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Nomenclature

- *a* Relative cost of producing new individuals to replace those lost through mortality
- **B** Total population biomass
- **B**_i Biomass of new individuals that recruit to the population at age j
- E Mean activation energy of cellular respiration
- **g** Instantaneous rate of biomass increase, includes both somatic growth of existing age groups and recruitment of new individuals to the youngest age group
- io Normalization constant
- k Boltzmann constant
- K Population carrying capacity
- Lact Population rate of energy expended on interactions with the environment
- L^a_{act} Population rate of energy expended on attacking prey
- L^s_{act} Population rate of energy expended on searching for prey
- L_{inf} Asymptotic length
- L_m Population rate of energy expended on basal maintenance costs
- L_R Population rate of energy loss to propagule (eggs/sperm) release
- L_z Population rate of energy loss to mortality
- M_{ind} Individual metabolic rate
- M_{pop} Average routine metabolic rate of individuals in a population that is at its carrying capacity.
- \bar{N}_i Average abundance of a cohort over its $[i+1]^{th}$ year of life.
- P Tissue production
- P_{cc} Production of a population at its carrying capacity.
- P_F Population rate of energy acquired from foraging
- P_{ε}^{max} Maximum rate of energy acquisition
- P_{ε} The rate of energy flow from the environment through a population
- ρ_F Proportion of energy available in forage that is acquired by population members

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- ρ_R The degree to which the energy of propagules released to the environment is augmented, over early life, to generate the energy of older individuals recruiting to a population.
- R Population rate of energy acquired from addition of newly recruited individuals
- r Proportion of adult body weight that is released as propagules at each breeding period.
- s Relative cost of synthesizing somatic tissue
- t Time
- **T** Environmental temperature (°K)
- *W_i* Weight of an individual
- \overline{W} Mean weight of individuals in a population that is at its carrying capacity.
- Wind Individual somatic weight
- W_{inf} Asymptotic weight
- z Instantaneous mortality rate; rate of biomass loss through mortality.

General introduction

Freshwater fisheries are essential economic, cultural and subsistence resources in many countries around the world, with freshwater fish harvests supplying enough food protein for an estimated 158 million people globally (McIntyre et al., 2016; Funge-Smith and Bennett, 2019). It has long been recognized (e.g., Leach et al., 1987) that sustainable harvests are determined by the capacity of natural populations to produce new biomass—their rates of biomass production. Historically, fisheries conservation was achieved mainly through focused efforts on fisheries regulation. More recently, the negative effects of anthropogenic stresses (i.e., climate change, habitat degradation, pollution, invasive species) on the fundamental processes supporting the viability of fish at both the individual and population level have been recognized, leading to an expansion of conservation efforts to include protection of both the quantity and quality of fish habitat (Sass et al., 2017).

Fishes are dynamic in time and space. They are influenced by a range of species-specific abiotic and biotic factors and require a minimum amount of usable habitat to be viable, resulting in both population abundance and production varying directly with the quantity and quality of available habitat (Fig. 1). Countries like Canada have recognized legislatively that the productivity of fish populations and communities are inextricably linked to habitat availability and have implemented policy requirements and



Fig. 1 Body size and temperature preference are the dominant traits that determine the capacity of an individual from a particular species to synthesize new biomass from its environment. The physical space available (e.g., lake size, river width/length) sets an upper limit on realized production. The degree to which realized production reaches that upper limit is determined jointly by the fraction of the available space that is usable as habitat by the target species, and the "quality" of that habitat space. This, in turn, is determined by: (i) the abiotic characteristics of the available space that define the fraction of that space that is usable = the relative amount of space that supports tolerable temperatures and water chemistry for the target species; (ii) the degree to which abiotic conditions in the usable space match species-specific optimal performance traits = the quality of the usable habitat (iii) the relative abundance of prey, competitors and predators that inhabit the usable habitat.

scientific approaches that focus on sustaining production through habitat conservation using regional productivity benchmarks (DFO, 2016). However, the effectiveness of this approach hinges on developing a sound understanding of the environmental and ecological forces that shape the productivity of freshwater fish populations in their natural environments. Currently our understanding of these forces is limited, due mainly to the time and cost of the field studies required to quantify how production varies among wild populations of limnetic and riverine fish.

Production at the population level is defined as the amount of tissue elaborated in the population over a time period (Δt), regardless of whether that tissue survives to the end of that period (Waters, 1977). Production is expressed as biomass elaborated per unit space per unit time (e.g., kg ha⁻¹ year⁻¹). It is determined by the three separate processes that add or subtract new biomass to that segment of the population (i.e., typically older juveniles to the oldest adults) that can be accurately tracked with existing technologies. Those processes are (i) tissue growth, which causes the weight of existing population members to increase from W_t to $W_{t+\Delta t'}$ (ii) reproduction, which causes new individuals to recruit to the population as members of the youngest observable group; and (iii) mortality, which causes the number of older population members to decrease. We illustrate the fundamental way in which these separate processes interact to generate production, can be approximated by a single value (g) representing the instantaneous fractional rate of biomass increase; and that (ii) the loss in population biomass associated with mortality can be approximated by a single value (z) representing the instantaneous fractional rate of biomass decrease. Therefore, the instantaneous rate of change in biomass (*dB/dt*) can be expressed as:

$$dB/dt = (g - z) *B \tag{1}$$

and the production generated over the interval Δt equals (see Gillespie and Benke, 1979 for a demonstration):

$$P_{\Delta t} = [B_{t+\Delta t} - B_t][g/(g-z)]$$
⁽²⁾

where B_t is the initial biomass density (kg ha⁻¹) at time *t*.

For a population at its carrying capacity (i.e., *B* is constant and therefore $\frac{dB}{dt} = 0$), growth (including both tissue synthesis and recruitment) and mortality rates must be equal and therefore, $g^*B = z^*B$, from Eq. (1). While Eq. (2) is undefined for g = z, Gillespie and Benke (1979) demonstrated that, *P_{cc}*, the production of a population at its carrying capacity, can be computed as

$$P_{cc} = g * B = z * B \qquad \text{when } (g - z) \to 0 \tag{3}$$

In nature, g and z are dynamic and sensitive to changes in both environmental conditions and population biomass. However, Eq. (3) should hold, provided B, g and z vary randomly around relatively constant mean values.

Ideally, production estimates are based on extended time series of comprehensive demographic information (i.e., abundance, biomass, growth and mortality; Dolbeth et al., 2012; Rypel et al., 2015) and hence are logistically demanding. However, the high value of population production estimates compensates for their cost since: (i) they provide direct measures of the degree to which individual populations extract energy from their supporting ecosystems (Downing et al., 1990; Downing and Plante, 1993); (ii) they provide indirect measures of sustainable harvest at the population level (e.g., Leach et al., 1987); and (iii) they provide the empirical basis for advancing our understanding of the forces that drive variation in production in the natural world (Downing and Plante, 1993). This last role is of value since it is fundamental to the development of new and better models for predicting the responses of production both to environmental changes, and to the management actions designed to mitigate those changes. In this chapter, we begin by first reviewing the standard methods used to estimate production in the field. We then go on to (i) review the fundamental bioenergetic processes that support production at the population level, (ii) summarize current knowledge regarding the sensitivity of those processes to changes in both abiotic and ecological conditions, (iii) identify recent methodological advances that promise to increase the precision and accuracy of production estimates, and (iv) suggest promising directions for increasing our knowledge of how production is determined in the wild.

Estimating production

Traditional methods

Production is typically estimated first within a given size-class or age-cohort. These results are then aggregated across classes or cohorts to give an overall estimate of production for the population or community of interest. A variety of estimation methods exist and the choice of method is largely dictated by the data available to calculate the estimate. In the simple situation where age-specific growth and survival rates are constant over time, the following elaboration (patterned after Benke and Huryn, 2017, assuming a time unit of 1 year) of Eq. (1) captures the basic information alluded to, or directly used, in all of these methods:

$$P = B_j + \sum_{i=j}^{i=n} \overline{N_i} * \Delta W_i \tag{4}$$

where:

- *P* is the production of new biomass generated by the entire population over 1 year,
- {*j*,*n*} is the range of ages for which both abundance (\overline{N}_i = the average abundance of a cohort over its [i + 1]th year of life) and size at age (W_i and $\Delta W_i = [W_{i+1} W_i]$) are known, and
- B_i is the biomass of new individuals that recruit to the population when they reach age *j*.

If j = 0, then this equation provides an unbiased estimate of production for the entire population. If j > 0, then B_j represents the accumulated tissue growth of individuals surviving from age 0 to age j; this equals the annual production of those age groups only in the unrealistic situation where all individuals survive from age 0 to age j. In the real world, where significant mortality occurs in early life, B_j underestimates the production of early age groups and thus P is underestimated. If B_j is omitted from the result, then P is an unbiased estimate of production over the age range [j, n]: the range of ages that can be effectively monitored. If the growth and mortality rates for a population are relatively constant over time, data from a point-in-time sample can be used in Eq. (4) to estimate the value of P that is typical for that population. If growth and mortality rates vary widely from year to year, consecutive annual samples are required to provide the year-specific estimates for $\overline{N_i}$ and ΔW_i that are needed to generate annual values for P over the time interval of interest. When applying any of the methods listed in Table 1, sampling programs need to be designed to minimize the biases in estimates of both $\overline{N_i}$ and ΔW_i that typically arise from such factors as size/age selectivity of sampling gear, variation in sampling efficiency across habitat types, life cycle complexity (e.g., migration or developmental changes in habitat), and, consequently, the completeness of sampling coverage of the population or community of interest.

While production estimation methods follow the basic concepts outlined above, accepted methods in the literature for calculating production estimates vary based on the data available. The Instantaneous Growth Rate (IGR) method (see Table 1) remains the most widely accepted and popular method for production calculations due to its greater precision. However, the price for this precision is the high data demand of the method (Hayes et al., 2007). While the size-frequency method is based on length-classes and does not require aging data, it too requires at least two consecutive sampling periods to calculate a single estimate. Older and less frequently used methods include the Allen curve and Summation (Removal and Increment) methods. The Allen curve is a graphical extension of the IGR method and is based on cohort-specific growth-survivorship curves. However, it is rarely implemented now because it lacks a variance estimator. Summation methods are based on estimates of the gain or loss of tissue by a population over time: removal summation focuses on estimating the loss rate of individuals, while increment summation focuses on estimating the tissue growth of individuals. Variance estimators for the removal summation method are also unavailable (Hayes et al., 2007). There are numerous worked examples for each of these methods in the literature, and a selection for each is listed in Table 1.

Recent refinements

Five of the seven methods listed in Table 1 require characterization of the life-time growth patterns of typical population members. Growth is a sensitive component of production estimates that offers insight into the state of a population. However, growth

Method	Summation (removal and increment)	Allen curve	IGR (instantaneous growth rate)	Simplified IGR	P/B ratios	Size-frequency	IGR modified with cohort-fitted growth curves
Examples	Newman and Martin (1983)	Waters (1977)	Newman and Martin (1983), Hayes et al. (2007), and Rypel et al. (2015)	Embke et al. (2019)	Newman and Martin (1983), and Randall and Minns (2000)	Garman and Waters (1983)	See "Recent refinements"
Data required							
For estimating rate	of change						
Two or more time periods	Y	Y	Y	Ν	Ν	Y	Y
Cohort size-at-age	Y	Y	Y	Y	Ν	Ν	Y
Size composition (weight, length; no age data)	Ν	Ν	Ν	Ν	Y	Y	Ν
For estimating abu	ndance						
Cohort density (number, biomass)	Y	Y	Y	Y	Y	Y	Y

 Table 1
 Overview of fish production calculation methods, examples, and data requirements.

Y denotes data types required for the estimation method, N denotes data types that are not required for the estimation method.

calculations within production estimation methods are often a significant source of error. Error introduced through growth calculations can arise from the under-sampling of age groups that is common in fisheries surveys: when few (e.g., <5) individuals are captured, weight data for age-cohorts or size-classes will be quite inaccurate. By replacing estimated weights for under-sampled age classes with predicted weights from growth curves fitted to individual cohorts, error will be reduced and the overall precision of production estimates will be increased.

Additional refinements include a simplified IGR method from Embke et al. (2019) that allows for the calculation of production estimates without consecutive annual measurements, while incorporating biomass lost to harvest. However, this method relies on simplifying assumptions that should be recognized (i.e., subsamples of ages and lengths determine relative age-class densities; age-specific mean weights are determined from ecosystem specific age-length keys). This method offers the opportunity to explore conservative "snap-shot" estimates of production based on limited data, particularly from harvested populations.

The bioenergetics of fish production

Seminal empirical work has shown that freshwater fish production is correlated with total phosphorus, primary production (Downing et al., 1990), standing biomass and mean body-mass of fishes, annual mean air temperature, latitude, and species richness (Downing and Plante, 1993). Since these associations are largely consistent with expectations generated from the Metabolic Theory of Ecology (MTE: Brown et al., 2004; Savage et al., 2004), we will use the MTE explicitly in our account of how individual-level bioenergetic processes support population-level production in wild freshwater fish populations (Fig. 1).

General principles: The Metabolic Theory of Ecology

The Metabolic Theory of Ecology (MTE) contends that the primary factors that shape the energy metabolism of individuals (i.e., body size and temperature) also shape the rates of energy gain and loss that determine the flow of energy through a population in the wild. This focus of the MTE makes it particularly relevant to the study of production since it is the flow of energy through a population that must underlie the rates of biomass gain and loss (g and z in Eq. 1) and therefore also determine population production. This is seen most clearly through the relationship that defines production for a population at its carrying capacity. From Eq. (3), at carrying capacity, production equals g^*B . Given that the synthesis of new biomass requires the input of new energy, changes in mass-specific production rates (i.e., changes in g) must reflect changes in energy flow. Hence, understanding the forces that drive changes in production. What follows is a brief summary of the MTE, focusing on its relevance to understanding the forces that drive production in the wild.

For most ectotherms, basal metabolic rate (M_{ind} , the flow of energy required to sustain life in an individual) is given by:

$$M_{ind} = i_0 W_{ind}^{3/4} e^{-E/kT}$$
(5)

where M_{ind} is individual metabolic rate, W_{ind} is the somatic weight of the individual, *T* is the environmental temperature (°Kelvin) the individual is experiencing, i_0 is a constant that is specific to each species, *E* is the mean activation energy of cellular respiration (0.60–0.70 eV) and *k* is the Boltzmann constant (8.62 10^{-5} eV/K; Brown et al., 2004; Gillooly et al., 2001). The routine and maximum metabolic rates typically seen in the wild roughly follow simple multiples of this basic equation (Peters, 1983).

Now that we have a bioenergetic description of individual metabolism (Eq. 5), we show how it can be used to describe the flow of energy through an entire population. Following Savage et al. (2004), the flow of energy through a population that is maintaining itself at its carrying capacity within its supporting habitat can be derived as follows:

- (i) replace individual somatic weight (W_{ind}) in Eq. (5) by the average weight of individuals (\overline{W}) when the population is at its carrying capacity (K),
- (ii) energy flow ($P\varepsilon$) through the population under an environmental temperature (T) is then given by:

$$P\varepsilon = (1 + s + a) * M_{\text{hold}}(\overline{W}, T) * K(\overline{W}, T)$$
(6)

where $M_{pop}(\overline{W}, T)$ is the basal metabolic rate of individuals in the population, *s* and *a* augment basal metabolism to account for costs associated with generating new somatic and reproductive tissue, respectively, at the rates required to maintain the population at its carrying capacity, and $K(\overline{W}, T)$ is the numerical abundance at carrying capacity.

(iii) the bracketed first term in Eq. (6) explicitly identifies the processes that underlie the growth term (g) in Eq. (3): tissue maintenance (1), somatic growth (s) and reproduction (a). It also clarifies how body size and environmental temperature (through $M_{pop}(\overline{W}, T)$ as defined by Eq. 5) act together with abundance to determine overall energy flow and consequently production.

Now, if we replace population abundance $[K(\overline{W}, T)]$ in Eq. (6) with its biomass equivalent $[K(\overline{W}, T)^*\overline{W}/\overline{W}]$ and expand M_{pop} with the temperature and weight effects from Eq. (5), then Eq. (6) becomes:

$$P_{\varepsilon} = (1 + s + a) * \left[K(\overline{W}, T) * \overline{W} \right] \left[i_0 * e^{-\frac{E}{kT}} * \overline{W}^{3/4} / \overline{W} \right]$$
(7)

and this simplifies to:

$$P_{\varepsilon} = (1 + s + a) * [population \ biomass] \left[i_0 * e^{-\frac{E}{kT}} * \overline{W}^{-1/4} \right]$$
(8)

where i_0 is the normalization constant from Eq. (5). Note that, since $\overline{W}/\overline{W}$ is equal to 1, multiplying Eq. (6) by $\overline{W}/\overline{W}$ to get Eq. (7) does not alter the validity of either equation. Given that production (*P*) must be supported by energy flow (*P_e*), it is reasonable to expect that production will also follow Eq. (8). This expectation is supported by the fact that there is a qualitative and quantitative match between Eq. (8) and the empirical analysis of production presented by Downing and Plante (1993). These authors showed that the statistical links between population production and standing biomass, temperature and mean body-mass are consistent with the form of Eq. (8) and that the fitted exponent for body weight (-0.17) in their analysis is similar to the expected value of -0.25.

Another important production metric is the production to biomass ratio (P/B). The P/B ratio is an expression of population growth that is linked to the productive capacity of a population's habitat (Randall and Minns, 2000) and has been used in a variety of contexts to estimate production when data intensive methods cannot be applied (e.g., Sprules and Stockwell, 1995; Shuter and Ing, 1997; Randall and Minns, 2000). By simply dividing both sides of Eq. (8) by population biomass, we arrive at:

$$\frac{P\varepsilon}{[population\ biomass]} = (1+s+a) * \left[i_0 * e^{-\frac{F}{kT}} * \overline{W}^{-1/4}\right]$$
(9)

which highlights the role of both temperature and somatic weight in determining the P/B ratio.

Support for the MTE rests on general summaries of empirical data on the performance of various plants and animals in the wild. Data on marine and freshwater fish populations have also played a supporting role in these analyzes, indicating that it is a relevant framework for considering the production of fishes. The following section provides a more detailed demonstration of the degree to which current knowledge of fish bioenergetics matches expectations from the MTE.

MTE and freshwater fish-Examining the role of body size and temperature in detail

The acquisition and allocation of energy towards biomass production occurs simultaneously with energy losses to maintenance and activity (L_m and L_a respectively), individual mortalities (L_z) and propagule release (eggs and sperm; L_R). Assuming that P is roughly proportional to P_{z} , this implies that:

$$P \propto P \varepsilon = \left[\rho_F * (\text{available forage}) + \rho_R * L_R - (L_m + L_{act}) - L_z - L_R\right]$$
(10a)

which simplifies to:

$$P \propto [P_F + R - (L_m + L_{act}) - L_z - L_R]$$
(10b)

where ρ_F is the proportion of available forage energy that is acquired by population members (i.e., foraging efficiency), P_F represents total energy acquired by the population from foraging, ρ_R is the degree to which energy released to the environment as propagules accumulates during offspring development to return to the monitored segment of the population as newly recruited individuals, and R is the product of ρ_R and L_R (Fig. 2). Notably, the degree of energy allocated towards propagule production is a positive reflection of the size and health of the individual and this, in turn, will contribute directly to the degree to which energy released as propagules returns to the population as newly recruited individuals (ρ_R ; e.g., Venturelli et al., 2009, 2010).

From the MTE, we would expect these processes of energy acquisition and recruitment to vary predictably with body size and temperature, following the allometric Arrhenius weight-temperature functional form defined in Eq. (5), with individual somatic



The Bioenergetics of Population Production

Fig. 2 Over any time period, realized production by the older individuals in a population derives from several different flows of energy through those individuals: For a population in equilibrium with its environment [dB/dt = 0], the following relationships should hold: (i) the production of new biomass (somatic tissue + reproductive tissue) is determined by the net gain in energy from foraging ($= P_F - (L_m + L_{act})$) where P_F depends on the amount of prey available in the environment and the foraging efficiency (ρ_F) of a typical individual. (ii) the increase in biomass from new individuals recruiting to the population is determined jointly by the biomass released as propagules (L_R) and the degree to which that biomass is augmented over early life (ρ_R) by the combined effects of individual growth and mortality. (iii) the total gain in biomass from growth and recruitment = losses from metabolic costs, propagule release and mortality.

weight replaced by the population mean somatic weight (Eqs. 6-8, following Savage et al., 2004) and the proviso that *T* does not exceed the tolerance range of the species in question. Thus, maintenance losses can be described as:

$$L_m = i_m \,\overline{W}^{\beta m} \tag{11a}$$

the maximum rate of energy acquisition, P_{ε}^{max} , as

$$P_{\varepsilon}^{max} = i_{\varepsilon max} \,\overline{W}^{\beta_{\varepsilon max}} \tag{11b}$$

losses to mortality as:

$$L_z = i_z \,\overline{W}^{\rho z} \tag{11c}$$

and losses to propagules as:

$$L_{R} = r * \overline{W} \tag{11d}$$

where:

$$\beta_m \approx \beta_{emax} \approx 3/4$$
 (11e)

$$\beta_z \approx -1/4$$
 (11f)

and $[i_m, i_{emax}]$ exhibit the temperature dependence evident in Eq. (5), i_z increases with temperature and r is a species-specific constant. For individuals, there is good empirical support for Eqs. (11a), (11b), (11d) (Fig. 3A and B) regarding maintenance losses and energy acquisition: (i) estimates of bioenergetic performance parameters for 58 fish species described in the fish bioenergetics model FB4 (Deslauriers et al., 2017) are consistent with the allometric form; (ii) typical values for β_m and β_{emax} are close to the expected value of $\frac{3}{4}$ (Eq. 11e); and (iii) over species-specific thermal tolerance ranges (Savage et al., 2004), the effect of temperature on i_m and i_{emax} is consistent with the Arrhenius relationship (Fig. 4A and B; Deslauriers et al., 2017).

For populations, there is also good empirical support for Eq. (11c) regarding losses to mortality (McCoy and Gillooly, 2008; Fig. 3C): the allometric form is followed, the exponent has a value close to the expected value of -1/4 (Eq. 11f), and i_z shows the expected increase (vertical offset) with increasing environmental temperature. In Eq. (11d), energy lost to reproductive activity ($r * \overline{W}$) is assumed to be proportional to somatic weight. This is consistent with the typical metric used in field studies for this quantity (i.e., GSI = gonad weight/body weight). For fish generally, values of *r* for mature females can range from 0.2 to 0.6 (Lester et al., 2004b).

The variable L_{act} (Fig. 2) measures the energetic cost to the individual of interacting with its environment and is often dominated by foraging costs. These separate into the cost of search (L^{s}_{act}) and the cost of attack (L^{a}_{act}). There is strong theoretical (Weihs, 1977; Ware, 1978) and empirical (Videler and Nolet, 1990; Ryan et al., 2015) support for asserting that search velocity in the wild will match the velocity that maximizes distance traveled per unit swimming cost. Travel at this velocity varies with (body length)^{0.45} with a metabolic cost, at the level of the individual, that is roughly proportional to basal metabolism. It then follows that the overall activity cost needed to provide a population with a fixed daily ration of prey biomass will vary with the overall attack cost ($L^{a}_{act} = [\# \text{ attacks}]^*[\text{cost/attack}]$). This will increase with the number of prey required to meet that ration and, all else being equal, that number and the overall attack cost will decrease as prey size increases. This effect of prey size on foraging cost has been observed in many natural populations (Paloheimo and Dickie, 1966; Kerr and Ryder, 1977; Sherwood et al., 2002a; Giacomini et al., 2013).



Fig. 3 Relationships of fish consumption (Panel A), metabolism (Panel B) and mortality (Panel C) with body mass. Histograms of fish mass exponents for consumption (Panel A, as g food per day) and metabolism (Panel B, as g 0_2 consumption or energetic units per day) both approximate 0.75. The median values for consumption and metabolism are 0.73 and 0.79, respectively and the shaded region highlights density of observations between 0.65 and 0.85. Instantaneous mortality (Panel C) scales negatively with body mass among fishes occupying cold, cool and warmwater habitats: the common slope across habitats approximates -0.25 (estimated slope = -0.263; note log scales on axes). Panels A and B: Data FROM Deslauriers D, Chipps SR, Breck JE, Rice JA, and Madenjian CP (2017) Fish bioenergetics 4.0: An R-based modeling application. *Fisheries* 42:586–596; Panel C: Data from McCoy MW and Gillooly JF (2008) Predicting natural mortality rates of plants and animals. *Ecology Letters* 11:710–716.



Fig. 4 Influence of thermal range on individual performance in fishes. Panel A: In fishes, both consumption and basal metabolism increase with temperature to a peak value and then decline rapidly, with death occurring at a critical maximum temperature. The green curve shows the thermal response of consumption for Walleye (*Sander vitreus*) when prey are abundant. The temperature range supporting optimal performance is characterized by the fundamental thermal niche (after Magnuson JJ, Crowder LB, and Medvick PA (1975) Temperature as an ecological resource. *American Zoologist* 19: 331–343, in gray) of 4 °C around the optimum temperature. The overall shape of the basal metabolism vs temperature curve is similar to that in Panel A but shifted to the right by 2C. For temperatures below the optimum, the pattern of increasing rates with increasing temperature approximates the Arrhenius temperature relationship in the MTE. This holds for both consumption and basal metabolism. Panel B shows that the peak consumption observed at the species-specific optimum temperature does not vary systematically across thermal guilds. Each point refers to a particular species; points are colored by thermal guild, where guild membership is set by optimum growth temperature (0GT, from Hasnain, SS, Escobar MD and Shuter BJ (2018) Estimating thermal response metrics for north American freshwater fish using Bayesian phylogenetic regression. *Canadian Journal of Fisheries and Aquatic Sciences* 75:1878–1885): cold-blue 0GT < 17.5; cool-green 0GT falls between 17.5 and 25.0; warm-red 0GT > 25. The mean peak consumption rate across all guilds = $0.46 \text{ g}^{-1} \text{ g}^{-1} \text{ day}^{-1}$. Panel C shows that thermal range (the difference between the optimal growth and lethal temperature, shown in orange in Panel A) narrows significantly from cold to cool to warmwater fishes. Data in panels A and B from Deslauriers D, Chipps SR, Breck JE, Rice JA and Madenjian CP (2017) Fish bioenergetics 4.0: An R-based modeling application. *Fisheries* 42:586

For a particular species, individual metabolic rates are relatively insensitive to temperature over a specific thermal range (Fig. 4A) where performance is optimal in regards to activity, feeding, growth, and reproduction (Fry et al., 1947; Pörtner, 2002; McMeans et al., 2020). This optimal range has been dubbed *the fundamental thermal niche* (Magnuson et al., 1979). The diversity of temperature constraints that have shaped ecological performance of freshwater fish has produced wide diversity in realized thermal niches, with species-specific optimal performance temperatures ranging from 5 °C to 30 °C (Hasnain et al., 2018). The center of the fundamental thermal niche has been used to group freshwater fish species into three discrete thermal guilds (McMeans et al., 2020): cold-water—optimal temperatures <17 °C; cool-water—optimal temperatures ranging from 17 °C to 25 °C; and, warm-water—optimal temperatures >25 °C (Fig. 4B and C). Although the peak feeding rate at the optimal temperature is similar across guilds (Fig. 4B), the width of the thermal niche declines progressively as the optimal performance temperature increases (Fig. 4C). Within a thermal guild, feeding rate (Fig. 4A) and basal metabolic rate respond in a similar way to temperature differences: for temperatures below the thermal niche, both rates approximate the Arrhenius temperature relationship; for temperatures above the thermal niche, both rates decline rapidly following rapid declines in enzymatic efficiency (Fry et al., 1947; McMeans et al., 2020; Pörtner, 2002).

The impetus for an individual to seek its optimal operating temperature shapes its habitat use and consequently its realized growth and mortality risk (e.g., Cruz-Font et al., 2019). This, in turn, shapes its productive capacity and, thus, the productive capacity of the population to which it belongs. Empirical data suggests that functioning at temperatures exceeding the preferred range can lead to energetic inefficiencies (e.g., metabolic costs increase faster than ingestion rates) that reduce population productive capacity (Gorman et al., 2016). However, at temperatures within and below the preferred range, temperature differences can promote variation in production in at least three ways:

- (I) By promoting changes in the overall abundance of new forage through changes in factors like primary production (e.g., Cross et al., 2015; Junker et al., 2020) and growing season length (Shuter and Ing, 1997; Gorman et al., 2016).
- (II) By promoting higher feeding rates on existing forage supplies: for freshwater fish, temperatures below optimal have similar exponential effects on both maximum consumption rates and metabolic costs (Deslauriers et al., 2017; Fig. 4A), therefore, temperature increases at the lower end of the tolerance range can promote higher net energy gain by promoting higher feeding rates on existing forage resources.
- (III) By promoting changes in the availability of existing forage supplies: for example, temperature change (e.g., seasonal warming or cooling in boreal lakes) can extend/limit the opportunities for a particular consumer to forage in some habitats by driving ambient habitat temperature into/out of the consumer's tolerance zone (Guzzo et al., 2017).

When forced to forage in habitats outside of their optimal thermal niche, reduced foraging efficiencies (Fig. 4A) and additional energetic costs reduce the net energy available for production of new tissue. Ultimately, this can impact fitness through impaired survivorship and/or reproductive success (Quince et al., 2008; Guzzo et al., 2017; Cruz-Font et al., 2019).

The role of habitat

Ecosystem size ultimately dictates the habitat available to support fish production. Additional characteristics such as light (Lester et al., 2004a), oxygen (Plumb and Blanchfield, 2009), and temperature (Guzzo and Blanchfield, 2017) determine the amount of habitat that is actually useable by that population (Fig. 1). These characteristics can then be further modulated by nutrients, such as dissolved organic carbon (DOC; Ask et al., 2009). Thermal habitat constraints on fishes have been thoroughly discussed in Section "MTE and freshwater fish—Examining the role of body size and temperature in detail", thus, our attention below turns specifically to the constraints set by space, oxygen and nutrients.

The role of habitat: Spatial limits

Production is often quantified on a per unit habitat basis (e.g., Downing and Plante, 1993; kg ha⁻¹ year⁻¹) with the implicit assumption that this value is independent of lake or river size. However, physical boundaries (e.g., lake shoreline, riverbanks) clearly limit fish population function in most freshwater ecosystems. In rivers compared to lakes, home ranges are smaller for a given fish size (Minns, 1995), while P/B ratios are larger (Randall et al., 1995). This is likely due to the greater role of throughput (i.e., more allochthonous than autochthonous inputs) in rivers. Similarly, since the fraction of littoral zone surface area typically decreases with lake size, allochthonous nutrient inputs and littoral benthic production often make a greater contribution to overall production in small lakes than in large lakes. This is important as ecosystem size can limit food chain length, and consequently top predator size, in both terrestrial and aquatic systems (Schoener, 1987). These effects are particularly evident among top predators living in lake ecosystems (Vander Zanden et al., 1999; Post et al., 2000, 2002). Simple energetic arguments and empirical findings (outlined below) support the contention that these effects will influence fish population production.

Given that:

- Metabolic demand increases with body size (Eq. 5), and
- Hydrodynamic constraints ensure that the metabolic cost of areal search is proportional to basal metabolism ($L_{act}^s \sim L_m$; Ware, 1978; Videler and Nolet, 1990).

It follows that:

- Foraging space, which is approximated by home range size, should increase with body size;
- Large piscivores will be absent from very small ecosystems;
- The adult size of piscivores will tend to be larger in the longer food chains that are common in larger systems; larger systems tend to support longer food chains because foraging spaces are larger, food web diversity is higher and forage species tend to be larger (e.g., Sherwood et al., 2002a; McGarvey et al., 2016).

Fig. 5 illustrates this congruence between individual capabilities (e.g., areal search rate), metabolic need (e.g., home range size), increased foraging opportunities (e.g., presence/absence of pelagic forage fish) in larger systems and population traits (e.g., mean adult size). Data used to generate the black and blue lines are from the Lake Trout (*Salvelinus namaycush*) life history data base documented in Lester et al. (2021). Here "Body Length" is typical adult body size, estimated as the mean of length at maturity and maximum length.



Fig. 5 Similarities across spatial scales of how body size influences the use of space by fish: (i) The lowest (red) line: the relationship (Ware, 1978) linking fish body size to prey search rate (ha time⁻¹), (ii) the orange line: the relationship (Minns, 1995) linking home range size to fish body size (ha) in lakes, (iii) The black line: the relationship linking lake size (ha) to adult body size for populations of Lake Trout (*Salvelinus namaycush*) where pelagic piscivory is negligible, (iv) The highest (blue) line: the relationship linking lake size (ha) to adult body size for populations of Lake Trout (*S. namaycush*) where pelagic piscivory is dominant.

All four relationships exhibit very similar slopes. Lakes below the horizontal dotted line are too small to support a top predator like Lake Trout (*S. namaycush*). The range of small body sizes marked by the two vertical dashed lines are only found in small lakes where pelagic piscivory is absent (dark gray rectangle).

In aquatic systems (freshwater and marine—Sprules and Barth, 2016) both numerical and biomass abundance (per unit habitat) decline as body size and trophic position increase (Andersen, 2019). Therefore, changes in prey size will affect the net benefit to predators through changes in both prey abundance and predator foraging efficiency. Eqs. (6), (8) and (9) can be used as guides to generate predictions of how these diverse effects will impact predator production *per individual* (Eq. 6) and predator production *per unit predator biomass* (Eqs. 8 and 9). They also identify the central role that overall population abundance (numerical and biomass) plays in determining total population production and consequently production *per unit habitat*. Eq. (10a) explicitly identifies the primary roles that available forage (i.e., forage *per unit habitat*) and predator foraging efficiency play in determining production *per unit habitat*.

Population biomass production (per unit habitat) should vary inversely with adult size (Eq. 8; Downing and Plante, 1993) and hence be higher in smaller ecosystems. Lester et al. (2021) quantified this effect for North American Lake Trout (*S. namaycush*) populations, showing that the equilibrium rate of biomass production (including growth and recruitment) among adults in unexploited populations was an allometric function of adult size ($\sim W_{inf}^{-1.63}$)—a result consistent with the theoretical work of Andersen and Beyer (2006). Here, and in other studies, the measure of adult size is the weight or length (W_{inf} , L_{inf} respectively) typical of the largest adults in the population. For two well studied Lake Trout populations (Lake 373: 27 ha, $L_{inf} = 425$ mm; Lake Opeongo: 5800 ha, $L_{inf} = 603$ mm; Cruz-Font et al., 2019), this implies that biomass production per hectare for Lake 373 is approximately five times the production for Lake Opeongo. This drop in production is roughly consistent with the drop in trophic efficiency (e.g., Andersen, 2019 p. 36) expected, given that Opeongo Lake Trout are feeding on pelagic fish, one trophic level higher than Lake 373 Lake Trout, which feed on zooplankton (Vander Zanden et al., 1999).

The role of habitat: Oxygen limitation

The physiological performance of ectotherms depends strongly on aerobic metabolic rate, which varies with both oxygen concentration and temperature. At high temperatures or during times of intense activity, oxygen supply can exceed demand, and the metabolic rate approaches a limit (Fry et al., 1947; Pörtner, 2002; Rubalcaba et al., 2020). The difference between basal metabolism and this metabolic limit represents the aerobic scope (i.e., the energy available) for fitness-enhancing activities such as movement, feeding, digestion, growth, and reproduction. From Eq. (5), we expect metabolic oxygen demand to increase with higher temperatures within the liveable thermal boundaries of fishes, and this expectation has strong empirical support (e.g., Rubalcaba et al., 2020). In the aquatic environment, oxygen and temperature act together to define the oxythermal habitat space that supports optimal performance by individuals of a particular species (Fig. 1). The size and positioning of this space within the larger habitat will vary with climate/latitude, with implications for behavior patterns, activity costs and, ultimately, population productivity. Behavioral telemetry studies have found that Lake Trout (*S. namaycush*) reduced their use of littoral regions due to shorter spring and longer summer seasons (Guzzo et al., 2017). This was accompanied by (i) loss of optimal oxythermal habitat; (ii) reduced access to littoral prey resources; leading to (iii) reduced individual growth rates and body condition. These findings are particularly important within the context of climate change, where warmer, longer summer seasons can lead to significant decreases in oxythermal habitat for cold-water fish and increases for warm-water fish (Guzzo and Blanchfield, 2017).

The role of habitat: Nutrient limitation

Nutrient limitation of ecosystem productivity is an important theme of freshwater ecology and this limitation is implicit in the population abundance terms in Eqs. (6)–(9): increased nutrient inputs are expected to increase production at lower trophic levels, promoting increased population abundance, and consequently higher production at higher trophic levels. Many studies have identified phosphorus as a correlate (Downing et al., 1990) and a driver (Mills, 1985; Rennie et al., 2019; Hecky and DePinto, 2020) of both fish biomass and production. This is nicely demonstrated in several whole lake experimental lake studies (Schindler 1990, Bristow et al., 2008) that involved nutrient additions and increases in total phosphorus concentration in small oligotrophic lakes. In one experiment, the production of the resident top predator (*Coregonus clupeaformis*), rose and fell with the initiation and cessation of nutrient additions (Mills 1985). These changes in production were the combined result of parallel increases in abundance, recruitment, and somatic growth (Mills 1985). In another experiment (Rennie et al., 2019), the abundance of both small forage fish (i.e., minnows) and the resident top predator (*S. namaycush*), rose and fell with the initiation and cessation of nutrient additions. The increases in top predator abundance were accompanied by parallel increases in somatic growth and maturation size and a parallel decrease in age at maturation.

Beyond the direct effects of nutrient levels on ecosystem productivity, other components of water chemistry (e.g., pH—Mills et al., 2002a,b; Schindler 1990) can indirectly modulate fish production through bottom-up effects on nutrient and habitat availability. For example, DOC attenuates light and thus can alter vertical temperature profiles (Pilla et al., 2018), primary productivity (Ask et al., 2009) and oxythermal habitat availability (Knoll et al., 2018). Increases in DOC can be accompanied by decreases in fish abundance (Seekell et al., 2018), growth (Benoît et al., 2016), and biomass production (van Dorst et al., 2019). Such effects are of immediate concern since DOC concentrations are increasing in aquatic ecosystems due to climate change and altered precipitation cycles (Solomon et al., 2015).

The role of community: Prey and competitors

Like production (as outlined earlier in Sections "General principles: The Metabolic Theory of Ecology" and "MTE and freshwater fish—Examining the role of body size and temperature in detail"), the life history of a population emerges from the bioenergetic processes that determine the amount of energy allocated to fitness-enhancing traits such as somatic growth and reproduction (Lester et al., 2004b; Shuter et al., 2016). As discussed in Section "MTE and freshwater fish-Examining the role of body size and temperature in detail", these bioenergetic processes are strongly dependent on prey availability and quality (Giacomini et al., 2013). Prey quality, and particularly prey size relative to predator size, (the predator/prey size ratio; Andersen and Beyer, 2006; Brose et al., 2006) can be just as important as prey availability in determining the energy budget of individual fish and populations (Fig. 6A). The net energetic benefit associated with acquiring a unit biomass of food typically increases as prey become bigger (e.g., Kerr, 1971; Shuter et al., 2016)—even if the biomass density of small prey is high, many individual prey captures are needed to meet the energy needs that arise with increasing predator size (Cruz-Font et al., 2019). The high attack costs that result can create a bioenergetic bottleneck where the value of reaching larger adult size (i.e., increased fecundity with larger size; Giacomini et al., 2013; Cruz-Font et al., 2019) is offset by the energetic cost of reaching and maintaining that size (Sherwood et al., 2002a,b). Life history theory dictates that this trade off will shape both the size-at-maturity and post-maturation growth pattern of the predator (Jensen, 1996; Charnov and Gillooly, 2004; Lester et al., 2004b): when larger prey are available, fitness is maximized by an increase in adult size and a reduction in reproductive allocation (Fig. 7A). These differences feed back, through their effects on adult size and somatic growth, to exert a strong influence on population production (Eq. 8).



Fig. 6 Forces affecting the balance of energy flow (gains vs losses) through a population when the overall supply of prey resources is fixed. (A) Relative prey size determines foraging costs for predators: very large prey are very costly (if not impossible) to capture; as prey become smaller, the cost per capture declines but the gain per capture also declines—acquisition of a fixed amount of biomass is accompanied by increasing activity costs; the net result of this tradeoff is that relative feeding costs reach a minimum (and feeding efficiency reaches a maximum) when the predator/prey weight ratio lies in the range [400,700]— Andersen, 2019. (B) Relative predator size determines mortality on prey. The relationship between predator benefit and prey size evident in panel A has a parallel effect on prey mortality risk. For the prey, mortality risk rises and falls with increasing predator size. Since predator feeding efficiency on very large and very small prey is low then, all else being equal, the mortality risk for prey should be correspondingly low, with highest risk associated with predators that are 400–700 times larger (by body weight) than prey.



Fig. 7 Prey availability and predation risk act together to determine the timing/extent of reproductive allocation and hence the lifetime growth pattern of a typical individual. Panel A: the theoretical relationships linking optimal life history traits (allocation of energy to reproduction and age at maturity) to both variation in prey size and mortality. Panel B: the observed relationships (after Fig. 3 in Shuter et al. (2005) linking life history traits to trophic position and mortality (L₂) for a sample of fish populations from freshwater lakes (number of populations: 14 Lake Trout *(Salvelinus namaycush)*, 17 Walleye *(Sander vitreus)*, 10 Cisco *(Coregonus artedi)*, 15 Yellow Perch *(Perca flavescens)*).

Competition for prey can also drive population production, with production decreasing as species richness increases (Downing and Plante, 1993). In particular, invasions of non-native species can alter fish production in potentially unpredictable ways. When introduced, Northern Pike (*Esox lucius*) often negatively impact native species (DeBates et al., 2003; Haught and von Hippel, 2011)—in some cases eliminating prey species, leaving pike monoculture lakes (Regmi, 2012; Nicholson et al., 2015). In lakes without an offshore prey fish population, the invasion of non-native Smallmouth Bass (*Micropterus dolomieu*) can negatively impact Lake Trout (*S. namaycush*) dramatically by reducing their access to larger nearshore prey (minnows), forcing an increased reliance on offshore zooplankton (Vander Zanden et al., 1999) leading to slower growth rates and reduced production. From an ecosystem perspective, it is currently unclear as to whether the production of invasive fishes can ultimately offset the loss of native fish production in invaded ecosystems such as these.

The role of community: Predator pressure

Trade-offs between predation mortality and growth are common in fishes, since mortality losses are driven by the relative size of predator and prey (Fig. 6B). Growth can provide an escape from predation, with prey fish (or, in cannibalistic species, juvenile life stages) growing rapidly and maturing earlier to exceed predator gape (Day et al., 2002; Biro et al., 2005; Urban, 2007). Ironically, the increased foraging required to achieve rapid early growth rates often leads to increased exposure to predation. However, this comes with the benefit of reaching an invulnerable size faster (Urban, 2007). Alternatively, if refuges (spatial or temporal) are available, fish may modify their behavior to avoid predation, but this may force a decrease in foraging opportunities (e.g., Peacor, 2003). Linked changes in both overall activity and foraging can generate wide variation in growth trajectories (Abrams and Rowe, 1996). In Yellow Perch (*Perca flavescens*), maximum size, size at maturity, growth rate and growth efficiency all increased with increased predation risk, despite negative correlations with consumption and activity (Rennie et al., 2010). These results suggest that increased use of refuges in these populations permitted increased growth when risk of predation was high.

This trade-off between mortality and growth impacts life history decisions in ways that are similar to the trade-off between prey size and growth (Fig. 7A). The value of reaching larger sizes through allocating most available energy to somatic growth is offset by the increases in mortality that accompany higher foraging rates. Life history theory dictates that individuals will reach a point where the benefits of growth will be outweighed by the risk of mortality and all surplus energy should be allocated to reproduction (Jensen, 1996; Charnov and Gillooly, 2004). This will lead to earlier maturity and reduced post-maturation somatic growth under high mortality, with consequences for production through changes in both adult size and somatic growth. This set of joint differences in mortality, growth and maturity schedules is typical of the differences observed between forage fish and top predators (Fig. 7B).

Future directions and conclusions

It should be clear now that bioenergetic theory provides a unified paradigm for developing explicit hypotheses regarding the forces driving variation in production in wild populations of freshwater fish. However, the empirical work needed to explicitly test these ideas has lagged behind theory development. In the 2017 summary of currently available data provided by Rypel and David (2017), less than 30% of production estimates were based on direct estimates of production and over 60% of these were published prior to 2000. This highlights the need for new direct empirical estimates of fish production to refine our understanding of how drivers like habitat limitation, temperature/climate change, and prey size/foraging efficiency shape production in the wild. In addition to new empirical studies, a wider application of methodological refinements and further development of logistically simpler predictive models of fish production are needed, both to extend our understanding of production and to develop more effective, evidence-based strategies for conserving fish productivity.

Addressing costs of reproduction in production estimates

In most fish species, energy assigned to biomass synthesis shifts significantly at sexual maturity from somatic tissue to the predominate production of energy dense reproductive products (i.e., propagules; Gunderson and Dygert, 1988; Henderson et al., 2000). This shift in energy allocation leads to significant changes in the growth curve of individuals and populations: (i) prior to maturation, body weight increases steadily as biomass production accumulates; (ii) after maturation, body weight increases prior to spawning but then declines suddenly at spawning with the expulsion of propagules (Fig. 8A). Failure to account for these changes in weight and energy allocation to reproduction can generate age-specific bias in production estimates (Fig. 8B and C, Box Fig. 1).

Biphasic growth models capture these energy shifts particularly well and have been widely accepted since they were first proposed (Charnov et al., 2001; Lester et al., 2004b), with empirical work demonstrating their efficacy in providing accurate descriptions of lifetime growth (Shuter et al., 2005; Quince et al., 2008). These models explicitly recognize the landmark change in energy allocation that occurs with sexual maturity (Fig. 8A) through depicting (i) pre-maturation length growth as a linear function of age and (ii) growth at, and post-maturation, as an abrupt switch to an asymptotic form that is consistent with the von Bertalanffy equation. These models are then able to quantify traits that are critical in determining individual fitness (i.e., age at first reproduction, reproductive investment; Charnov et al., 2001, Shuter et al., 2005). This provides the opportunity to test hypotheses regarding how age-at-maturity and reproductive allocation (and hence lifetime growth pattern) should change with changes in mortality rate, prey availability (Fig. 7) and other environmental and ecological factors. Lastly, biphasic model fits can provide an



Fig. 8 Growth in fishes is often approximately linear when immature, but slows following maturity once allocation to reproduction (*L_R*) is initiated (Panel A, size at age of Lake Opeongo lake trout). The deviation from the initial linear pattern increases progressively with higher allocation of energy to reproduction. This growth pattern can be characterized by a von Bertalanffy growth function (Green dashed line), but more recently bi-phasic models of growth (orange) that explicitly recognize linear immature growth are more common. Absence of information on immature fish (common in commercial fisheries; shown in purple) can lead to overestimation of immature fish size if the growth curve for older ages is extrapolated to younger ages. When these growth curves are used to measure instantaneous growth (as they are in common production estimation methods), the bi-phasic model more accurately describes observed growth on average (Panel B). Growth curves fit to only mature fish are variable relative to observed growth (Panel B) and tend to greatly overestimate immature growth (Panels B and C). The traditional von Bertalanffy fit to all age classes is also variable and tends to underestimate instantaneous growth (Panel B), especially at the smallest age classes and immediately post-maturation (Panel C). (A) Data from Shuter BJ, Giacomini HC, de Kerckhove D and Vascotto K (2016) Fish life history dynamics: Shifts in prey size structure evoke shifts in predator maturation traits. *Canadian Journal of Fisheries and Aquatic Sciences* 73:693–708.

indirect estimate of reproductive energy allocation Shuter et al. (2005) that can be used to scope the magnitude of potential bias in empirical studies that do not cleanly allow for its cyclic gain and loss over a typical growing season. For example, the biphasic fit to the data in Fig. 8A generates an estimate of annual reproductive investment by females that is equivalent to \sim 23% of body weight.

This highlights the importance of ensuring that the production that is allocated to reproductive tissue is accounted for in production calculations, as well as the production allocated to somatic tissue. This requires:

- Accounting for the greater energy density of reproductive tissue (particularly eggs—see summaries in Gunderson and Dygert, 1988; Shuter et al., 2005) over somatic tissue;
- Scheduling field sampling to allow for the fact that seasonal patterns of reproductive allocation can exhibit accelerated allocation just prior to spawning and that most reproductive tissue is expelled when spawning ceases.

Failure to recognize these issues can lead to significant underestimates of population production—as illustrated in Box 1.

Refining the P/B ratio approach

The P/B ratio method for estimating production is founded on statistical regression models that summarize patterns in observed population production data. It is simple to apply, requiring only estimates of biomass and mean fish size for a given population, community, or ecosystem. Further development of this method along the following lines is needed both to confirm its reliability and broaden its applicability to a wider range of ecological contexts:

- Challenge the basic P/B model with new empirical data on how the relationship between production and biomass is affected by cofactors such as climate, food web diversity, habitat type (e.g., lake vs. river), and habitat size and complexity (e.g., Minns, 1995; Randall et al., 1995);
- Include size composition data in a weighted mean P/B and compare resultant production estimates with those derived from more data-intensive methods (such as the IGR method—Table 1);
- Use estimates of (*d*W/*d*t)/W from individual growth models (e.g., biphasic models) to derive species or stock-specific P/B ratios and compare with those derived directly from empirical data;
- Evaluate whether key life history parameters (e.g., growth coefficients), along with phylogenetic and environmental variables, can be used to derive species- and site-specific P/B values (see Thorson, 2020).

Currently, there is limited appreciation of how basin-wide production is shaped by scale and habitat factors (Oberdorff et al., 2011); recent work with Alaskan Pacific Salmon (*Oncorhynchus tshawytscha*) populations (Brennan et al., 2019) suggests that the integration of biocomplexity across large spatiotemporal scales can act to stabilize production basin-wide. Development of a more diverse and precise set of P/B models may provide the tools needed to design logistically feasible studies of variation in production across entire watersheds. The new knowledge of basin-wide patterns in production, obtained from such studies, could provide the empirical foundation needed for developing more effective, evidence-based strategies for assessing fisheries and conserving productivity at broader spatial scales (e.g., Rypel and David, 2017; Jarvis et al., 2020).

Box 1 Consequences of missing reproductive biomass in production estimates.

Access to prey resources and habitat suitability can exert a strong influence on the age or size at which an individual begins to allocate acquired energy to reproduction (Shuter et al., 2016). This key life-history trait is important to the overall productivity of a population since it dictates both adult maximum size and life-time fecundity. Current production estimation methods do not explicitly account for the energy or biomass lost through propagules (eggs/sperm) during spawning. By not accounting for loss of reproductive tissue, such estimates may underestimate the overall productivity of a population. This is of particular concern if field sampling occurs at times that do not coincide with spawning events, when investment in gametes is highest prior to release.

We aimed to assess the extent to which sampling of non-spawning individuals could underestimate overall production by failing to account for the production of reproductive tissue. Using long-term Lake Trout size-at-age data from Lake 375 in the IISD-Experimental Lakes Area (ELA), we calculated production estimates using the IGR method from 1989 to 2002 under population scenarios reflecting different sex ratios (50:50 and 80:20 females:males; the latter represents an extreme case of potential biomass allocation to gametes). Reproductive investment scenarios were set by the GSI (gonad weight expressed as a percentage of body weight: 15% for females, 5% for males) values observed for Lake Trout in Lake Opeongo in Algonquin Park, Ontario (Pazzia et al., 2002).

Since ELA Lake Trout data were collected in the fall during spawning, we felt justified in assuming: (i) our observed weight-at-age values included the full weight of tissue allocated to reproduction, and therefore (ii) these data provided the ideal dataset for evaluating potential bias as outlined below. A weighted average for population gonadal investment was calculated using female and male GSI values (0.1 and 0.13 for 50:50 and 80:20 females:males populations, respectively). These values were then multiplied against the weight of all aged individuals greater than 6 years of age, under the assumption that fall spawning Lake Trout *(Salvelinus namaycush)* spawn for the first time at the end of their 6th growing season. These amounts were then subtracted from the age class specific mean weight of all mature individuals, simulating spawning losses in the population. This allowed us to determine the degree to which we would underestimate production if our sampling occurred outside of the spawning period. Production estimates that excluded reproductive tissue were up to 50% lower than estimates based on the full observed weight of individual fish at spawning (Box Fig. 1; $t_{18} = -3.7628$, P < .001), with little difference between the 50:50 and 80:20 scenarios.

We demonstrate that underestimates of production may be substantial when reproductive biomass is not captured through appropriately timed sampling. This highlights the need to carefully consider the timing of field surveys such that reproductive energy allocation can be included when developing field sampling protocols designed to estimate production, or components of production.



Box Fig. 1 Comparison of annual production estimates that include reproductive biomass versus estimates that exclude reproductive biomass. Estimates are based on Lake (*S. namaycush*) Trout from lake 375 at the IISD-Experimental Lakes Area. A female:male sex ratio of 50:50 was assumed and reproductive biomass was estimated using sex specific mean values for the ratio of gonad weight to body weight (the GSI). Error bars represent estimate variance.

Conclusions

Our summary of current knowledge suggests that the primary drivers of production in freshwater fish populations can be divided in two distinct categories:

- 1. Forces that drive food availability:
 - (i) Production at lower trophic levels sets the level of available food;
 - (ii) The presence of competitors reduces available food through sharing;
 - (iii) The presence of predators limits access to available food by imposing additional mortality risk.
- 2. Forces that shape life history and hence determine adult size:
 - (i) Temperature, as a modulator of growth rates through its effects on both foraging efficiency and basal metabolic costs;
 - (ii) Ecosystem size;
 - (iii) Relative prey size, through its effects on foraging efficiency;
 - (iv) Predation-induced mortality.

The fundamental link between environmental temperatures and foraging as it relates to production is worth stressing here. The empirical findings and theory discussed earlier demonstrate that bottom-up influences—which control prey resource availability—appear to be critical drivers of fish production. This is consistent with other theoretical work suggesting that prey resources may often be the primary factor driving animal production, overriding direct effects arising from temperature and/or metabolic limitations (Cross et al., 2015; Junker et al., 2020).

On this basis, we offer the following testable hypotheses to guide future research:

- 1. Given that prey body size is a main determinant of predator body size, an increase in prey body size in the absence of changes in prey trophic level and abundance should lead to an increase in both predator foraging efficiency and predator size, with the following consequences for production: *increases* in both predator production per unit habitat area and predator production per individual (as per Eqs. 10a and 6); a parallel *decrease* in predator production per unit biomass, as per Eq. (8). The fact that the predicted direction of change depends very much on the units used to measure production highlights the importance of clearly defining those units.
- 2. As habitat size increases, top predators tend to occupy higher trophic levels. This is accompanied by the following changes in the dominant prey species: *increases* in both trophic level and individual size; *decreases* in both numerical and biomass abundance (Sprules and Barth, 2016, see chapter on the Biomass Size Spectrum, Andersen, 2019). The consequences for predator production will be diverse: at the population level, production per unit habitat will decrease (assuming increased foraging efficiency cannot compensate for the overall reduction in prey abundance), production per unit biomass will also decline (as per Eq. 8) but production per individual will increase (as per Eq. 6).
- 3. P/B ratios can be used as logistically simpler surrogates of detailed fish population production estimates, particularly for population and community production estimation on larger regional scales such as watersheds and lake regions.
- 4. Oxythermal habitat loss as a consequence of climate change will decrease production in stenothermic predators.
- 5. As DOC increases, light limitation increases, reducing the overall productive capacity of freshwater ecosystems, with negative consequences for fish production.

Fish production has long been recognized as the ideal metric for understanding the state of fish populations since it is the outcome of a major pathway of energy flow (Waters, 1977). Establishing the mechanisms that drive fish production within freshwater ecosystems through exploring the hypotheses we have laid out above will advance current knowledge in useful ways by: (i) answering fundamental questions around freshwater ecosystem function, and (ii) promoting the development of the practical management tools needed to mitigate future stresses on these systems from climate change, human development, invasive species, and exploitation.

Knowledge gaps

- New and defendable empirical estimates of production from a diversity of freshwater systems
- A better accounting for reproduction costs in production and MTE approaches
- How the relationship between production and biomass is affected by cofactors such as climate, food web diversity, habitat type (e.g., lake vs. river), and habitat size and complexity
- Refine the upscaling of individual growth models to population levels
- Accounting for phylogenetic diversity in production models

Further reading

- Bioenergetics and energy budgets
- The biomass size spectrum
- Benthic algae and food webs
- Fish populations
- Fish communities
- Lake food webs
- Inland Fisheries Management—Exploitation and Livelihoods
- Societal values of inland fishes

See Also: Emerging methods and topics: Electronic Tagging and Tracking of Animals in Inland Waters; Freshwater Ecoacoustics—A New Addition to the Limnologists' Methods Toolkit; Fundamental concepts and theories: Bioenergetics; Diel Vertical Migration; The Biomass Size Spectrum; Human pressures and management of Inland Waters: Freshwater Biota as Indicators of Impact: Case Studies and Examples of the Major Groups in Surface Water Assessment; Implications of Climate Change for Freshwater Fisheries; Inland Fisheries Management - Case Studies of Inland Fishe; Inland Fisheries Management - Exploitation and Livelihoods; Social/societal values of Inland waters: Societal Values of Inland Fishes; The Gender Gap: Women as Authors and Leaders in International Publications in Fisheries Science; Structures and functions of Inland Waters - Lakes: Fish Populations; Predation on Zooplankton; Structures and functions of Inland Waters - Rivers: Energetics and Food Webs in Large Rivers; Structures and functions of Inland Waters - Wetlands: Patterns in Freshwater Fish Diversity

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