other parameters were fixed across populations and over time. Each population was assumed to have been at equilibrium before and including the first year of data, which was modeled with a lake-specific  $H$ ,  $H_{lake}$ , and all other parameters shared between lakes. From the second year on, the growth in each lake and year was modeled as above, but with  $H_{lake}$  multiplied by a year-specific multiplier,  $\gamma_{l,y}$ . Essentially, growth within a lake (*lake*) and lake-year (*l,y*) was defined by the expression

$$\frac{dW}{dt} = H_{lake}\gamma_{l,y}W^d f_c(T) - mW^n f_m(T). \quad (2)$$

Size at age in 1 year built upon the size at age defined by parameters of the previous years by updating  $\gamma_{l,y}$  as the integration proceeded over the years of the study.

The model was fit to length-increment data of wild fish by finding the estimated age of each recaptured individual that minimized the following likelihood (Walters and Essington 2010):

$$\begin{aligned} LL_{Ri}(a_{li}) &= - \frac{(L_{1i} - \bar{L}(a_{li})\hat{R}_i(a_{li}))^2 + (L_{2i} - \bar{L}(a_{li} + \Delta t_i)\hat{R}_i(a_{li}))^2}{2\sigma_m^2} \\ &\quad - \frac{\hat{R}_i(a_{li}) - 1)^2}{2\sigma_R^2}, \end{aligned} \quad (3)$$

where  $a_{li}$  is the age of individual  $i$  at capture,  $L_{1i}$  and  $L_{2i}$  are observed length at capture and recapture,  $\bar{L}(a_{li})$  and  $\bar{L}(a_{li} + \Delta t_i)$  are estimated ages at capture and recapture and  $\sigma_m^2$  and  $\sigma_R^2$  are measurement and process error, respectively. The term  $\hat{R}_i(a_{li})$  is the growth deviation of individual  $i$  and is given by

$$\hat{R}_i(a_{li}) = \frac{\bar{L}(a_{li})L_{1i} + \bar{L}(a_{li} + \Delta t_i)L_{2i} + \frac{\sigma_m^2}{\sigma_R^2}}{\bar{L}(a_{li})^2 + \bar{L}(a_{li} + \Delta t_i)^2 + \frac{\sigma_m^2}{\sigma_R^2}}. \quad (4)$$

The model was fit to length-at-age data of wild fish by minimizing the following negative log-likelihood:

$$LL_{ai} = -w_a \frac{L_{ai} - \bar{L}(a_{li})}{\sigma_m^2 + CV_a \bar{L}(a_{li})}, \quad (5)$$

where  $CV_a$  in this equation is the coefficient of variation (SD/mean) in length of aged fish and  $w_a$  is a weighting factor for downweighting the importance of aged fish in the likelihood. The total likelihood of all data given model structure and parameters was found by calculating the sum of equations (3) and (5) combined.

## METHODS

We analyzed data from eight study lakes located on the Bonaparte Plateau in south-central British Columbia (Figure 1). The region is a low-relief, mid-elevation (~1,500 m) area where low productivity lakes experience a short open-water season (Taylor et al. 2005). The lakes are covered with ice from October through May. Summer water temperatures rarely exceed 20°C. All eight lakes are within 5 km of one another and experience similar weather and depth-temperature patterns, although lakes farther downstream are slightly warmer (D. S. O'Brien, Fisheries and Oceans Canada, unpublished data; B. T. van Poorten, unpublished data).

Fish populations in each study lake were expected to exhibit varying growth rates owing to among-lake variation in productivity, water temperatures, and fish community structure. Lakes farther downstream in each of the two watersheds typically had higher productivity and higher mean annual temperatures (Taylor 2006). An important additional source of variation

was that brought on by size-structured competition for resources. Trout in the study lakes typically resided in the same lake for their whole lives (~6% straying rate, B.T.v.P., unpublished data), resulting in similar size-structure across lakes. Conversely, pikeminnow exhibited a complex spatial ontogeny, which led to variation in size-structure between lakes in the same watershed (Taylor 2006). Adult pikeminnow were present in all study lakes, but adults living in the most upstream lakes typically spawned in outflow streams. Hatched age-0 pikeminnow drifted to lakes below those occupied by their parents and reared for 2 to 3 years until they were large and strong enough to migrate between lakes. The result was upstream (“headwater”) lakes that were devoid of the youngest age-classes and lakes farther downstream (“nursery lakes”) that had high densities of young pikeminnow as well as some adult pikeminnow. This may have caused complex intercohort competition among pikeminnow that may have affected growth in these lakes. Further, trout in these nursery lakes might have supplemented their diet with young pikeminnow, thereby resulting in increased trout growth in these lakes. Headwater lakes in this system included Moms, Nestor, Cheryl, and Wilderness lakes; nursery lakes included Dads, Moose Pasture, Cath, and Meghan lakes. Cath and Meghan lakes appeared to have extremely high densities of young pikeminnow owing to their relative position within the watershed (Figure 1).

Among-year differences in growth might have occurred because of shifts in relative density of the two fish species over time owing to differential removals of the two species. Early in the study, two lakes (Wilderness: 2001; Nestor: 2002) were partially depleted of adult trout and three lakes (Cheryl: 2001; Moms: 2001; Moose Pasture: 2002) were partially depleted of adult pikeminnow. Dads, Cath, and Meghan lakes were not depleted of any one species and were intended to serve as “control” systems for assessing the impacts of depletion removals. Further, all lakes were partially depleted of both species in the last 3 years of the study using a combination of gill nets set in a standardized configuration (Post et al. 1999; Askey et al. 2007) and small-mesh fyke nets. These changes to the fish community in each lake over time were expected to lead to variations in growth among years and lakes owing to variation in intraspecific and possible interspecific competition for resources.

*Data collection.*—Fish sampling occurred throughout the open-water season from 2001 to 2008, although not all lakes were sampled in every year. Cheryl, Dads, Moms, and Moose Pasture lakes were not sampled in 2004, Wilderness Lake was not sampled in 2004 or 2005, and Cath and Meghan lakes were only sampled between 2006 and 2008.

Sampling was conducted throughout the study primarily using fyke nets and gill nets. Individual fish sampled with fyke nets were measured, and fish larger than 120 mm were marked with an individually numbered spaghetti tag and released alive. Recaptured individuals were checked for spaghetti tags and measured. Fish captured with gill nets were all measured and checked for spaghetti tags, but usually died owing to sampling

and so were effectively removed from the population. These removals would not affect our growth estimates, although in cases where large numbers died (i.e., owing to intentional depletions) they would probably influence competition and predation in the systems, and therefore result in changes in consumption and growth rates from year to year. Fish with obvious misidentification errors because of either misread tags or transcription errors (identified as growth rate greater than 200 mm/year or length decrease greater than 5 mm) were removed from the data set, as were fish moving between lakes (which account for 6.6% of records) because the date of migration is unknown. In total, 915 trout and 2,881 pikeminnow tagged and later recaptured were included for analysis. Subsamples of fish collected in most years were sampled for aging structures. Trout were aged using scales collected between the dorsal fin and lateral line, and pikeminnow were aged using lapilli otoliths. All ages were estimated by two independent readers and any differences were resolved by a third reader. Additionally, scales of known-age trout were randomly included among samples to verify reader accuracy. In total, 6,247 trout and 7,602 pikeminnow ages were obtained across all lakes. Readers agreed on 49% of ages from trout scales and 89% of ages from pikeminnow otoliths. Validation from known-age trout showed 41% accuracy.

Water temperatures were derived from observed temperatures measured in each lake at various occasions over the course of the study. Observations were used to parameterize an annual sinusoidal water temperature model with a minimum winter temperature (similar to Taylor and Walters 2010).

Known numbers of hatchery-reared trout were stocked into the study lakes in the last 3 years of the study to examine intercohort differences in growth and consumption within a lake-year (Table 1). Fish were raised from gametes collected from a wild population in Pennask Lake, British Columbia, and reared to one of four size-classes. Age-0 trout were raised until they were a sufficient size to fin-clip (~0.5 g) and released in approximately mid-August of 2007 and 2008. Age-1 trout were raised for approximately 11 months at three different temperatures to create three size-classes with little or no size overlap. Age-1 trout were released in early June of each year (see Table 1 for stocking details). All size-classes were given a unique combination of fin clips to identify size- and year-class. Subsets of released fish from each size-class were measured to obtain length at release and the corresponding coefficient of variation (CV) in length. Intensive netting in late September of each year was used to recapture stocked fish to estimate growth rates of each size-cohort in each year.

Diet data were collected from both species on three separate monthly occasions from six lakes in 2006. Fish were captured using randomly placed gill nets set overnight in the benthic and pelagic zones. Stomachs were sorted into 30-mm size bins to a maximum of 10 stomachs per species per bin. Diet composition of each age-class was assumed to be represented as the proportion of each diet organism (biomass calculated by multiplying numbers by mean dry weight of sampled zooplankton

TABLE 1. Mean size and CV, date of stocking, and numbers of stocked fish from each cohort of hatchery-reared rainbow trout in each lake-year. All estimates of mean and CV in length are based on subsamples of 100 individual fish from each cohort in each year.

Size-class	Stocking date	Mean length (mm)	CV (mm)	Stocking density (fish/ha)							
				Cheryl	Cath	Dads	Meghan	Moms	Nestor	Moose Pasture	Wilderness
Small age 1	12 June 2006	96	0.12	12	12	12	12	12	12	12	12
Medium age 1	12 June 2006	118	0.13	12	12	12	12	12	12	12	12
Large age 1	12 June 2006	159	0.17		10	10	10			70	
Age 0	12 June 2007	43	0.08	1,650	1,650	500	1,650	1,650	500	500	500
Small age 1	12 June 2007	89	0.11	17	20	8	20	17	8	8	8
Medium age 1	12 June 2007	110	0.11	17	20	8	20	17	8	8	8
Large age 1	12 June 2007	142	0.12	17	20	8	20	17	8	8	8
Age 0	12 June 2008	43	0.07	500	3,500	3,500	3,500	500	500	3,500	500
Small age 1	7 June 2008	89	0.10	8	25	17	25	8	8	17	8
Medium age 1	7 June 2008	116	0.09	8	25	17	25	8	8	17	8
Large age 1	7 June 2008	153	0.11	8	25	17	25	8	8	17	8

and benthic invertebrates) across all size-bins that the fish of this age-class grow through over each year. As size at age changes across years, the same age-class may have incorporated different size-classes, resulting in small changes in diet proportions over time. Diet was assumed to be unchanged for fish larger than 240 mm and 150 mm for trout and pikeminnow, respectively, so all bins were combined beyond this size.

*Parameter estimation and model evaluation.*—The full model was used to evaluate changes in growth and consumption for both the trout and pikeminnow populations in the Bonaparte lakes. All populations for each species were run simultaneously, with  $m$ ,  $Q_c$  and  $Q_m$  shared among populations. We simplified analysis by fixing the anabolic and catabolic scalars to values assumed in von Bertalanffy growth (i.e.,  $d = 2/3$  and  $n = 1.0$ ; Essington et al. 2001). The  $H_{lake}$  term was estimated for each lake, and one  $\gamma_{l,y}$  was estimated for each lake-year for which data were available after the initial year of data collection on each lake. Therefore, across all lakes and years, the parameter vector being estimated included a vector  $H_{lake}$  equal to the number of lakes, a vector  $\gamma_{l,y}$  equal to the number of lake-years where data exist, minus the first year,  $m$ ,  $Q_c$ , and  $Q_m$ . We referred to this model as the Time-Varying Consumption model.

The number of lake-years where data exist varies across the two species owing to the differential ability to recapture marked individuals. Lake-years where no fish were recaptured had  $\gamma_{l,y}$  set equal to the last year where data exist. In total, 50 parameters were estimated for trout (47 lake-years of data) and 45 parameters were estimated for pikeminnow (42 lake-years of data). Prior distributions for all parameters except  $Q_m$  were assumed to be uniform with bounds given in Table 2. The metabolic  $Q_{10}$  parameter ( $Q_m$ ) is commonly confounded with  $Q_c$  and difficult to estimate. Walters and Essington (2010) recommend setting  $Q_m$  at or close to 2.0 based on the meta-analysis of Clark and

Johnston (1999). We chose to include an informative normally distributed prior distribution function for  $Q_m$  with a mean of 2.0 and SD of 0.02. Finally, the influence of aged fish on the likelihood was downweighted for each species by setting  $w_a$  to 0.5.

To determine whether estimating year-specific variation in net consumption rate results in an improvement in fit of the model to the data, we compared the model fit of the Time-Varying Consumption model with one similar to the original general bioenergetics model, which we refer to as the Time-Invariant Consumption model. As above, we assumed that all parameters apart from net consumption rate are shared among lakes and years. We further assumed that the net consumption rate is unique to each lake but does not vary over years. This was akin to the Time-Varying Consumption model above, with  $\gamma_{l,y}$  set to 1 for each year after the first year. In both species, this resulted in 11 parameters being estimated:  $H_{lake}$  for eight lakes,  $m$ ,  $Q_c$ , and  $Q_m$ , which are shared among lakes. We referred to this as the Time-Invariant Consumption model.

For each species, the most parsimonious model was selected using the Bayesian information criterion (BIC; Schwarz 1978). The principal of parsimony states that one should balance the fit of a model against the number of parameters used to generate the fit. As the number of parameters increases, bias declines, but variance increases (Hilborn and Walters 1992; Burnham and Anderson 2002). The BIC can favor lower dimension models more strongly than Akaike's information criterion (AIC; Burnham and Anderson 2002), especially when the number of observations is large (Schwarz 1978), resulting in a more conservative measure of model parsimony.

We assumed the same model and parameter structure for size-year cohorts of stocked trout as was used for the wild populations above (cohort-specific  $H$ , all other parameters shared). Growth of stocked fish was only estimated over one to several

TABLE 2. Fixed parameters and prior distributions for parameters allowed to vary that were used in the general bioenergetics model for predicting growth. Prior distributions are denoted as either  $U(l,u)$ , indicating a uniform prior distribution with lower and upper bounds in parentheses, or  $N(\mu,\sigma)$ , indicating a normal prior distribution with mean and SD in parentheses.

Parameter	Description	Parameter value / prior distribution		Units
		Rainbow trout	Northern pikeminnow	
$a$	Intercept coefficient of length–weight relationship	$1.08 \times 10^{-5}$	$1.16 \times 10^{-5}$	$\text{g}\cdot\text{mm}^{-b}$
$b$	Power coefficient of length–weight relationship	3.01	3.00	–
$H_{lake}$	Net food consumption rate per $W^{-d}$	$U(0,100)$	$U(0,100)$	$\text{g}\cdot\text{g}^{-d}\cdot\text{year}^{-1}$
$\gamma_{l,y}$	Year-specific net food consumption multiplier	$U(0,10)$	$U(0,10)$	
$m$	Standard metabolic rate per $W^{-n}$	$U(0,20)$	$U(0,20)$	$\text{g}\cdot\text{g}^{-n}\cdot\text{year}^{-1}$
$d$	Food consumption power parameter	0.67	0.67	
$n$	Metabolism power parameter	1.0	1.0	
$Q_c$	Proportional increase in feeding rate per 10°C temperature increase	$U(0,10)$	$U(0,10)$	
$Q_m$	Proportional increase in metabolism per 10°C temperature increase	$N(2,0.02)$	$N(2,0.02)$	
$\theta$	Slope parameter for decreasing allocation to structural tissue as $W_s/W$ varies around $f_s^*$	0.2	0.02	
$g$	Steepness parameter for decrease in feeding at high temperatures	1.76	3.0	$^{\circ}\text{C}^{-1}$
$T_m$	Water temperature at which feeding drops by half	23.5	24	$^{\circ}\text{C}$
$W_{ma}$	Weight at maturity	131	27	g
$p_{gonad}$	Proportion of body weight lost to spawning	0.15	0.15	
$CV_{L-L}$	Coefficient of variation of individual maximum body lengths	0.4	0.4	$\text{mm}^2$
$CV_{L-A}$	Coefficient of variation of individual maximum body lengths for aged fish	0.2	0.1	$\text{mm}^2$
$w_a$	Weighting factor for aged fish	0.5	0.5	
$\sigma_m^2$	Measurement variance for $L_1$ and $L_2$	1.3	2.45	$\text{mm}^2$
$a_e$	Assimilation efficiency	0.8	0.8	
$SDA$	Specific dynamic action	0.172 <sup>a</sup>	0.163 <sup>b</sup>	

<sup>a</sup>Rand et al. (1993).

<sup>b</sup>Petersen and Ward (1999).

months so it was not possible to estimate curvature in growth rate owing to either seasonality or allometry. It was therefore necessary to assume metabolism and temperature dependence was similar between wild and stocked trout populations by using the posterior distribution functions for  $m$ ,  $Q_c$ , and  $Q_m$  from the wild population as prior distribution functions for the stocked cohorts. A separate net consumption rate ( $H_{coh}$ ) for each cohort of size-classes stocked into each lake in each year was estimated. We assumed a hierarchical structure for net consumption rates within size-classes across years and lakes. The hierarchical Bayesian analysis allowed information from other similar sampling units to be incorporated by assuming that other units were not independent, but were exchangeable units within a defined population of similar units, resulting in improved individual estimates. Exchangeability implies that lake- and year-specific prior distributions for net consumption rates were independently drawn from a common distribution defined by hyperparameters (Askey et al. 2007). Therefore, in addition to estimating  $m$ ,  $Q_c$ ,

$Q_m$ , and cohort-specific  $H_{coh}$ , hypermeans, ( $\mu_{coh}$ ) and hyperprecisions ( $\tau_{coh}$ ) of net consumption rates were also estimated, which defined the shape of the prior distributions for each size-class. Hypermeans for each age-class were normally distributed with mean of 6.0 and CV of 100. Hyperprecisions for each age-class were gamma distributed with shape and scale of 0.01. Likelihoods for estimating parameters for the stocked cohorts based on individuals that were captured or captured, tagged, and recaptured were similar to those from wild fish (equations 5 and 3, respectively) except ages of all fish were known owing to cohort-specific fin clips. Therefore, any fish that were tagged after stocking and later recaptured were evaluated at the known age for that cohort in equations (3) and (4), rather than searching over all ages.

To compare growth rate estimates between wild and stocked trout, as well as to determine if growth varies within a year among differentially sized fish, we estimated instantaneous growth of wild and stocked fish. Instantaneous growth was



TABLE 3. Energy densities and sources for all prey items included in calculating consumption. Sources are 1: Cummins and Wuycheck (1971); 2: Mills and Forney (1981) based on juvenile yellow perch *Perca flavescens* of comparable size.

Prey group	Energy Density (J/g dry weight)	Source
<i>Daphnia</i>	21,051	1
<i>Bosmina</i>	21,905	1
Copepoda	24,036	1
Cyclopoidae	24,233	1
Amphipoda	16,756	1
Hirudinea	22,789	1
Diptera	17,903	1
Trichoptera	20,930	1
Ephemeroptera	22,898	1
Odonata	21,424	1
Coleoptera	22,487	1
Northern pikeminnow	20,704	2
Other	21,492	Average invertebrate

estimated as  $\log_e(\text{initial length} - \text{final length})/\Delta t$ , where  $\Delta t$  is the time interval between date of stocking and date of final removals in the fall. Initial and final lengths for stocked fish represented the mean length at stocking and estimated mean length in fall sampling for each cohort in each lake. For wild fish, we estimated what the final length would have been given the estimated parameters if a wild fish had the same initial length as each stocked cohort. This allowed direct comparison between the mean growth rate estimated across body lengths for wild fish and size-specific growth rates estimated for each stocked size-class.

For all models, we approximated the posterior distribution using Markov chain Monte Carlo (MCMC) simulation with

the Hastings–Metropolis algorithm found in AD model Builder (Fournier et al. 2012). We ran four chains with a thinning interval of 100. Burn-in, the number of iterations needed to reach the joint posterior distribution of all parameters, was evaluated using the Gelman and Rubin convergence statistics (Gelman et al. 1995) and by visual examination of trace plots. After burn-in removal, a chain of 10,000 samples was saved as an approximation of the posterior distribution.

Daily consumption per gram body weight was estimated using the equation

$$C_t = \frac{H_{lake} \gamma_{l,y} W_{s,t}^d f_c(T_t)}{W_t \cdot e \cdot 365}, \quad (6)$$

where  $W_{s,t}$  is structural weight at time  $t$  and  $e$  is growth efficiency, calculated as

$$e = a_e(1 - SDA) \frac{\sum_{i=1}^I p_i E_i p_{d,i}}{\alpha + \beta W_t}.$$

Here,  $a_e$  is the assimilation efficiency,  $SDA$  is the specific dynamic action,  $p_i$  is the proportion of diet organism  $i$  in the diet,  $E_i$  is the energy density of prey organism  $i$ , and  $p_{d,i}$  is the proportion of diet organism  $i$  that is digestible. Given information on diet composition, it is then possible to estimate total consumption of a specific diet group by multiplying total consumption by estimates of prey-specific proportions of energy in the diet (i.e.,  $C_t \cdot W_t \cdot W_i E_i / \sum_{i=1}^I W_i E_i$ , where  $W_i$  is the estimated diet mass of diet group  $i$ ). Information on prey items are shown in Table 3. The proportion of diet organisms indigestible ( $p_{d,i}$ ) was set to 0.9 for invertebrates and 0.97 for fish (Stewart et al. 1983). All unidentified prey were invertebrates, so the mean energy density across invertebrates was used for this diet group. The denominator of the growth efficiency formula depicts the energy density of the predator (trout or pikeminnow), which we

TABLE 4. Diet organisms found in stomachs of rainbow trout and northern pikeminnow grouped into 30-mm length bins (values < 0.01 refer to trace populations).

Prey taxon	Length bin (mm)													
	Rainbow trout ( $n = 177$ )							Northern pikeminnow ( $n = 134$ )						
	60	90	120	150	180	210	240	270+	30	60	90	120	150	180+
<i>Daphnia</i>	<0.01	<0.01	0.02	0.04	0.01	0.01	0.01	0.01	0.02	0.01	0.00	0.00	0.00	0.00
Amphipoda	0.00	0.06	0.03	0.02	0.02	0.42	0.08	0.16	0.9	0.37	0.15	0.05	0.00	0.94
Hirudinea	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.32	0.2	0.00	0.00
Trichoptera	0.01	0.02	0.03	0.08	0.01	0.01	0.04	0.01	0.07	0.1	0.03	0.06	0.02	0.06
Odonata	0.00	0.00	0.00	0.01	0.01	0.01	0.00	<0.01	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	0.91	0.67	0.13	0.19	0.22	0.10	0.37	0.06	0.00	0.00	0.06	0.14	0.37	0.00
Diptera	0.00	0.12	0.64	0.19	0.60	0.21	0.19	0.63	0.00	0.5	0.25	0.45	0.17	0.00
Northern pikeminnow	0.00	0.00	0.00	0.00	0.00	0.00	<0.01	<0.01	0.00	0.00	0.00	0.00	0.00	0.00
Other or unidentified	0.03	0.05	0.07	0.06	0.08	0.12	0.14	0.04	0.00	0.02	0.03	0.02	0.05	0.00

TABLE 5. Model selection statistics for both model types and species evaluated. Bayesian information criteria (BIC) are calculated as  $-2\log_e(L) + k \cdot \log_e(n)$ , where  $\log_e(L)$  is the log-likelihood,  $k$  is the number of free parameters, and  $n$  is the number of observations (see text). The  $\Delta$ BIC column is the difference between the BIC of each model and the minimum BIC for that species. Values in bold italics represent the minimum BIC and therefore the selected model.

Species	Model	Number of parameters ( $k$ )	Maximum posterior probability	BIC	$\Delta$ BIC
Rainbow trout	Time-Invariant Consumption	11	-16,542.00	33,181.64	-7,327.61
	Time-Varying Consumption	50	-12,705.1	<b>25,854.03</b>	<b>0.00</b>
Northern pikeminnow	Time-Invariant Consumption	11	-2,647.62	5,397.07	-553.16
	Time-Varying Consumption	45	-2,213.66	<b>4,843.91</b>	<b>0.00</b>

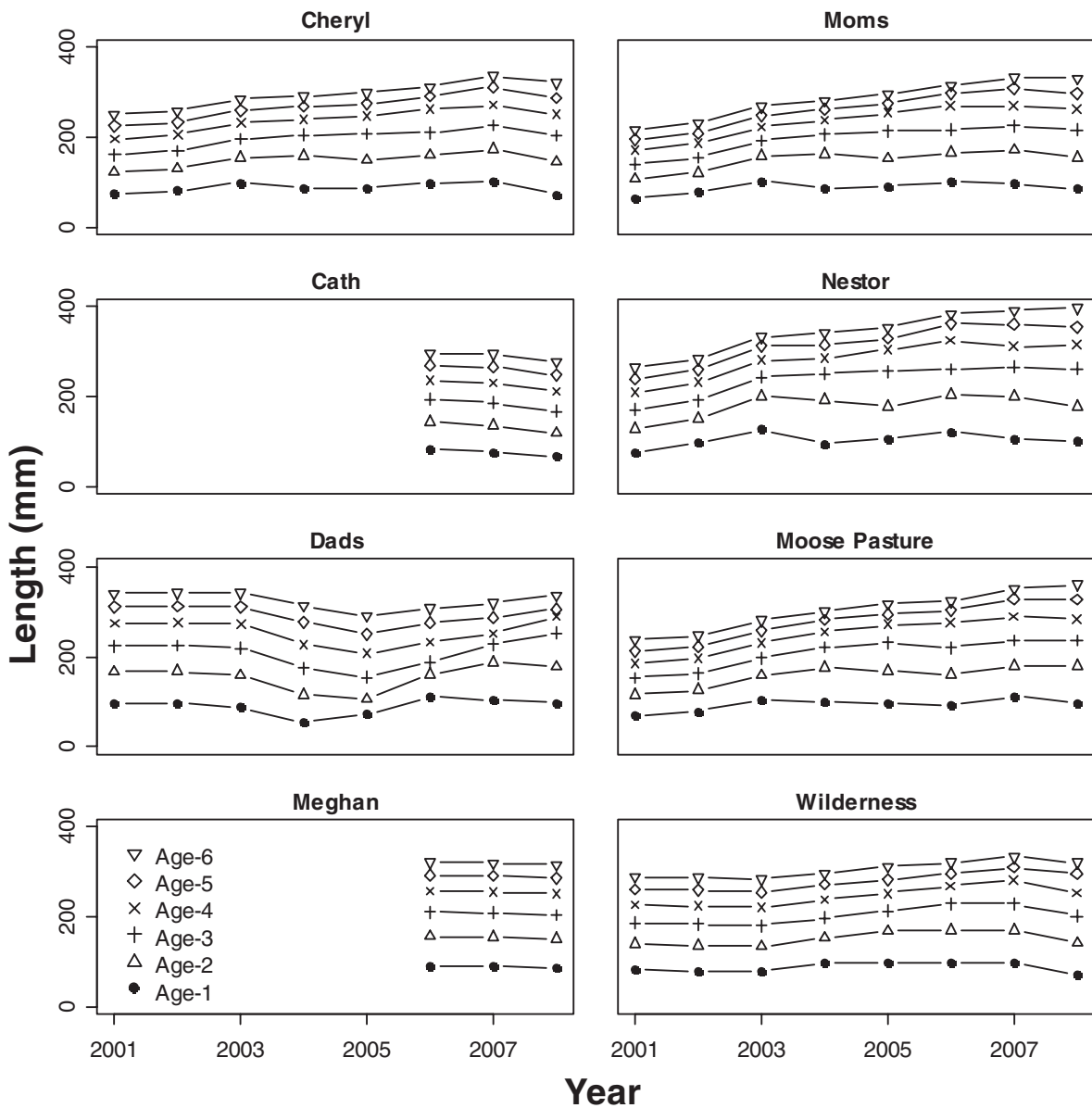


FIGURE 2. Length at age for rainbow trout in each lake across all study years.

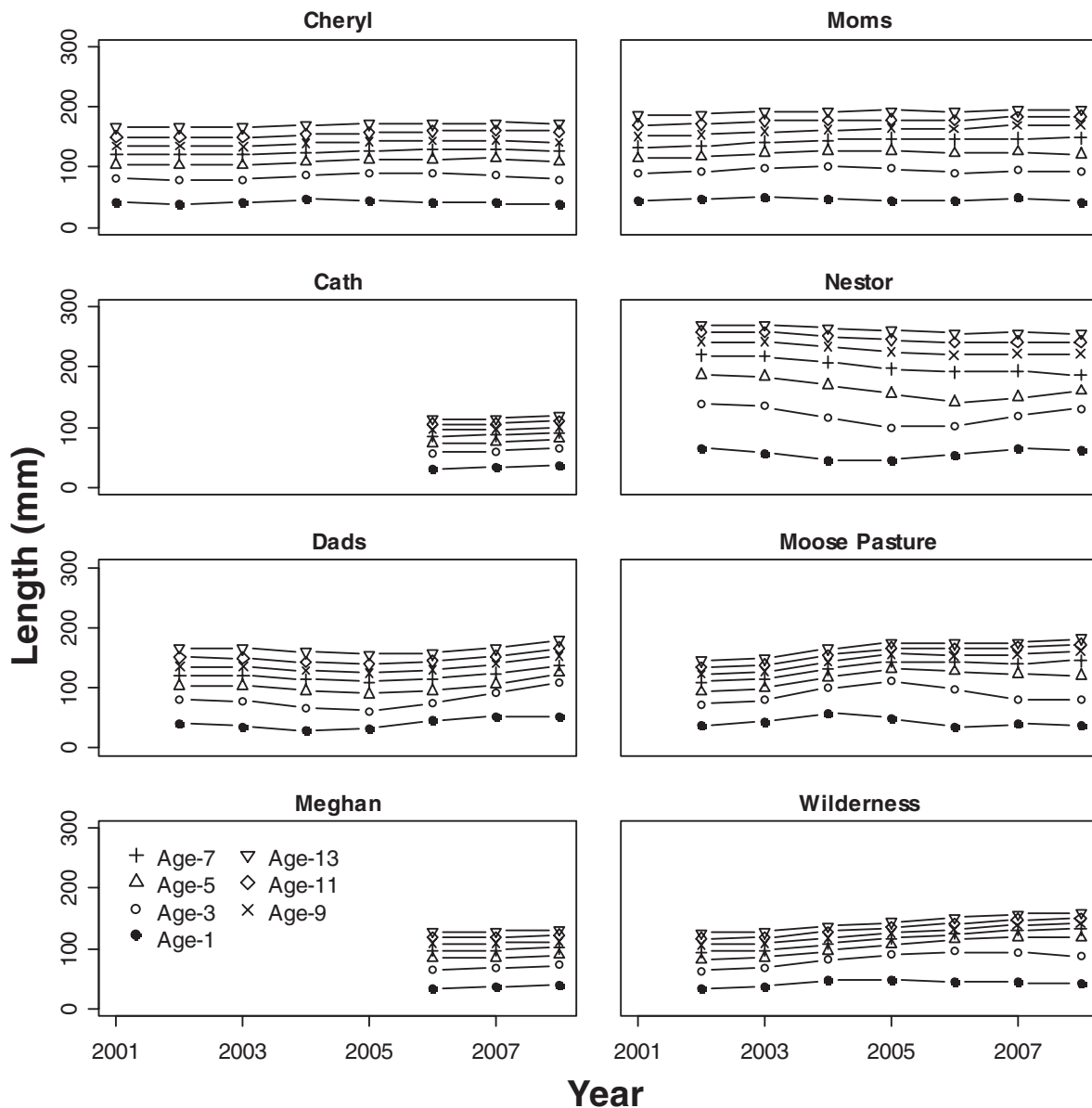


FIGURE 3. Length at age for northern pikeminnow in each lake across all study years. Note only every other age is shown.

assumed to increase linearly with weight for trout ( $\alpha = 0.99$ ,  $\beta = 5764$ ; Rand et al. 1993) and to be constant for pikeminnow ( $\alpha = 0$ ,  $\beta = 6703$ ; Petersen and Ward 1999). Parameter values are shown in Table 2. Proportional abundances of diet items found in different size-classes of each species are shown in Table 4. Diet information was only available for the open-water season, so consumption was only estimated from June to October each year. Additionally, age-0 individuals from each species were not assessed for diet, so consumption was only estimated for age-1 and older fish.

## RESULTS

Both the Time-Invariant Consumption model and the Time-Varying Consumption model were fit to the growth data for

both trout and pikeminnow (Table 5). In both species, the Time-Varying Consumption model was found to be the most parsimonious. The Time-Varying Consumption model had a BIC value of 7,328, 553 units lower than the Time-Invariant Consumption model, essentially giving full support to the more complex Time-Varying Consumption model.

Length at age estimated for trout and pikeminnow demonstrated obvious spatial and temporal variation (Figures 2, 3). In several lakes, this resulted in an increase in the maximum sizes for trout by the final year of the study (Figure 2). Trout in other lakes, such as Cath, Meghan, and Dads lakes, which were pikeminnow nursery lakes and not depleted of one species alone, showed constant or slight declines in length at age over the years studied, whereas all other lakes generally

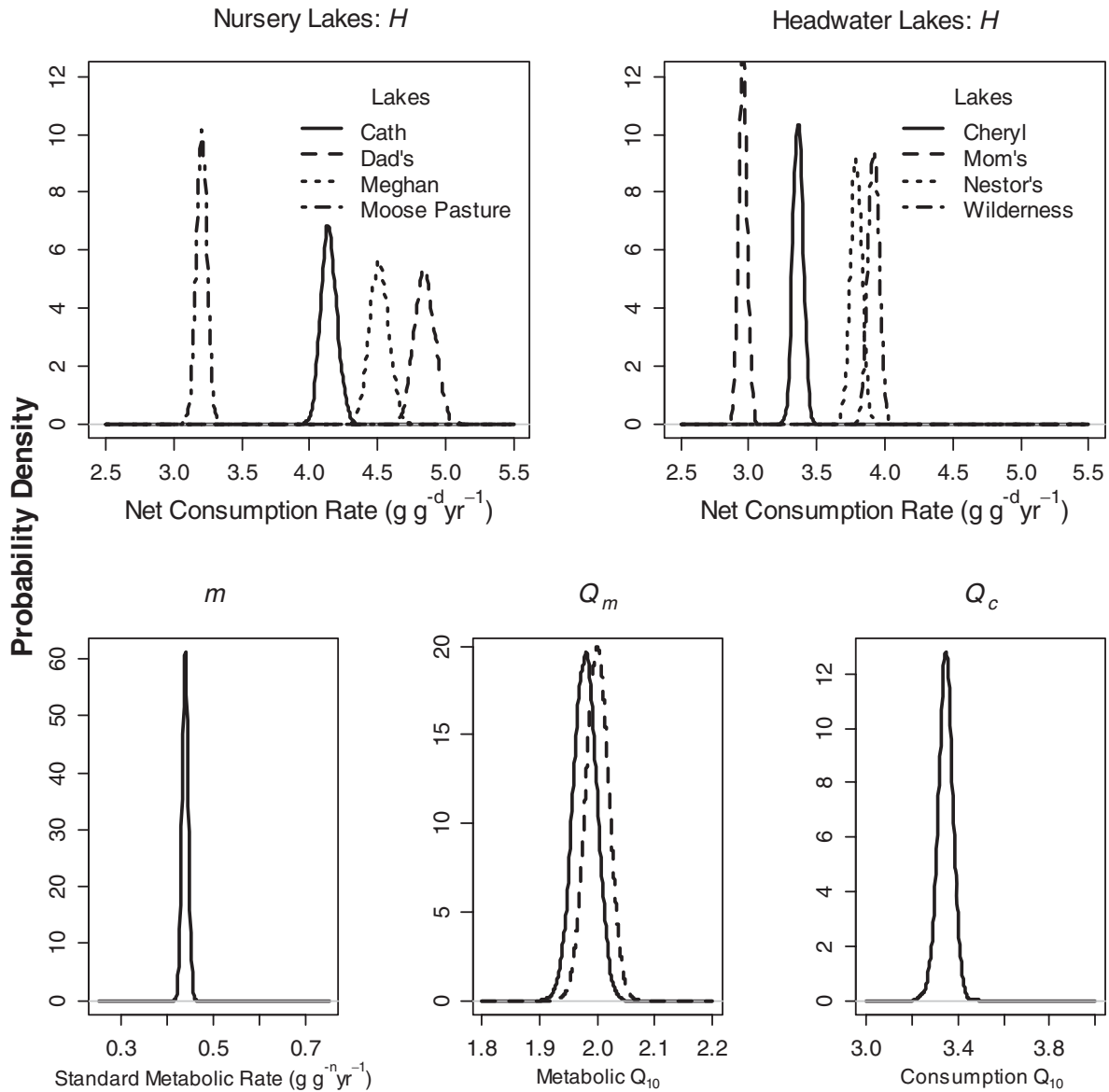


FIGURE 4. Posterior probability densities for mean (over years) first-year net consumption rates ( $H_{l,1}$ ) in all eight lakes, standard metabolic rate ( $m$ ), consumption and metabolic  $Q_{10}$  ( $Q_m$ ,  $Q_c$ ) parameters for rainbow trout. Net consumption rates are separated into those from populations in nursery lakes and those from headwater lakes. Prior and posterior probability distributions for  $Q_m$  are shown as dashed and solid lines, respectively.

showed slight increases in length at age in the same years. These results indicate that the model findings reflect our biological understanding of the system. In contrast pikeminnow growth rates were much more consistent over time resulting in similar lengths at age for different year-classes (Figure 3). However, the model detected varied growth rates across lakes for pikeminnow, with populations in some lakes exhibiting markedly slower growth (e.g., Cath, Meghan, and Wilderness lakes) than others (e.g., Nestor Lake).

Net consumption rates ( $H_{lake}$ ) for trout at the start of the study were quite variable, ranging from 2.9 to 4.8  $g \cdot g^{-d} \cdot year^{-1}$  (Figure 4). Trout net consumption rates were typically lower

in headwater lakes than in pikeminnow nursery lakes as might be expected if the two species compete for some shared food items. There was little information in the data to update the prior probability distribution of the  $Q_{10}$  for metabolism ( $Q_m$ ); hence, the posterior distribution was similar to the prior distribution. The  $Q_{10}$  for consumption ( $Q_c$ ) was much higher than  $Q_m$ , indicating that consumption increases faster than metabolism as temperature increases resulting in increased growth rates at higher temperatures.

Net consumption rates ( $H_{lake}$ ) for pikeminnow do not appear to be influenced by the size-structure of the population in each lake, as evidenced by similar ranges in nursery and headwater

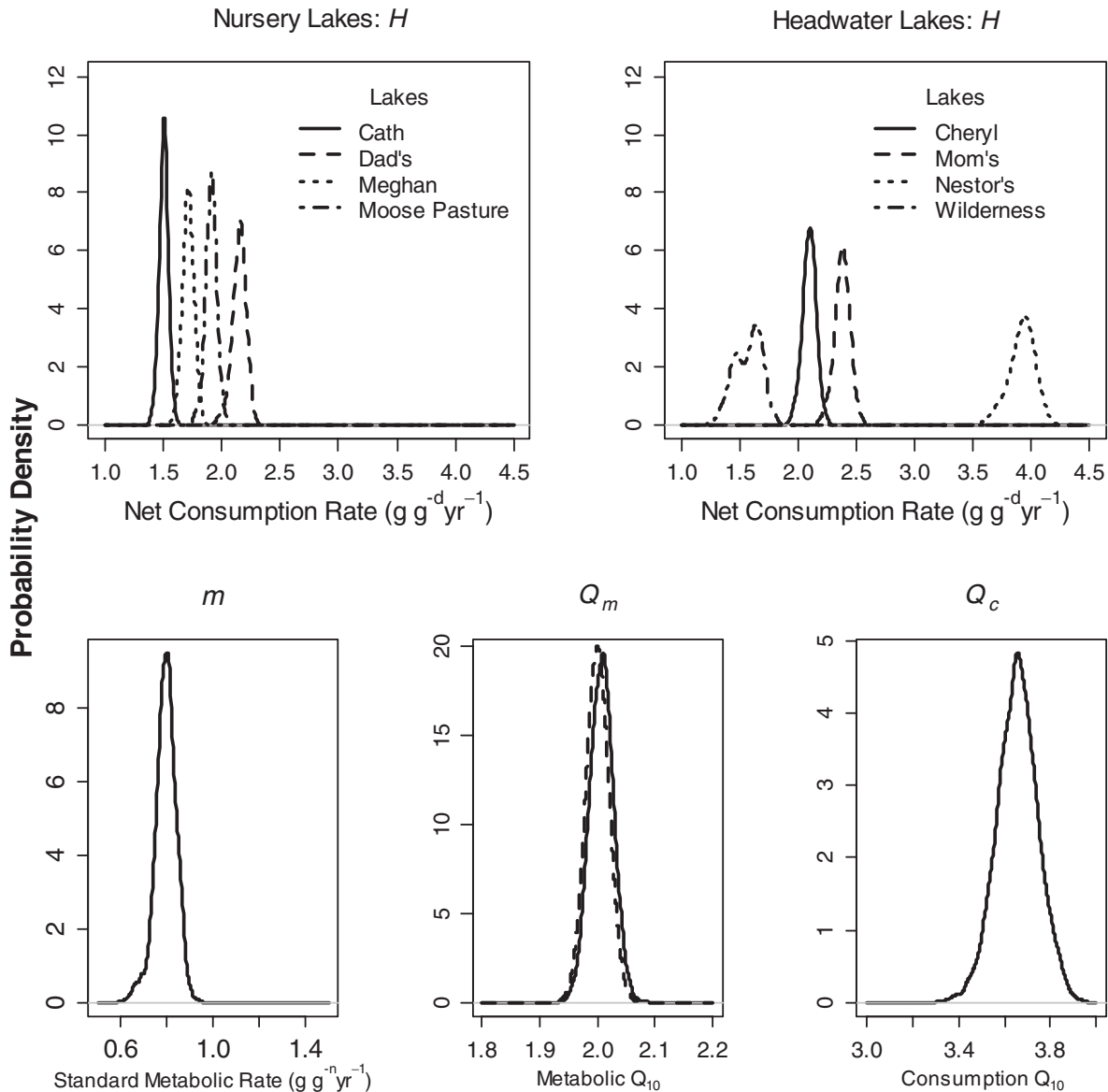


FIGURE 5. Posterior probability densities for mean (over years) first-year net consumption rates ( $H_{l,1}$ ) in all eight lakes, standard metabolic rate ( $m$ ), consumption and metabolic  $Q_{10}$  ( $Q_m$ ,  $Q_c$ ) parameters for northern pikeminnow. Net consumption rates are separated into those from populations in nursery lakes and those from headwater lakes. Prior and posterior probability distributions for  $Q_m$  are shown as dashed and solid lines, respectively.

lakes (Figure 5). The exception is pikeminnow in Nestor Lake, which had a net consumption twice that in most other lakes. As with trout, there was little information in the data to update the prior probability distribution of the metabolic  $Q_{10}$  ( $Q_m$ ), but net consumption does increase with temperature at a much faster rate than metabolism as shown by the difference between  $Q_m$  and  $Q_c$ .

The model was able to detect differences in net consumption rate both within populations over time and among populations (Figure 6), as reflected in differences in growth indicated in Figures 2 and 3. The model shows that both trout and pikeminnow

net consumption rates are relatively insensitive to pikeminnow removal experiments (Figure 6, top panels) since all three lakes follow the same annual pattern despite different treatment years. While this may seem like the model detected a general trend for trout across lakes, there is a different pattern in the control lake (Dads; Figure 6, bottom-left panel). Similarly, no clear pattern in trout net consumption rate appeared in lakes where adult trout were removed in 2001 (Figure 6, center-left panel). Overall, the model demonstrated that trout net consumption rate, and therefore growth, showed considerable variation across populations and years that appeared to be independent of density

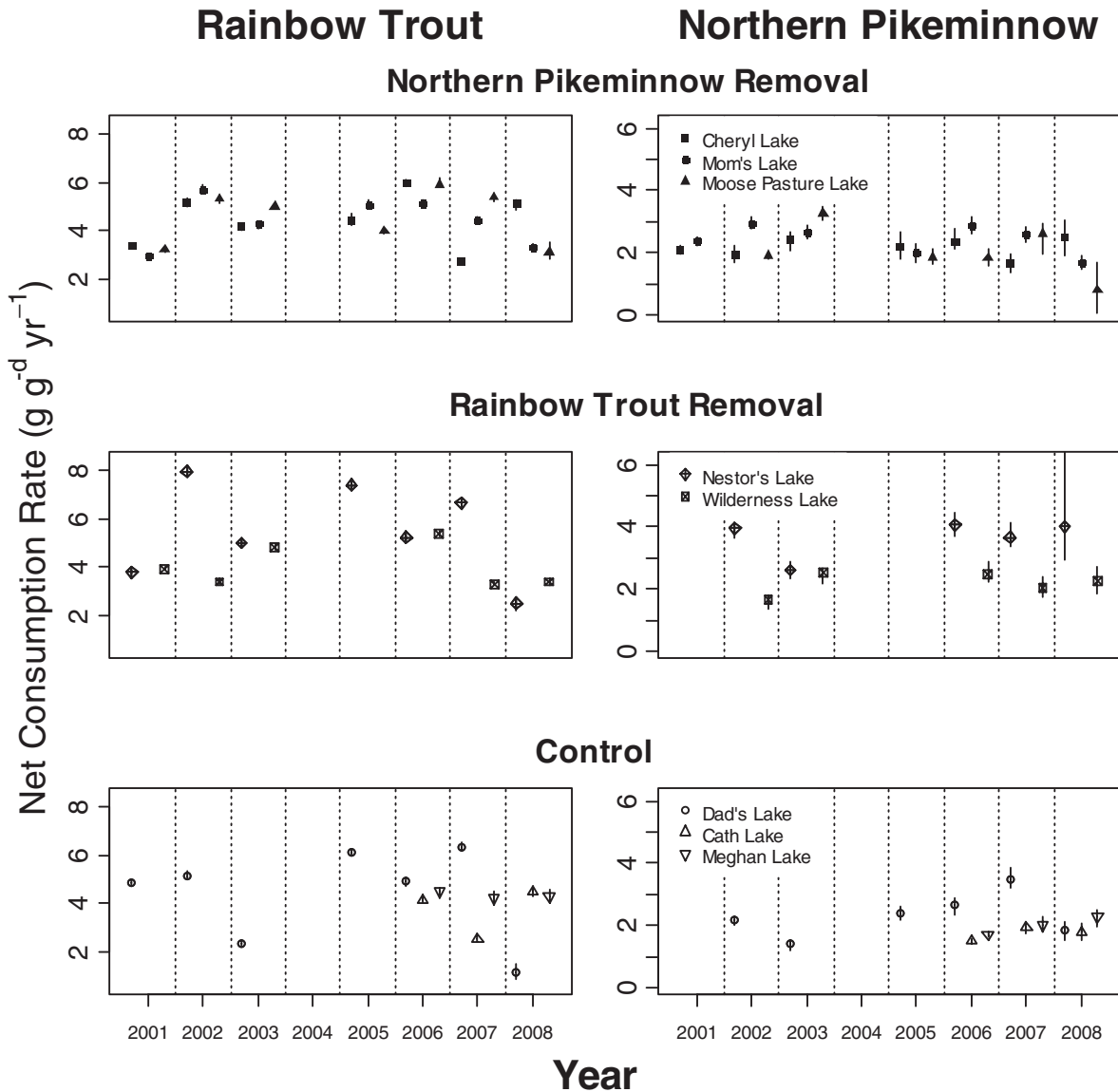


FIGURE 6. Net consumption rates for rainbow trout and northern pikeminnow across all 8 years of the study. Lakes are grouped by treatment type: northern pikeminnow removal in 2001 (Cheryl and Moms lakes) and 2002 (Moose Pasture Lake); rainbow trout removal in 2001 (Nestors and Wilderness lakes) and control lakes (Dads, Cath, and Meghan lakes). Years where lakes are not represented are years in which lakes were not studied or sample size was fewer than 10 individuals. Vertical bars represent 95% credible limits; some credible limits are obscured by the size of the marker.

manipulations of either species. The model showed that pikeminnow demonstrated less variation than trout in net consumption rate and growth over time (Figure 6, right panels). Changes in net consumption rates and growth were determined to be more consistent across populations than in trout as well.

The bioenergetics model estimated similar interannual trends in instantaneous growth between stocked and wild trout (Figure 7). This finding supports the bioenergetics model estimates of lake- and year-specific differences in net consumption rates for wild trout since the two data sets were estimated independently. Although absolute instantaneous growth estimates sometimes differed between wild and hatchery trout, there were

no consistent directions in differences across years, lakes, and size-classes.

The model was also used to estimate mean daily consumption, which varied across years and lakes for both species (Figures 8, 9). Lake-year interactions in growth were common, but did not necessarily reflect changes in density of either species owing to partial depletions. For example, growth increased in trout across most cohorts in 2002, despite wide-ranging reductions in abundance of either species in several lakes, but not in others (Figure 8). The model predicted definite changes in consumption within a lake across cohorts for trout, but year-cohort interactions in consumption rates were rare.

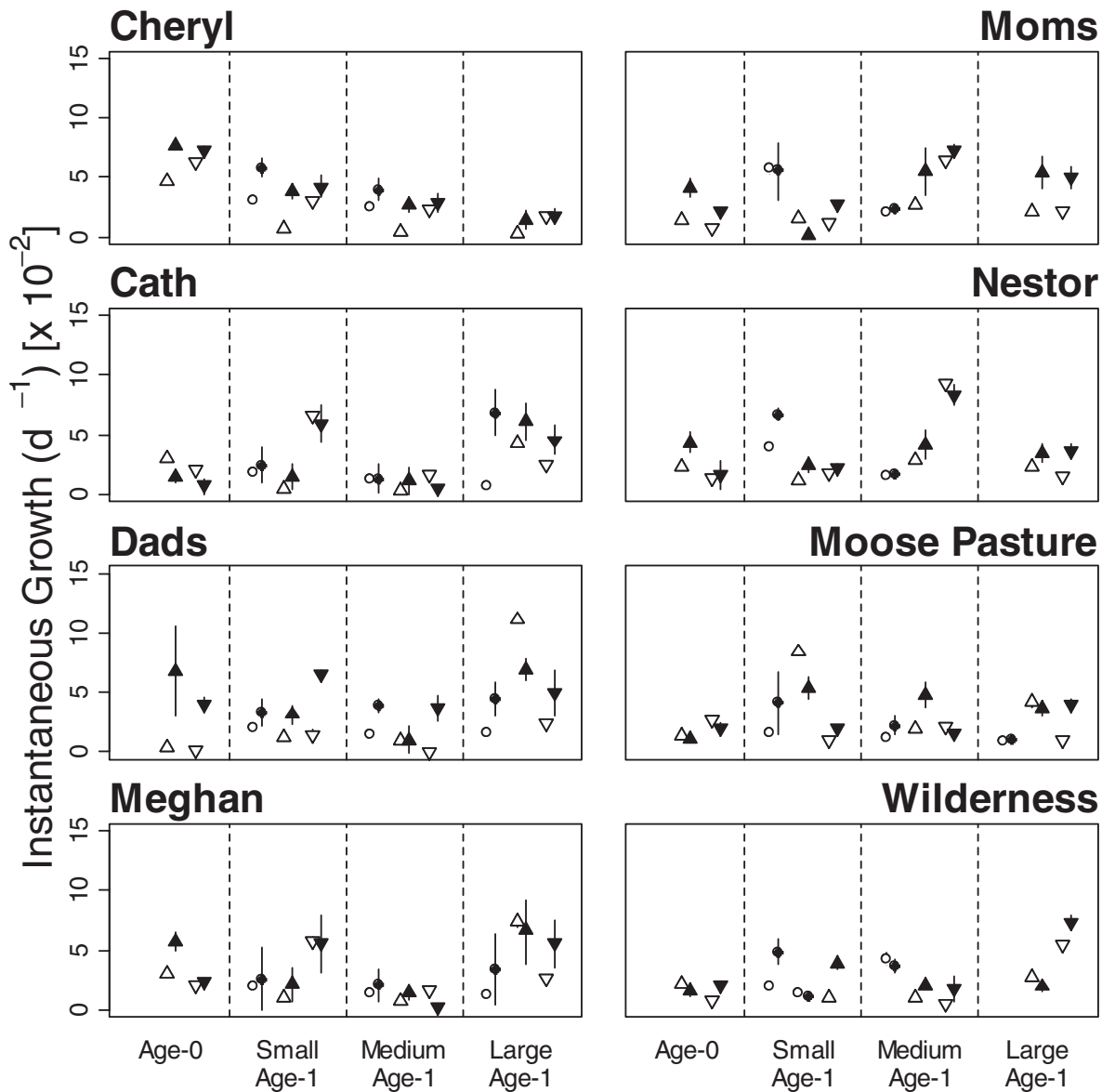


FIGURE 7. Instantaneous growth [ $\log_{10}(\text{initial length} - \text{final length})/\Delta t$ ] for four size-classes of stocked fish over 3 years in each of the study lakes. Squares, circles and triangles represent size-classes stocked from 2006 to 2008, respectively. Filled symbols represent growth of stocked hatchery trout, while open circles represent the expected growth of wild fish with identical initial size and time at large, given estimated wild trout parameters. Age-0 rainbow trout were not stocked in 2006, nor were large age-1 trout stocked in all lakes in 2006. Vertical bars represent 95% credible limits; some credible limits are obscured by the size of the marker.

## DISCUSSION

The new parameterization of the general bioenergetics model was able to detect differences in growth and consumption for trout and pikeminnow within and between populations in spatially distinct lakes that experienced similar environmental conditions (Taylor 2006). The direction and magnitude of the estimated differences in growth within and between populations was corroborated using hatchery trout stocked into the same lakes in several years and at various sizes. While includ-

ing additional parameters to explain variation in consumption over time and among populations will lead to an increase in parameter uncertainty (Hilborn and Walters 1992), in situations where finer-scale understanding of growth is needed, the additional flexibility may be warranted. However, our comparison with the simpler Time-Invariant Consumption model demonstrated that the Time-Variable Consumption model was much more parsimonious and the use of additional explanatory parameters was warranted. Overall, we found the flexibility of the

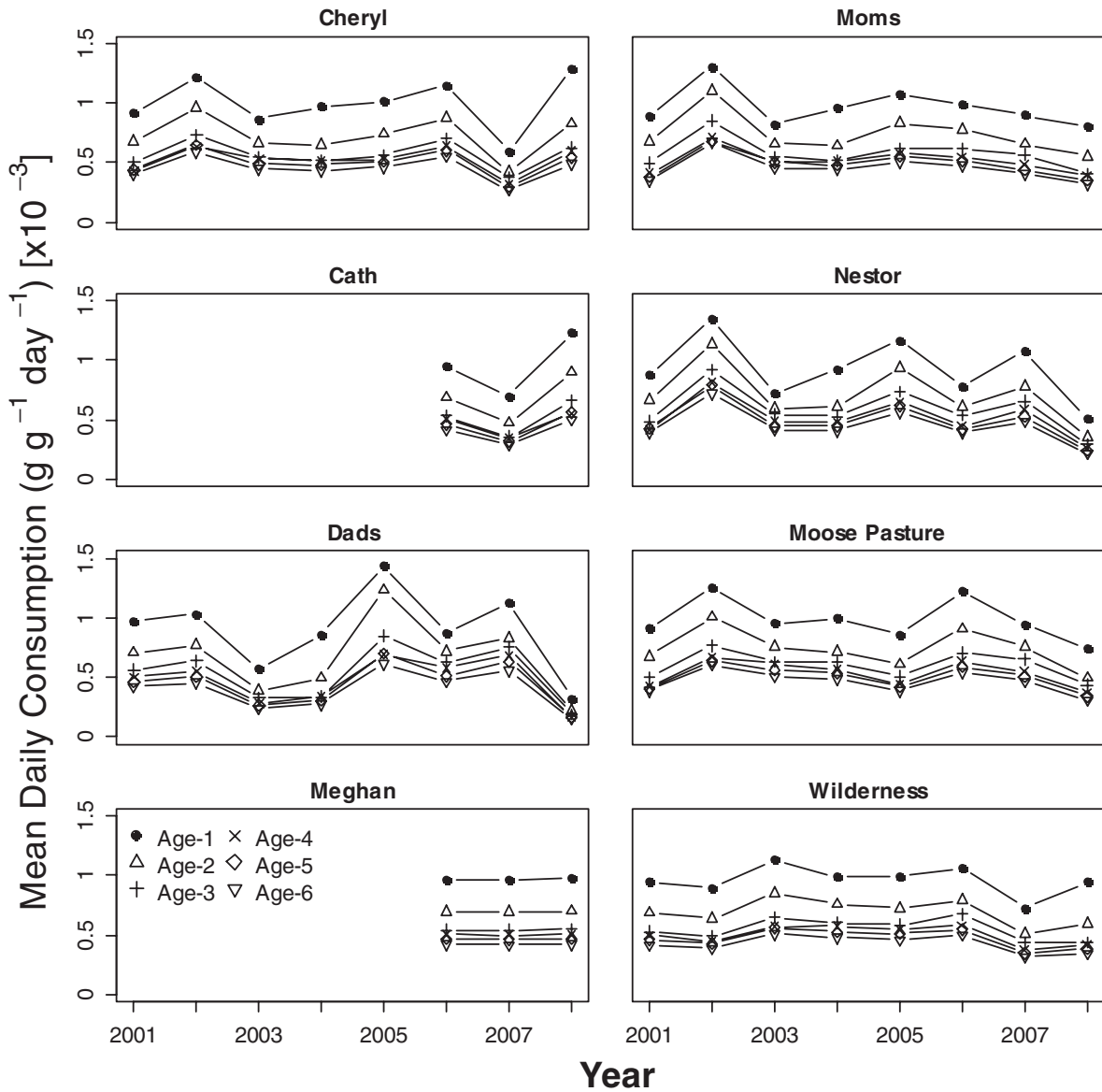


FIGURE 8. Mean daily consumption rates for wild rainbow trout in each lake studied across all study years. Consumption for trout of ages 1 to 6 years are shown.

general bioenergetics model to be significantly improved as a result of including the year- and lake-specific multipliers on net consumption rate.

We assume metabolism-related parameters are shared among populations within a species. Many authors warn against the concept of “parameter borrowing” (Ney 1993), where functions and parameters developed from laboratory studies on one species or population are used for predicting the growth or consumption of another. Recent empirical work suggests that metabolic rates and processes experienced by different population within species can vary significantly, and this will result in varied estimates of growth and consumption in bioenergetics models (Munch and Conover 2002; Tyler and Bolduc 2008). Es-

timates of metabolic rates using the same general bioenergetics model as used in the present study suggested that groups of white sturgeon *Acipenser transmontanus* had different metabolic rates despite the fish being found in the same contiguous span of the Columbia River (van Poorten and McAdam 2010). One of the benefits of the Bayesian analysis used to estimate parameters in the bioenergetics model is the estimation of parameter uncertainty in parameters such as metabolism. Estimating metabolism as a population-independent parameter means that the uncertainty within and among populations is combined, thereby permitting potential differences between populations to be exposed. This means that parameters are not borrowed as in the Wisconsin model (Ney 1993; Tyler and Bolduc 2008), thereby eliminating



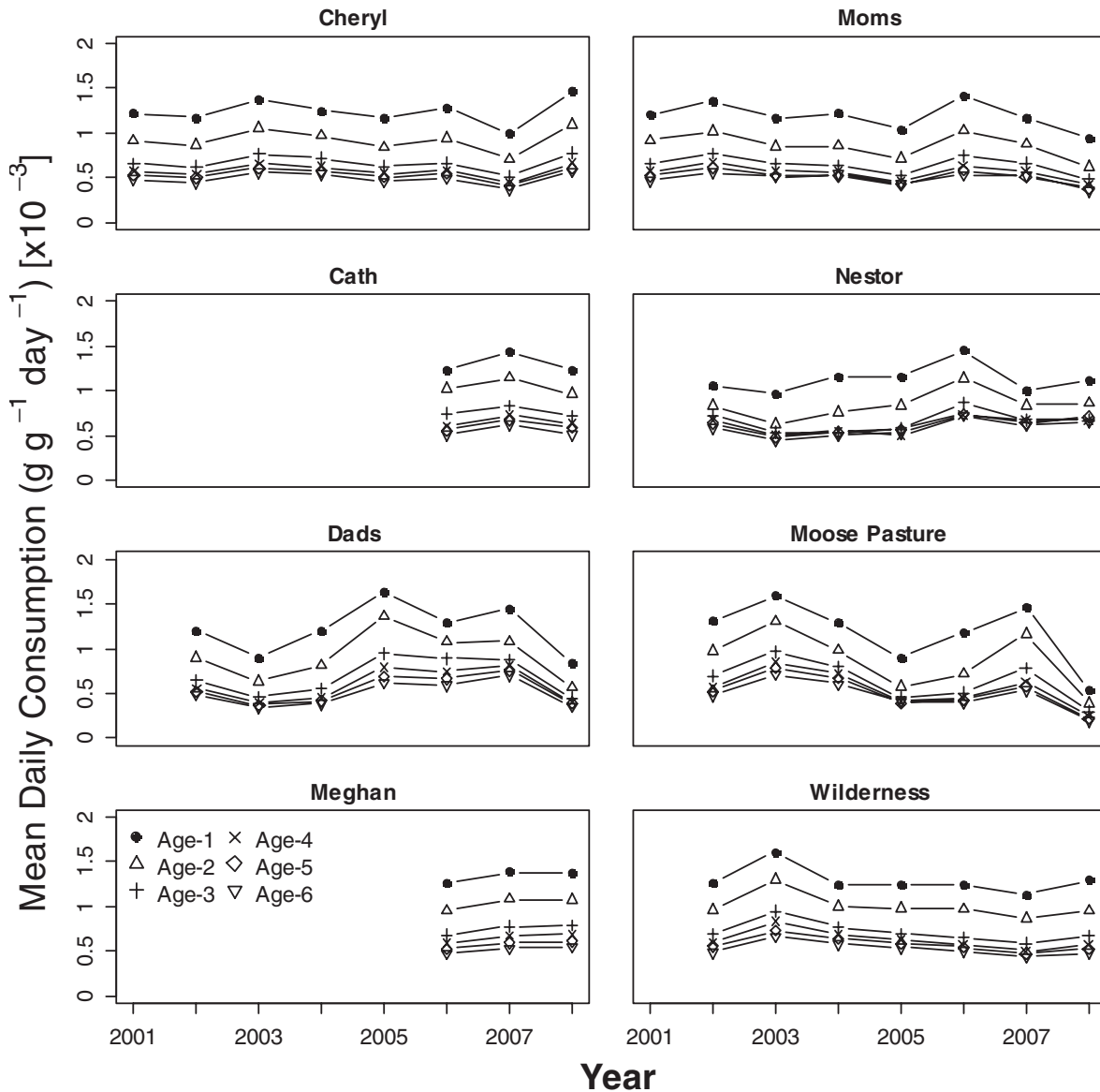


FIGURE 9. Mean daily consumption rates for northern pikeminnow in each lake studied across all study years. Consumption for pikeminnow of ages 1 to 6 years are shown.

the misgivings of parameter-borrowing common in analysis of most bioenergetics models.

The general bioenergetics model was also used to estimate growth rates of different size-classes of stocked trout to determine if growth rates of differently sized fish deviated from the population mean estimated for the wild fish. Overall growth estimates between stocked and wild fish were similar, both validating the year-specific net consumption rate estimates and indicating that little ontogenetic variation in growth occurs within trout in these lakes. While we attempted to account for ontogenetic changes in diet through separation of diet analysis into discrete size-classes, this does not account for changes in net consumption rates as fish grow. Specifically, as fish grow, their

gape size (Mittelbach and Persson 1998) and gill raker spacing (Keeley and Grant 2001) increases, allowing for larger and potentially more energetically rewarding prey to be consumed (Madenjian et al. 1998; Post 2003). As fish switch to larger diet organisms, their anaerobic activity may drop, probably owing to a decrease in burst swimming accompanying fewer foraging attempts (Pazzia et al. 2002; Sherwood et al. 2002). The result is more energy gained in fewer predation attempts, which may result in little ontogenetic variation in growth, as appeared to occur in the present study. Alternately, if fish largely maintain their feeding activity, ontogenetic diet changes could result in much higher energy input, resulting in relatively rapid increases in growth in one or more periods throughout the lifetime of a

fish (Osenberg et al. 1988; Madenjian et al. 1998). Accounting for ontogenetic diet shifts in growth can conceivably be done using the generalized bioenergetics model in the same way as is done when modeling a multiphased growth model (He and Stewart 2002): estimate parameters for two growth phases and estimate the rate and size at which the diet shift occurs. This approach would require sufficient data for most or all sizes of fish in the population to ensure that parameters are estimable. Again, this would add extra parameters to the model and should only be attempted in situations where obvious ontogenetic shifts in the population are suspected and when the need to account for this change in growth rate is warranted. Our stocked trout of various size-classes indicate that no consistent shift in diet occurred in the study populations.

Shifts in consumption rates may have implications for other organisms in the ecosystem. With this in mind, a useful application for our modification of the general bioenergetics model will be to include growth and consumption estimates in an ecosystem model where ecosystem implications can be modeled and estimated directly. Several bioenergetics models have been integrated into foraging or ecosystem models to examine the interaction of several trophic levels (Nibbelink and Carpenter 1998; Hayes et al. 2000; Aydin et al. 2005; Rose et al. 2008; Kishi et al. 2011). These models often use the Wisconsin model as the framework with which fish bioenergetics are estimated, primarily owing to the flexibility of the model. The present study shows that substantial growth information can be estimated directly from field data rather than predicted based on empirical relationships derived using laboratory studies. This information would be of use for ecosystem models, thereby permitting a direct evaluation of how changes in growth rate and species targeting will affect the community in general (Werner and Gilliam 1984). For example, with size- or age-structured abundance estimates for the trout and pikeminnow in the study lakes, it would be possible to estimate total consumption of both species, which could be used to help estimate mortality for all other groups of species in the lakes, in a way similar to that of the EcoPath with EcoSim model framework (Walters et al. 2000). The merger of bioenergetics and ecosystem models is still in its infancy, largely owing to the large number of parameters and substantial parameter uncertainty inherent in both approaches individually. We hope that the model described here will help to promote further integration as this avenue of research develops.

Our modification to the general bioenergetics model increases the utility of a field-based bioenergetics model for predicting changes in growth and consumption over time. Like the Wisconsin model, our modification makes it possible to estimate how growth might have changed over a period of system perturbations. It is possible to apply additional parameters to the bioenergetics model to predict cohort-specific effects on lifetime growth (He and Bence 2007) or variation in consumption or metabolism to account for ontogenetic shifts in these rates (Quince et al. 2008). Alternately, net consumption rate (or some other) parameters can be estimated with covariates (Kimura

2008) such as relative abundance of primary food organisms, stream flows, or relative competition or predation risk. While an infinite number of possibilities exist for increasing flexibility to the general bioenergetics model, it is always necessary to balance the need for increased model precision and parameter uncertainty (Hilborn and Walters 1992). Further, it is inherently difficult and time consuming to attain the high number of recaptures necessary to estimate growth deviations in the general bioenergetics model. If sufficient data do not exist, it may not be possible to estimate growth using the general bioenergetics model as we have done here.

## ACKNOWLEDGMENTS

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