



## Describing growth based on landscape characteristics and stocking strategies for rainbow trout

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### ABSTRACT

The achievement of target growth rates of stocked fish in a particular environment is an important component of recreational fisheries management; if stocked fish do not achieve a desired size structure, then angling effort and satisfaction may be lower than anticipated. We developed a growth model for rainbow trout (*Oncorhynchus mykiss*) based on a Bayesian hierarchical analysis of growth data from 142 gillnet assessments across the province of British Columbia. The growth equation was defined as a von Bertalanffy function with environmental and stocking covariates applied to the function's asymptotic length ( $L_{\infty}$ ) and metabolic rate ( $K$ ) parameters. Key factors defining growth for the best performing model were the time spent in lake based on accumulated growing degree days, the life-stage at stocking, stocking density, and the stocked strain. Calculating time in-lake in terms of growing degree days experienced by fish instead of calendar days in-lake improved the prediction of growth. We explore examples of how to use this information, such as identifying stocking rates needed to achieve particular size thresholds given size-structure objectives for a stocked lake fishery. This analysis helps managers determine how to efficiently distribute hatchery-reared fish across the landscape and recognize limits to growth given particular environmental constraints while also tailoring to the diversity of angler preferences and expectations of the fishery.

### 1. Introduction

Fish size and catch rates are two of the primary catch-related motivations driving decisions on whether and where an angler will fish (Dabrowska et al., 2017). Growth in many stocked freshwater species, is “inherently plastic” (Lorenzen, 2016) and affected by a broad suite of biotic and abiotic factors (van Poorten and Walters, 2016). Recreational anglers vary in the types of fisheries experiences sought (Aas and Ditton, 1998; Hunt et al., 2013; Parkinson et al., 2004); the success of stocking programs depends on the ability to reliably provide a variety of population size structures on lakes across the landscape to meet the needs of a diverse angling community (Johnston et al., 2010). Despite the importance of factors that lead to variation in growth rates, stocking policies often do not explicitly consider quantitative predictions of growth potential that may be attainable with particular stocking

densities in particular environmental conditions. Although experiential models and rules of thumb for growth potential in particular lakes may exist for many managers, quantitative models may allow stocking decisions to be better communicated among managers and stakeholders and improve overall fishery performance.

Gillnetting-based sampling methods have commonly been adopted by North American biologists to assess fish populations in smaller lakes (Willis, 1987; Appelberg, 2000; Ward et al., 2012). Gillnet assessment data are usually used to monitor the performance of the fisheries on a lake-by-lake basis, yet these data provide an opportunity to explore landscape-level patterns in growth variation that would not be possible experimentally. These data integrate growth information over a broad suite of lakes across a large geographic area, providing much greater contrast in environmental and demographic data than would be possible in time-series data on a single lake (e.g. He and Stewart, 2002; He

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and Bence, 2007). Further, stocked lakes offer contrasts in initial fish density for exploring density dependent effects on fish growth. Combining data from multiple assessment datasets over many populations provides a unique opportunity to explore growth, productivity, and density trade-offs across the landscape (Helsler and Lai, 2004).

Growth is an important biological process, which is influenced by energy surplus. Factors that influence consumption (anabolism) or metabolism (catabolism), or both govern growth plasticity (van Poorten and Walters, 2016). In stocked lake fisheries, average individual food consumption by fish can be limited by competition with conspecifics (Walters and Post, 1993; Post et al., 1999). Likewise, environmental conditions can have variable impacts on growth through direct impacts on metabolism and indirect impacts on consumption (through availability of prey) (Boisclair and Sirois, 1993; Hewett and Kraft, 1993). The extent of these effects may be determined by a combination of life history and environment; for example, Askey et al. (2013) showed that environmental conditions, primarily growing season length determine the magnitude of the density effect. When considering growth potential for fish in any given environment, each of these factors should be considered with respect to their impact on consumption and metabolism.

We estimate the relative influence of various biotic and abiotic factors on growth of rainbow trout populations distributed over a large number of stocked British Columbia lakes. We utilize standard sampling data gathered over multiple years, taking advantage of a broad suite of environmental conditions and stocking densities. We develop multiple models and evaluate their performance based on three criteria: (i) parsimony, (ii) model fit perspectives, and (iii) ability to predict out-of-sample data. The results of the best performing model are used to calculate expected stocking densities across the British Columbia landscape to achieve a variety of size-based management objectives.

## 2. Methods

### 2.1. Study system and data collection

British Columbia (BC) is a large jurisdiction for recreational fisheries management: this includes approximately 20,000 angling lakes that support a clientele of 350,000 licensed anglers (FFSBC, 2011). Approximately 675 small lakes, generally between 100 and 1000 ha, are annually stocked (FFSBC, 2015) with rainbow trout (*Oncorhynchus mykiss*) and more than half of the total angling effort on small lakes is concentrated on these stocked populations (Gislason et al., 2009). Though lakes < 1000 ha are stocked, the majority of the stocked lakes are smaller than 100 ha. A large proportion of the stocked lakes are those which are not connected to other waterbodies via inlet or outlet streams. Most of these lakes are only stocked with Rainbow trout and are essentially monoculture lakes maintained for the purpose of recreational fishing. Though there are stocked lakes that have natural recruitment, in the majority of cases, fish density is determined by stocking densities. Survival of Rainbow trout is understood to be higher in monoculture lakes compared to lakes with other species on account of competition for food resources and predation on young stocked fry.

Stocked lakes cover a large portion of southern BC (Fig. 1). Lakes range in elevation from 0 to 2000 masl and range from a latitude of 48.3 to 58.5 °N. The productivity of BC lakes is known to vary considerably between inland and coastal regions; coastal lakes have higher flush rates and lower productivity while inland lakes with lower flush rates have higher productivity (Ashley and Nordin, 1999). Lakes in the south of the province have a longer growing season (> 1000 growing degree days calculated above base temperature of 5 °C; GDD) compared to lakes in the north (< 1000 GDD).

Rainbow trout stocked in BC small lakes are predominantly either 'fry' or 'yearling' from one of several strains. Fry are stocked in the fall (September–October) at age-0+; yearlings are stocked in summer (May–June) at age-1. Yearlings are larger in size and stocking densities

are generally lower than for fry. Rainbow trout strains included in the analysis are 'Pennask', 'Blackwater', 'Tzenzaicut', 'Carp Lake', 'Fraser Valley domestic', 'Gerrard', and mixed strain stockings. All strains hatch in spring except for the domestic, 'Fraser Valley' strain. Fraser Valley strain hatch in late fall and are stocked in spring; hence, their age in-lake is approximately half a year younger than their wild-strain counterparts. Each strain is defined as having unique feeding, aggression and competitive characteristics (Pollard and Yesaki, 2008; Northrup and Godin, 2009). Blackwater and Tzenzaicut strains of rainbow trout were aggregated in our analysis because of similarity in behavior and because they are often stocked together. Sterile (triploid) fish are also stocked in some lakes to produce higher condition fish and/or preserve the genetic diversity of native stocks.

Fisheries managers have assigned stocked lakes into one of four fishing categories: Trophy (low density, large body size), Urban (high density catchable), Family (high density, low body size) or Regional (average density and body size). The sets of fishery attributes provided by these lake categories have been formed to match findings about angler preferences in the province (Dabrowska et al., 2017). Decisions about stocking densities and strains are made on a lake-by-lake basis with respect to these categories. Stocked fish become vulnerable to fishing at sizes 22 cm and higher which roughly corresponds to fish age 2 and higher (Askey et al., 2013). Because of the trade-off between growth and survival, size structure and abundance is quite variable, providing a range of fish size and catch rates across lakes. Lake categories 'Urban' and 'Family' tend to provide fisheries with high catch rates but smaller average fish sizes (ages 2–3). Urban lakes are located close to population centres, are generally smaller than 20 ha, and are stocked at high densities of age-2 'catchable' fish. Lake category 'Trophy' cater to specialized anglers targeting large fish (ages 3, 4, and 5); these lakes generally tend to have several restrictions on harvest, for example catch and release or one fish over 50 cm allowed to be harvested. Trophy lakes tend to be located far from large urban centres, have the lowest stocking densities among the different lake categories and must be productive enough to achieve fish of larger size. Regional lakes provide a fishery where fish sizes are generally higher than in 'Family' lakes and the catch rates and opportunities to keep the fish are expected to be higher than in 'Trophy' lakes. Biologists take into account the environmental attributes (e.g., pH, shoal area, growing degree days, flushing rate) of each lake with the aim of achieving objectives for fish sizes and densities and fishing experiences that are associated with the lake's fishing category.

Between 60 and 100 stocked lakes are surveyed each autumn with a standardized gill-net configuration (Ward et al., 2012) to assess rainbow trout density and size structure. Surveys are conducted using one pelagic and one benthic gang of gillnets according to standard protocol consisting of seven panels of varying size arranged in a fixed order (25, 76, 51, 38, 89, 64 and 32 mm) attached at the top and bottom of the net. Nets are set overnight in each lake to improve catching efficiency from crepuscular fish activity. Captured fish are identified to species, measured for length, examined for tags or fin clips (which may have been used at stocking to identify age-class or strain) and have scales or otoliths removed for aging.

The BC Small Lakes Database has data from 1070 gillnet assessments across many years and lakes. Of these, 632 assessments have paired data on lengths and ages. For this analysis, individual lake assessments were removed when: (1) multiple age-classes were stocked in the same year which obscured records of time in-lake; (2) covariate information on stocking density, strain, ploidy or total dissolved solids were unavailable; and (3) fewer than three age-classes or fewer than 20 fish over age-1 were captured. These criteria reduced the total data to 142 assessments from 91 lakes, which were used for the analyses. The assessments used in the analysis extended over much of the distribution of stocked rainbow trout in the province (Fig. 1). Assessments that did not satisfy criterion 3 but satisfied all other criteria were used to assess out-of-sample model prediction.

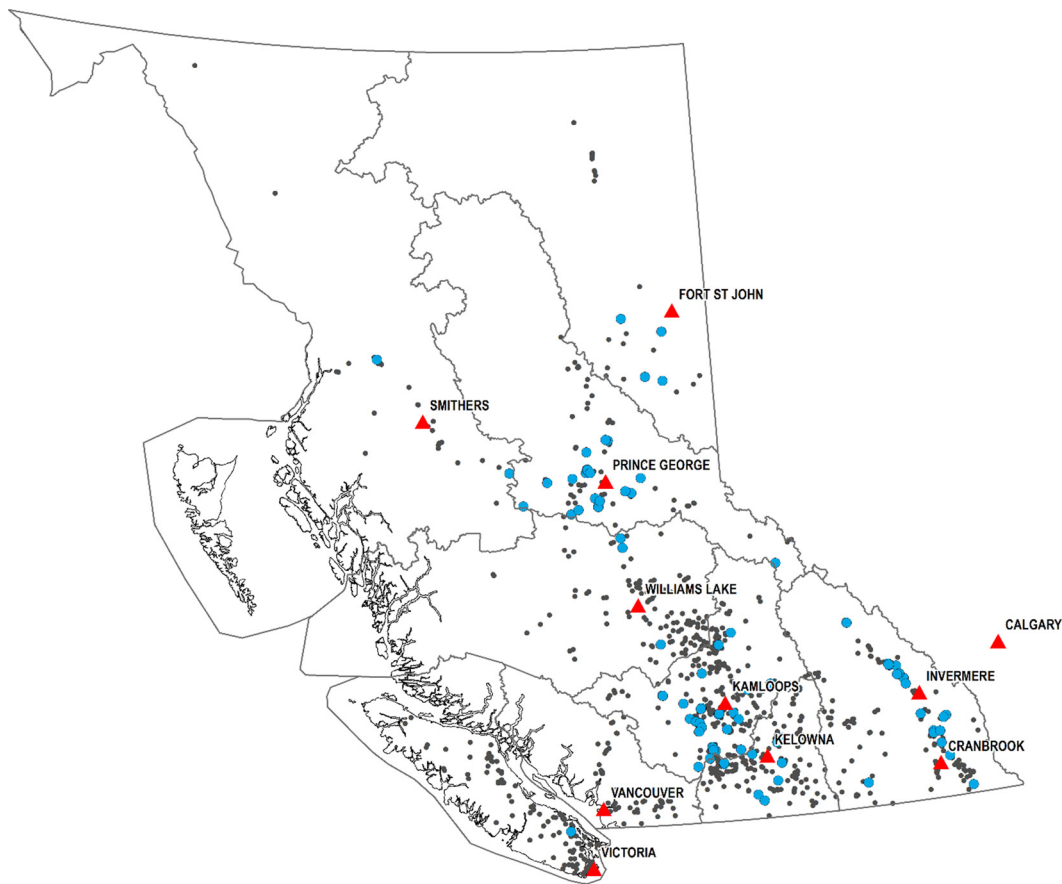


Fig. 1. Stocked lakes in British Columbia, Canada. Black dots show lakes stocked with rainbow trout since 2000; blue dots show lakes assessments that were used in the analysis presented here; red triangles show larger municipalities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

## 2.2. Model development

We assume growth of rainbow trout can be characterized using the specialized von Bertalanffy growth rate function:

$$\frac{dL}{dt} = q - KL \quad (1)$$

where growth in length is the difference between anabolism  $q$  (approximately proportional to consumption) and catabolism  $KL$  (metabolic and reproductive cost). Integrating Eq. (1) over time results in the specialized von Bertalanffy growth function (VBGF) assuming allometry in growth across the age range considered. Length can be predicted based on a starting length ( $L_0$ ) such as length at stocking and intervening time (Mangel, 2006):

$$L_{l,i} = L_{0l} e^{-K_{l,i} \Delta t_{l,i}} + L_{\infty l} (1 - e^{-K_{l,i} \Delta t_{l,i}}) \quad (2)$$

where  $L_{l,i}$  is the length of fish  $i$  observed in lake  $l$ ,  $L_{0l}$  is the mean size at stocking and  $\Delta t_{l,i}$  is the time since stocking for fish- $i$ .  $L_{\infty l}$  and  $K_l$  are von Bertalanffy growth parameters indexed by lake  $l$ . Time in-lake since stocking ( $\Delta t_{l,i}$ ) was calculated either as time in days/365 between the release and assessment dates or as accumulated growing degree days (AGDD) calculated as the average daily air temperature greater than 5 °C summed over the total number of days between stocking and assessment netting. AGDD is an index of ‘ambient thermal energy’ (Neuheimer and Taggart, 2007; Venturelli et al., 2010) and has been shown as an important explanatory factor describing growth (Venturelli et al., 2010). AGDD was calculated from latitude, longitude, and lake elevation information using ClimateBC\_v51, a Visual Basic 6.0 application that can be used to generate annual and monthly climate data for BC locations (Wang et al., 2012, 2015).

Because the VBGF is based on a simple bioenergetics framework (Eq. (1)), it is possible to evaluate how environmental and demographic variables will affect overall growth (van Poorten and Walters, 2016). Asymptotic length,  $L_{\infty l}$ , in Eq. (2) is actually a ratio of assimilated energy and standard metabolic rate per body length ( $\frac{q_l}{K_l}$ ). Therefore, covariates that affect consumption alone, due to either direct effects on appetite and aggression or indirect effects on prey availability, are modelled as covariates on  $L_{\infty l}$ . Covariates that similarly affect both consumption and metabolism are modelled as covariates on  $K_l$ ; since  $L_{\infty l}$  is a ratio of consumption and metabolism, covariates that affect both terms will cancel out. Finally, covariates that affect metabolism alone will be modelled as a direct effect on  $K_l$  and as an inverse effect on  $L_{\infty l}$ .

Consumption was assumed to be influenced by prey availability and competition. Measures of prey densities were not available, so proxies of system productivity were used, including total dissolved solids (TDS), and mean annual precipitation (MAP). Though several studies indicate that TDS is correlated with organic production, there are also suggestions that very high levels of TDS could limit production (Sorensen, 1977). MAP was included as a covariate based on the opinion of biologists that coastal lakes are less productive than lakes in the interior due to higher rainfall input and related nutrient flushing. Competitive effects on consumption were modelled as: 1) a direct impact of effective stocking density; 2) a density dependent impact of effective stocking density; and 3) a density dependent impact of effective stocking density and effective competitor density. Effective stocking density ( $dRB$ ) for a particular year-class ( $y$ ) in lake ( $l$ ) of rainbow trout was formulated as

$$dRB_{y,l} = S_{y,l} L_{0,y,l}^2 \quad (3)$$

where  $S_{y,l}$  is the stocking density for year-class  $y$  associated with lake assessment  $l$  and  $L_{0,y,l}^2$  is the squared length at stocking of fish in year-class  $y$  for assessment  $l$ . Walters and Post (1993) suggested consumptive pressure is related to effective density (sum of squared body lengths) assuming allometric consumption and von Bertalanffy growth; this was later empirically demonstrated by Post et al. (1999). Effective competitor density was calculated as the sum of squared lengths of all other species captured in lake assessments:

$$dOS_l = \frac{\sum_{j=1}^C L_{l,j}^2}{E_l} \tag{4}$$

where  $C$  is the total number of non-rainbow trout captured in assessment  $l$  and  $E_l$  is a measure of fishing effort based on the number of net panels and length of time fishing. Note that  $dOS_l$  may not accurately represent actual competitor density since gillnet assessments may actively avoid non-target species and/or not all non-target fish are recorded. Further, competition was also represented using the count of other (non-rainbow trout) species ( $cOS_l$ ) as a covariate.

Metabolism was assumed to be influenced by ploidy of stocked fish. Triploid fish are developed to forego maturity, which nearly eliminates energy loss to reproductive behavior and tissue; however, triploid male fish invest some energy in developing secondary sex characteristics and engaging in false spawning behavior. We assumed the reallocation of energy away from reproductive losses will be realized as a direct effect on metabolism alone (Benfey, 1999).

Several variables were assumed to influence both consumption and metabolism. Water temperature affects consumption through activity and prey availability and metabolism through direct effect on enzyme activity. Temperature effects were evaluated using mean annual air temperature (MAT) experienced on a lake. Life-stage (fry/yearling) at stocking was also assumed to affect both consumption and metabolism. Genetic strains of fish exhibit differences in aerobic scope and swimming performance (Scott et al., 2014). Because of the physiological and behavioral differences between the different rainbow trout strains, we assumed strain affects both consumption and metabolism.

We created multiple nested models to evaluate which covariates most strongly influence population-scale size-at-age (covariates described in Table 1), thereby building a final growth model using a stepwise design. In the base model (model 1, Table 2), von Bertalanffy growth parameters ( $L_{\infty l}$  and  $K_l$ ) are estimated as mixed-effects across 91 lakes without any covariates.

$$L_{\infty l} \sim \text{lognormal}(\ln(\mu_{L_{\infty}}), \sigma_{L_{\infty}}^2) \tag{5}$$

$$K_l \sim \text{beta}(\alpha_K, \beta_K) \tag{6}$$

where  $\mu_{L_{\infty}}$  and  $\sigma_{L_{\infty}}^2$  are the mean and variance in asymptotic lengths across lakes and  $\alpha_K$  and  $\beta_K$  are the shape parameters for the beta density function for  $K$  across assessments. All subsequent models applied covariates to the structure of Eq. (2) to account for influences on

consumption and/or metabolism.

Covariates were applied in various ways depending on how they were linked to metabolism and/or consumption and whether links were phenomenological or mechanistic. Covariates attributed to both consumption and metabolism (and therefore only applied to  $K$ ) were applied in the following linear form using a log-link function

$$K_{l,i} = K_l e^{\sum a_j X_{(CM)j}} \tag{7}$$

where  $X_{(CM)j}$  is a measured covariate that affects consumption and metabolism (CM) similarly and  $a_j$  is an estimated effect size. Two model structures were evaluated for applying the covariate effects on consumption alone (and therefore only applied to  $L_{\infty}$ ). The first is a linear form using a log-link function

$$L_{\infty l,i} = L_{\infty l} e^{\sum \beta_j X_{(C)j}} \tag{8}$$

where  $X_{(C)j}$  is a measured covariate that affects consumption (C) and  $\beta_j$  is an estimated effect size. Eq. (8) assumes both environmental and density effects are included as log-linear covariates. The second model structure is a non-linear form based on theoretically derived relationships between  $L_{\infty}$  and density from van Poorten and Walters (2016), which assumes a marginal effect of density dependence with increasing effective density.

$$L_{\infty l,i} = \frac{L_{\infty l} e^{\sum_{j=3}^J \beta_j X_{(C)j}}}{1 + (\beta_1 dRB + \beta_2 dOS)} \tag{9}$$

Eq. (9) assumes only environmental effects are included as log-linear covariates in the numerator, while effects in the denominator set an upper bound on asymptotic length based on effective density of rainbow trout at stocking and (if included) other species.

Covariates applied to only metabolism must reflect the bioenergetic origins of the VBGF, which show metabolism as  $K_l$  and inversely related to  $L_{\infty l}$ . Therefore, covariates attributed only to metabolism were applied directly to  $K_l$  and inversely to  $L_{\infty l}$  using a log-link function. The two von Bertalanffy parameters with covariates applied appear as

$$K_{l,i} = K_l e^{\sum a_j X_{(CM)j} + \sum \gamma_j X_{(M)j}} \tag{10}$$

$$L_{\infty l,i} = L_{\infty l} e^{\sum \beta_j X_{(C)j} - \sum \gamma_j X_{(M)j}} \tag{11}$$

where  $X_{(M)j}$  is a measured covariate that affects metabolism (M) and  $\gamma_j$  is an estimated effect size. Note that the same  $\gamma_j$  is applied to both von Bertalanffy parameters.

All parameters were set up with uninformative prior probability distributions with the exception of  $L_{\infty l}$  and  $K_l$ , which had hyper-prior probability distributions, as described in Eqs. (5) and (6). All covariates were standardized before applying the model (Table 1). TDS and MAP were mean standardised. Fry densities were standardized at stocking of 5 cm fry at 150 per hectare. Yearling densities were standardised at stocking 10 cm fry at 200 per hectare. The lifestage effect was estimated

**Table 1**  
Details about covariate standardization and model parameters estimated.

Covariates	Description
$K_L$	Lake-level von Bertalanffy $K$
$L_{\infty l}$	Lake-level von Bertalanffy $L_{\infty}$ (cm)
$mat$	MAT (mean annual temperature) standardised on mean
$AGDD$	Accumulated growing degree days, release to sampling (°000 days > 5 °C)
$lfs$	Life-stage effect (The effect of life-stage when stocked; the effect calculated with respect to fry; fry and yearling represented as 0 and 1 respectively in the model)
$dRB$	Stocking density of rainbow trout ( $n \text{ cm}^2 \text{ ha}^{-1} 10^5$ ). Fry densities were standardized at stocking of 5 cm fry at 150 per hectare. Yearling densities were standardised at stocking 10 cm fry at 200 per hectare.
$dOS$	Density of other species (species other than Rainbow trout) in the lake ( $\text{cm}^2 \text{ panel}^{-1}$ ).
$cOS$	Count of other species (species other than Rainbow trout) observed in the lake as a covariate.
$stn$	Strains 6 levels: (Blackwater; Carp Lake, Gerrard, Fraser Valley, Mixed stockings, and Pennask; standardised on Pennask strain)
$pld$	Ploidy (3 levels: 3n, Mixed stockings, and 2n; Ploidy effect was standardised on 2n)
$tds$	TDS (total dissolved solids) standardised on mean
$map$	MAP (mean annual precipitation) standardised on mean



**Table 2**

Model structure and selection criteria. Covariates applied to  $K$  include  $\alpha$  (coefficient for *mat*), lifestage (*lfs*), strain (*stn*), and ploidy (*pld*). Covariates applied to  $L_{\infty}$  include *map*, *tds*, rainbow trout density (*dRB*), density of other species in the lake (*dOS*) and (*cOS*) count of other species in the lake. Bold text in  $\Delta$ DIC and RMSE columns show the top performing models under the respective criteria.

Model	K	$L_{\infty}$	$\Delta t$	Deviance	DIC	$\Delta$ DIC	RMSE
1	$K_L$	$L_{\infty L}$	ndays	67766	68,138	1,791	8.02
2	$K_L e^{\alpha mat}$	$L_{\infty L}$	ndays	67766	68,122	1,775	7.86
3	$K_L$	$L_{\infty L}$	AGDD	66514	66,942	595	6.16
4	$K_L e^{lfs}$	$L_{\infty L}$	AGDD	66491	66,911	564	6.27
5	$K_L e^{lfs}$	$L_{\infty L} e^{\beta dRB}$	AGDD	66187	66,627	280	6.34
6	$K_L e^{lfs}$	$L_{\infty L} / (1 + \beta dRB)$	AGDD	66164	66,604	257	6.36
7	$K_L e^{lfs+stn}$	$L_{\infty L} e^{\beta dRB}$	AGDD	66021	66,461	114	6.17
8	$K_L e^{lfs+stn}$	$L_{\infty L} / (1 + \beta dRB)$	AGDD	65997	66,434	87	6.16
9	$K_L e^{lfs+stn+pld}$	$L_{\infty L} e^{-pld} / (1 + \beta dRB)$	AGDD	65919	66,348	1	6.18
10	$K_L e^{lfs+stn}$	$L_{\infty L} e^{\beta tds} / (1 + \beta dRB)$	AGDD	65996	66,450	103	6.09
11	$K_L e^{lfs+stn}$	$L_{\infty L} e^{\beta map} / (1 + \beta dRB)$	AGDD	65997	66,425	78	<b>5.74</b>
12	$K_L e^{lfs+stn+pld}$	$L_{\infty L} e^{\beta tds-pld} / (1 + \beta dRB)$	AGDD	65915	66,349	2	6.14
13	$K_L e^{lfs+stn+pld}$	$L_{\infty L} e^{\beta map-pld} / (1 + \beta dRB)$	AGDD	65920	66,374	27	6.09
14	$K_L e^{lfs+stn+pld}$	$L_{\infty L} e^{\beta tds-pld} / (1 + \beta dRB + \beta dOS)$	AGDD	65912	66,355	8	6.24
15	$K_L e^{lfs+stn+pld}$	$L_{\infty L} e^{\beta map-pld} / (1 + \beta dRB + \beta dOS)$	AGDD	65913	66,347	0	<b>5.99</b>
16	$K_L e^{lfs+stn+pld}$	$L_{\infty L} e^{\beta tds+\beta cOS-pld} / (1 + \beta dRB)$	AGDD	65918	66,350	3	6.11
17	$K_L e^{lfs+stn+pld}$	$L_{\infty L} e^{\beta map+\beta cOS-pld} / (1 + \beta dRB)$	AGDD	65920	66,393	46	<b>5.91</b>

relative to fry stocking. Strain effects were structured as effect size relative to performance of Pennask strain and ploidy effects were standardised on diploid stockings. Individual models were designed based on inclusion of different covariates for  $K_{L,i}$  and  $L_{\infty L,i}$  (Table 2). Model 1 measured time  $\Delta t$  as calendar days from release date to assessment date; model 2 included the covariate MAT on model 1, while models 3 and higher measured  $\Delta t$  in accumulated GDD (AGDD). Model 4 included the life-stage at stocking as a covariate. Models 5 through 8 evaluated stocking density either as a log-linear covariate (Eq. (8)) on asymptotic length ( $L_{\infty L,i}$ ; models 5 and 7), or as a mechanistic description (Eq. (9)) of density dependence on  $L_{\infty L,i}$  (models 6 and 8). In models 7 and 8, strain effects were added as a covariate and in model 9 ploidy effects were added. Models 10 through 17 explored two different measures to account for lake productivity: TDS (models 10, 12, 14, 16), and MAP (models 11, 13, 15, 17). The analysis was performed in three different sets: (a) models 10 and 11 added the two productivity covariates respectively to model 8; (b) models 12 and 13 add ploidy to models 10 and 11; (c) models 14 and 16 add the density of other species as a density dependent factor to models 12 and 13; and (d) models 16 and 17 added count of other species as a covariate.

The posterior probability distribution for the models were numerically approximated using Markov Chain Monte Carlo (MCMC) simulation implemented in JAGS 3.4.0 (Plummer, 2003) via R (R Core Team, 2017) using the R2Jags package (Su and Yajima, 2012). Posterior distributions were calculated from 100,000 iterations after an initial burn-in of 50,000 iterations and further thinned to provide a final sample of 10,000 from each of three MCMC chains. Convergence was evaluated using visual examination of trace plots of MCMC chains and Gelman-Rubin convergence diagnostics available through the CODA package of R (Plummer, 2003).

### 2.3. Model performance

Model performance was evaluated based on parsimony and predictive performance. Model parsimony was evaluated using the deviance information criterion (DIC), which balances posterior model deviance against the number of effective parameters ( $p_D$ ; Spiegelhalter et al., 2002). Predictive performance was explored based on how each model predicted fish length data for 60 assessments that were not used in parameter estimation. The 60 assessments were not included in the assessments because these lakes did not satisfy the selection criteria in

terms of the minimum number of fish captured or the minimum number of fish of different ages recorded in a gill-net sampling assessment; however, all other selection criteria were met. Across the 60 assessments, the out of sample observations were for a range of fish lengths that included a wide range of fish sizes, environmental conditions, and stocking options, even though individual data sets included might have a had limited range of lengths. Model parameter estimates from the “in-sample” data estimation for each of the candidate models were applied using the out-of-sample covariates to produce predicted length values for trout sampled from the out-of-sample lakes and these predicted lengths were compared with the observed lengths. This enabled an evaluation of how well the parameters obtained and model structures obtained could predict the-out-of-sample length observations using the out-of-sample covariates. We calculated root mean squared error (RMSE) for the predictions of out-of-sample fish lengths.

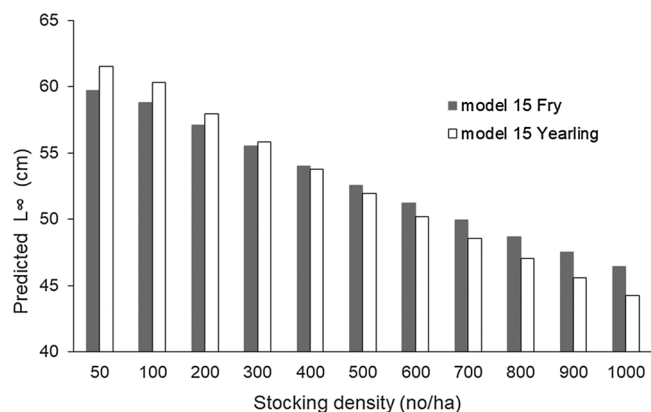
## 3. Results

### 3.1. Model performance

We found that performance in DIC did not directly correspond with RMSE for out-of-sample predictions. In model 2, the MAT effect was not significant, but model performance still improved over model 1 (Table 2). Model 3, which measured  $\Delta t$  in accumulated GDD (AGDD) spent in the lake from stocking to assessment, performed better than both model 1 and model 2. The largest drop in DIC and RMSE was obtained when time in lake calculation ( $\Delta t$ ) was modelled using AGDD instead of calendar days,

Adding the life-stage at stocking (model 4) effect led to improvement in DIC but not RMSE (Table 2). In all models that included life-stage as a covariate, the positive effect on metabolism ( $K_{L,i}$ ) of stocking yearlings was consistent and similar (see Table A1). On average, fish stocked as yearlings have an approximately 1.3% higher  $K_{L,i}$  than those stocked as fry. In all following models, life-stage was included as a covariate.

Including density effects showed improvements in DIC: model 6 with a mechanistic description of density dependence performed better than model 5 and similarly model 8 performed better than model 7. However, models 5 through 9 were approximately equivalent in performance of out-of-sample predictions. The estimated coefficient ( $\beta$ ) governing density dependence for fry was higher than that for yearling



**Fig. 2.** Density dependence in  $L_{\infty}$  based on estimated parameters. Predicted values for  $L_{\infty}$  for fry and yearling against stocking density are shown based on estimates from model 15. Fry are shown in grey bars and yearlings in open bars. Stronger density dependence in yearlings is indicated in the steeper slope of the open bars.

but the total density dependent effect after including the size of stocked fish was higher for yearlings (Fig. 2). At low stocking densities, yearlings produce higher asymptotic size; the effects balance out between fry and yearling stockings at a stocking density of about 300–400/ha (Fig. 2). Higher stocking densities result in a much stronger decrease in asymptotic size for yearling stockings compared to fry stockings. The remaining models (models 10–17) were based on the mechanistic description of density dependence (Eq. (9)).

Adding the strain (models 7 and 8) and ploidy effects (model 9) showed improvement in DIC. Model 9 with density, strain, and ploidy effects on  $L_{\infty}$  had one of the lowest DIC values. Positive effects were estimated for Fraser Valley, Blackwater strain, and mixed strain stockings; the effect-size was larger for Fraser Valley strain (Table 3) compared to Blackwater strain and mixed strain stockings. Gerrard strain stockings were found to have negative effects. Both 3n and mixed ploidy stockings were estimated to have approximately 7–10% lower metabolism than 2n stockings.

Among all combinations evaluated, the best performance measured in terms of DIC was obtained for model 15 which included MAP as the

**Table 3**

Comparison of posterior parameter means for selected models. Parameter names and descriptions are in Tables 1 and 2. \* $lfs = 0$  for fry, \*\* $stn = 0$  for Pennask, \*\*\* $pld = 0$  for 2N.

Parameter	Effect	Models				
		9	11	12	15	16
$L_{\infty}$	$L_{\infty}$	55.400	56.821	55.844	57.967	59.900
K	K	0.285	0.282	0.281	0.286	0.282
$lfs^*$	Yearling	0.130	0.130	0.135	0.132	0.133
$stn^{**}$	Blackwater	0.106	0.084	0.106	0.105	0.107
$stn^{**}$	Carp	0.340	-0.345	-0.342	-0.344	-0.342
$stn^{**}$	Fraser Valley	0.426	0.417	0.428	0.430	0.427
$stn^{**}$	Gerrard	-0.066	-0.065	-0.065	-0.065	-0.064
$stn^{**}$	Mixed	0.085	0.138	0.084	0.085	0.083
$pld^{***}$	3N	-0.062		-0.062	-0.062	-0.062
$pld^{***}$	Mixed	-0.119		-0.120	-0.119	-0.122
$\beta_{dRB}[1]$	Rainbow Density [fry]	1.106	0.981	1.108	1.169	1.143
$\beta_{dRB}[2]$	Rainbow Density [yearling]	0.378	0.385	0.379	0.387	0.377
$\beta_{map}$	map		-0.499		-0.503	
$\beta_{tds}$	tds			0.037		0.038
$\beta_{dos}$	Other Species Density				0.235	
$B_{cos}$	Other Species Count					-0.125

covariate for productivity. Other models with  $\Delta DIC \leq 5$  were models 9, 12, and 16. In comparison, the models with the highest performance in predicting out-of-sample data were models 11, 15, and 17. The biggest gain in DICs and out-of-sample prediction was observed when the time was changed from actual number of days in the lake to accumulated growing degree days spent in the lake. The model with the lowest DIC (model 15) did not have the lowest RMSE in out-of-sample prediction; RMSE for model 15 was 5.99 compared to 5.74 for model 11.

Parameter estimates are similar between the different models with  $\Delta DIC$  values  $\leq 5$  and model 11 with the lowest RMSE for prediction of out-of-sample data (Table 3); this is true for all parameters other than the productivity covariate—model 9 does not include productivity, model 11 and 15 are based on MAP, and model 12 and 16 are based on TDS. TDS coefficient estimates are positive indicating that higher levels of TDS contribute to larger  $L_{\infty}$  and hence fish tend to attain larger sizes in lakes with higher TDS. MAP coefficients are negative indicating higher precipitation resulted in lower food density and hence lower consumption and growth.

For simplicity, all further evaluations were conducted on model 15, which is among the best performing models based on both DIC and RMSE.

### 3.2. Landscape patterns in growth

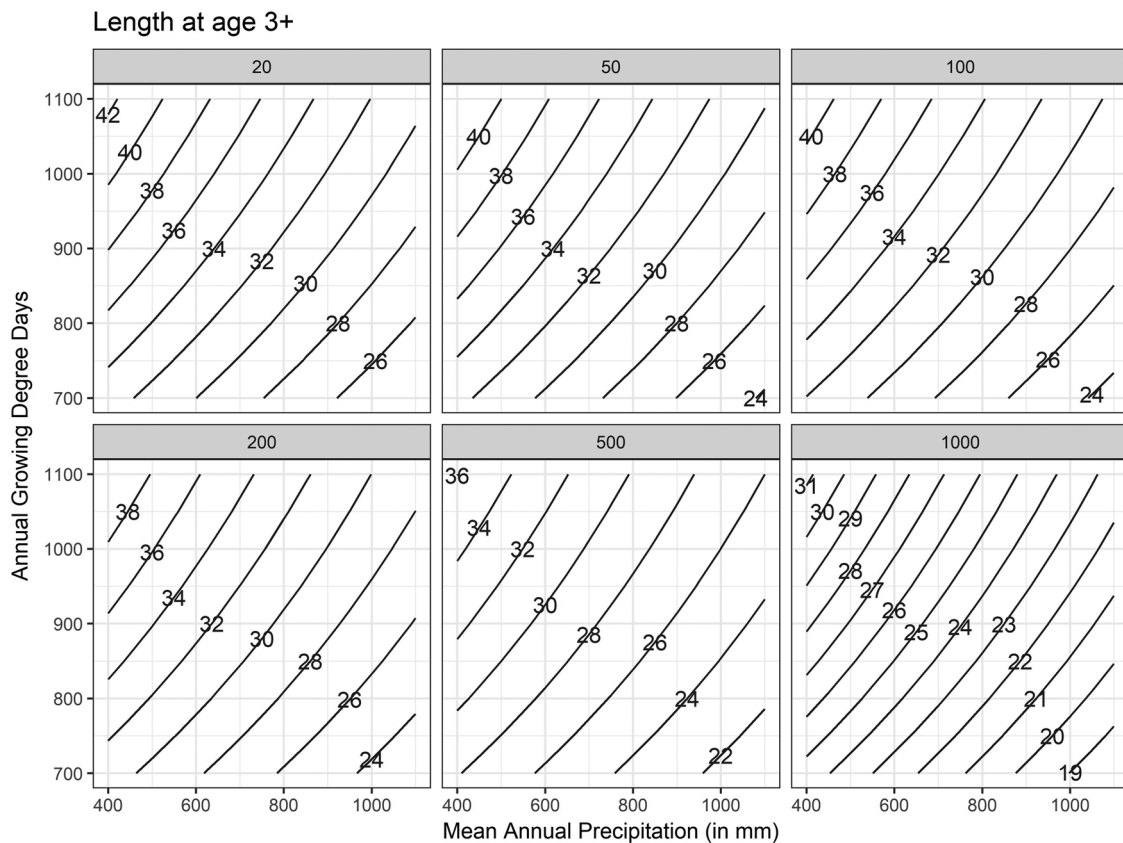
Fitted growth models predicted growth and demonstrated responses to both stocking policies and lake characteristics. For example, model 15 showed how potential size structure, based on asymptotic length ( $L_{\infty}$ ) declined with stocking density and how this expectation differed depending on whether fry or yearlings were stocked (Fig. 2). At low stocking densities, yearling stockings yield larger fish but as stocking density increased, the negative effects of density dependence were more noticeable in yearling stockings. The interactive effect of stocking density, MAP, and GDD on length-at-age of stocked fry showed that ‘trophy fish (> 40 cm) could be obtained only at stocking densities of 100 fry/ha or lower across the range of growing degree days and precipitation rates in British Columbia (Fig. 3).

Lakes with high growth potential at high stocking densities are more common in the southern and central interior of BC than in the northern and eastern interior and coastal regions (Fig. 4) due to site-specific combinations of GDD, TDS and rainfall. A higher proportion of lakes in the southeastern region of the province have potential to produce larger trout but at lower stocking densities than in south-central interior region (Fig. 5). This may be due to there being on average lower GDD, higher rainfall and lower TDS in lakes in the southeastern region compared to the south-central interior regions of B.C. Lakes in the southern coastal region of B.C. that have potential for higher growth at higher stocking densities are confined mostly to the southeastern coastal belt where GDD is higher, rainfall is lower and TDS is higher than in other parts of this region (Figs. 4 and 5). Also, across the entire landscape of B.C. the same lakes that have high growth potential at different fry stocking densities also have high growth potential but mostly at slightly lower yearling stocking levels than the indicated fry stocking levels (Fig. 5).

## 4. Discussion

### 4.1. Influence of stocking strategy on growth performance

Examining in-lake growth of stocked fish presents a number of unique opportunities that would not be possible for wild fish (Post et al., 1999). Each of the fish populations examined in our study have information on mean size- and age-at-stocking, ploidy (diploid or triploid), strain and stocking density. Information on density and size of new recruits would not be available for most wild-stock populations. Taking advantage of the unintentional experiment of stocking in many lakes across a wide range of environmental conditions provides the



**Fig. 3.** Surface plot of fish length at age-3+ across gradients of mean annual precipitation (MAP – representing productivity levels), growing degree days (GDD), and stocking density (fish/ha) choices. Stocking density of 5 cm fry is shown in panel headings. Calculations are based on model 15. In the first panel, the isoclines show size of age 3+ increases with GDD but decreases with increase in precipitation. As stocking density increases from left to right in the figure panels, the size of age 3+ fish decreases for any given GDD-precipitation combination. Given the environmental features at a lake (GDD and precipitation), the figure enables a manager to choose a stocking density for a management target for size of age 3+ fish.

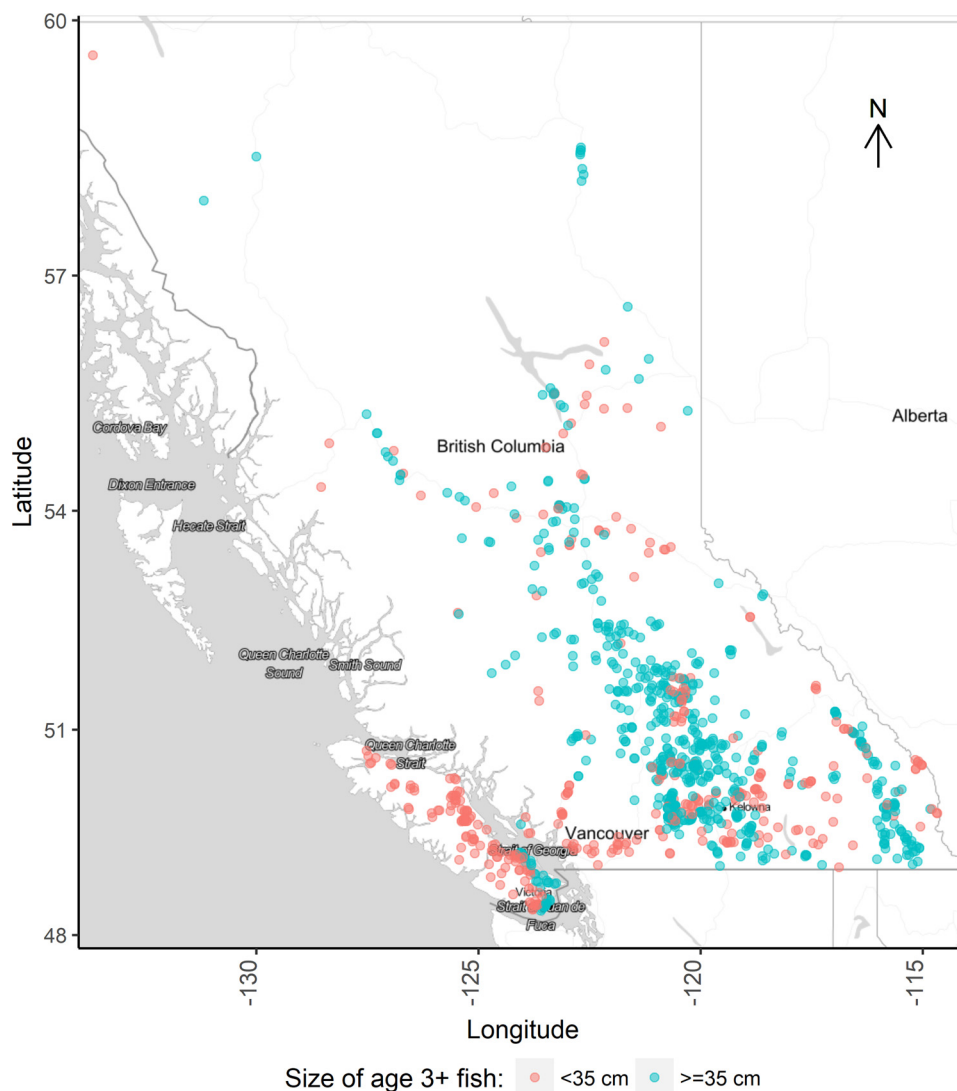
opportunity to more precisely evaluate how growth is influenced by these factors than would be possible with direct experiments on a limited number of populations (Post et al., 1999; Askey et al., 2013). While stocked fish may have behavioral or genetic differences from wild strains, the lessons learned can be of great value for understanding how growth of natural populations will vary across the landscape.

Growth models that incorporate environmental and demographic covariates and drivers should be easily interpretable (He et al., 2005). In constructing and evaluating our models, it was relatively clear how each variable may have influenced growth. Moreover, we allow for model uncertainty in certain drivers, such as temperature and density dependence, by providing alternate model structures and using model selection criteria such as DIC and out-of-sample prediction as a means of determining which mechanism suits our study system (Burnham and Anderson, 2003). However, the mechanisms driving some processes are not explicitly included in the models we present. These mechanisms (life stage, strain, ploidy, productivity indices) are included as covariates with a log-link, but the exact ways in which these variables influence consumption and metabolism (and other processes) are likely to be much more complex.

Angling effort on lakes (e.g., boat days per hectare) is known to vary considerably across the BC landscape (Parkinson et al., 2018) based on travel distances to nearby and distant population centres (Post et al., 2008), angler motivations (Dabrowska et al., 2017) and the attractiveness of fishing opportunities available in any particular area. Fishing effort is assessed on small lakes in BC by aerial counts and camera counts. Fishing effort surveys are not necessarily in tandem with gillnet samplings; these effort assessment methods are expensive and provide information for a small proportion of stocked lakes. It is

known that fishing effort is high in the southern regions in B.C. and lower in the north, but even locally, fishing effort may vary tremendously depending for example on stocking density, stocked fish attributes, angling regulations, proximity to population centres and highways (Post et al., 2008; Parkinson et al., 2018). Hence, including an index of angling effort for each lake or lake-year was not possible for this study. Understanding growth processes could be improved further by detailed analyses of how the various attributes of angling effort (e.g., size-targeting, proportion retained-at-age, gear used and seasonality) impact fish density and thereby fish growth.

Inland fisheries are “multidimensional” and observational studies in inland fisheries could be biased due to influence of management, governance, multiple stakeholders, or natural processes (Lorenzen et al., 2016). The data for this study are not from a designed experiment but from opportunistic gillnet surveys collected over several years. As discussed previously, stocking densities and proximity to population centres (i.e. ease of access for anglers) are different in different lake categories e.g. ‘Family’ versus ‘Trophy’. It is not possible to explore any biases on account of these categories because these categorizations were developed recently, and in many cases, management measures have changed over time. We believe that by including a large sample of the different categorizations across the spatial distribution of stocked lakes, we have reduced possible biases to the extent possible. For broad landscape patterns, simple solutions such as those presented here may be sufficient to describe growth variation while still being relatively intuitive to managers. However, providing more information on management approach (bag/size limits) and fishing effort in a lake level stock assessment model may provide more accurate predictions of a fish population’s age structure and its response to different stocking



**Fig. 4.** Predicted mean lengths for age-3+ fish on the BC landscape. Red dots indicate lakes where mean length for age 3+ < 35 cm and blue dots indicate lakes where mean length for age 3+ fish are  $\geq 35$  cm (the length at which fish are expected to recruit to the fishery). All results are based on stocking 10 g yearlings at 200/ha (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

strategies.

#### 4.2. Landscape patterns in growth

Rainbow trout have been successfully stocked in lakes and rivers around the world (MacCrimmon, 1971). Though our study is confined to populations stocked in BC, some of our findings could be broadly applicable to populations in other jurisdictions as well. One benefit of modelling using a Bayesian approach is our posterior predictive distributions may be used as prior probability distributions for future predictive growth models. Future work based in other jurisdictions could for example consider the key structural features of our best performing growth model, e.g., GDDs for time units, and explanatory variables such as strain, ploidy, stocking density, and life-stage at stocking. In BC, priors for parameters in growth model can be used to develop and improve stock assessment modelling.

Recognizing anglers' preferences, recreational fisheries managers of stocked lakes often use specific growth rates and densities as their primary management targets when assessing stocking policies (Parkinson et al., 2018). Given the importance of growth as a management metric, it is essential to have accurate and biologically plausible models to predict variation in growth potential across the

landscape (Helsler and Lai 2004). A key function of the growth model presented here is to predict growth on any lake on the landscape, based on readily available environmental information and stocking decisions. It is increasingly recognized that anglers are heterogeneous in their preferences and seek a variety of fishing experiences (Dabrowska et al., 2017; Beardmore et al., 2014). The trade-off curves showing comparative results of stocking policies and lake characteristics could help identify the type of lake and the management policies that are required to meet size-based management objectives (Fig. 3). Given the environmental features at a lake (GDD and precipitation), the management outcome for fish size can be predicted from stocking density (Fig. 3.) thereby enabling a manager to make a decision on stocking details. Together with environmental covariates for a given set of lakes these trade-off curves could be used to (1) determine which lakes could meet a specific objective based on one of a variety of candidate stocking regimes (e.g. ability to achieve 35 cm if stocked at 200 yearling per ha, Fig. 4) or (2) determine stocking rates and lakes that could meet other specific objectives (e.g. stocking densities required to produce 40 cm fish as in Fig. 5). This information allows managers to make stocking decisions. For example, one popular management target is the provision of 'trophy-sized fisheries' which provide low densities of large fish (Arterburn et al., 2002) and according to the model presented here



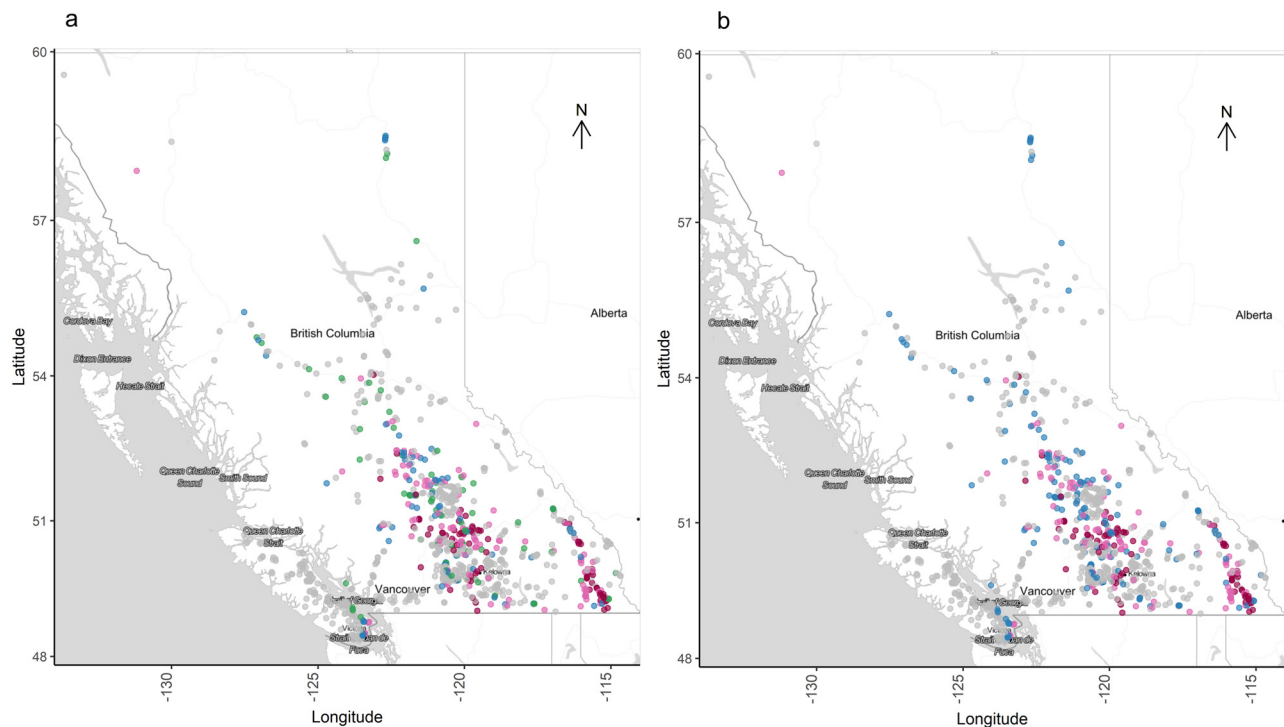


Fig. 5. Stocking densities that produce 40 cm fish from fry (a) and yearling (b) stockings. Grey points indicate lakes that do not produce a fish mean length of  $> 40$  cm at age 3 + . Blue, magenta, and green represent stocking density ranges 20–200/ha, 200–500/ha, and  $> 500$ /ha that produce  $> 40$  cm fish at age 3 + (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

(Fig. 3), very few combinations of fry stockings could produce 40 cm fish by age-3. When combined with environmental information, model results can be used to communicate landscape limitations and evaluate lake-specific capacity to meet size-based management objectives (Figs. 4 and 5). For example, all the lakes in 'grey' (Fig. 5) are unable to produce 'Trophy' fish at any stocking density. These findings allow managers to compare current stocking policies with model predictions and evaluate if stocking strategies could be improved to meet lake-specific management objectives. When mapped, these management-specific lake attributes reveal pronounced regional and within-region patterns across the landscape of B.C. The locations of the highest productivity lakes within broader regions, e.g. the southern interior, conform to the locations that tend to have higher GDD, lower rainfall and lakes having higher TDS. On the coast, only a small fraction of the lakes are capable of producing larger trout due mainly to higher rainfall amounts and a tendency for higher lake flushing rates; managers and anglers in this region would need to lower their expectations for the size "Trophy" fish can attain. And in northern regions, managers would need to stock lower densities to produce "Trophy" fish. Similar landscape level evaluations can be performed for different size-based management objectives and the findings used to help managers to more precisely tailor hatchery production to model-predicted stocking needs and more efficiently distribute their available hatchery products between lakes.

When imbedded in a more comprehensive management model (e.g. Askey et al., 2013; Varkey et al., 2016), a growth model could be used to quantify the effect of this size-density trade-off on angling quality and identify lakes that are able to produce fish sizes and catch rates that are high enough to attract trophy anglers. A better match between the set of opportunities and the attributes of anglers (trophy, urban, family, regional) should increase overall angler satisfaction. The growth modelling presented in this paper can help managers set fisheries objectives and stocking densities on individual lakes that will achieve their objectives at the regional scale, given geographic constraints influencing productivity, thereby improving region-wide fishery utility and angler

satisfaction (Johnston et al., 2010).

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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2018.06.015>.

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