Metabolic life tables: the sockeye salmon example

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Key words: life history; demography; energy budget; ecosystem; conservation; sustainable harvest; steady-state; metabolic theory of ecology; population

Abstract

We resurrect the metabolic life table (MLT), a combination of life table and energy budget that quantifies how metabolic energy is acquired and allocated to survival, growth and reproduction over the life cycle. To highlight its broad implications and utility, we apply this framework to John Brett's classic data on sockeye salmon. In the life cycle of Skeena River sockeye, a pair of breeders dies in fresh water after spawning, and the offspring move to the ocean where they feed, grow and suffer mortality before returning to freshwater and migrating upstream to spawn and die. Most of the accumulated biomass energy is transported into freshwater ecosystems and expended on respiration for migration and breeding or is transferred to

consumers. Reanalyzing Brett's data in the context of a MLT has broad implications and applications: i) for basic ecology, because of the unusual physiology, life history and ecosystem impacts of wild salmon; and ii) for conservation and management, because of the enormous economic importance of wild-caught and farmed salmon. Moreover, the MLT highlights the intimate relationships between two universal biological processes: i) demography as a function of age; and ii) metabolism—the balancing of uptake, transformation, and allocation of metabolic energy over the life cycle. Linking these two universal processes provides a general MLT framework that can be applied across the diversity of life.

Introduction

Empirical and theoretical research on metabolic ecology uses energy as a common currency to make explicit linkages between ecology, life history and evolution (e.g., Lotka 1922; Odum & Pinkerton 1955; Hall 1972, 1995; Van Valen 1976; Brown et al. 2004, 2018; Koopijman and Kooijman 2010; Sibly et al. 2012; Burger et al. 2019). These linkages connect anatomy, morphology, physiology and behavior at the level of individual organisms to patterns and processes of ecological organization at population, community and ecosystem levels. They also have important implications for applied issues in science including conservation, management and exploitation of animals for human use.

Canadian fisheries biologist John "Roly" Brett (1983, 1986) introduced the concept of a "life table of energetics," which combines the demographic framework of a traditional life table with the energy balance framework of physiological ecology. Brett illustrated the conceptual approach and practical applications using data on sockeye salmon collected over decades of field and laboratory research. Here, we resurrect Brett's seminal ideas in the context of recent advances in metabolic scaling theory. We compile and reanalyze his data to address theoretical and empirical, basic and applied problems. We show how updated metabolic life table (MLT) analysis offers new insights into the fundamental general features of demography and metabolic ecology that govern the diversity of life (Brown et al. 2018; Burger et al. 2019). Sockeye salmon provide an exemplary model system for MLT analysis illuminating the keystone energetic roles of salmon in ecosystems and human economies.

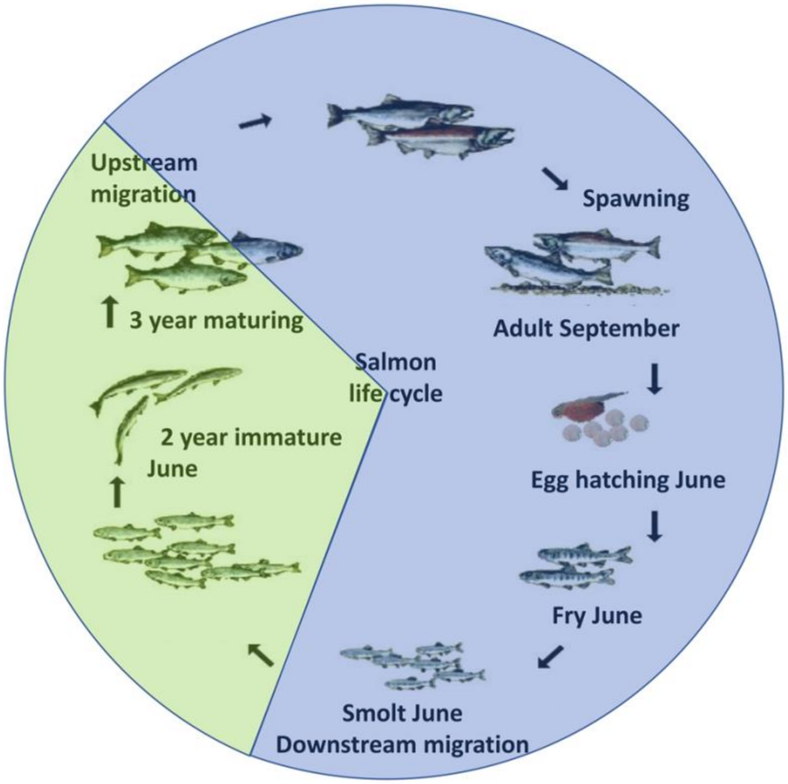

Figure 1. Life cycle of Babine Lake sockeye salmon after Brett (1983). The parts of the life cycle spent in fresh water and the oceans are indicated by green and blue shading, respectively, but not to scale; salmon spend nearly equal time, two years, in freshwater and marine environments. Figure modified from

https://www.google.com/search?q=salmon+life+cycle&rlz=1C1CHFX_enUS555US555&source=lnms&tbm=isch&sa=X&ved=0ahUKEwj7rZiC3PXWAhWBLmMKHRIiAM8Q_AUICigB&biw=1067&bih=423#imgrc=WiztTrFdqAKvPM.

Brett's seminal 1983 paper "put together a comprehensive estimate of the life energetics of an average sockeye salmon that commences life as a fertilized egg weighing 0.013 g containing 372 cal … and terminates growth as a 2,270 g adult containing 4,200 kcal when entering fresh water on its final journey ... to examine the life energetics in detail—namely, the Babine Lake sockeye salmon" Brett 1983, p.30). Brett combined a *life table*, which quantifies changes in the number of individuals with age due to survival and reproduction; and an *energy budget*, which accounts for the flows and stocks as energy is taken up from the environment and allocated to maintenance (survival), growth and reproduction. Pacific salmon (*Oncorhynchus spp.*) provide an excellent empirical model organism for two reasons: they have an unusual life history that facilitates quantification (Fig. 1); and they have been studied intensively – long prized as food for humans, wild fisheries and aquaculture are worth billions of dollars (Quinn 2018; http://www.iser.uaa.alaska.edu/Publications/2013_04-TheEconomicImportanceOfTheBristolBaySalmonIndustry.pdf; https://en.wikipedia.org/wiki/Aquaculture_of_salmonids). Here we reassembly and revive Brett's "life table of energetics" of sockeye (Brett 1983; Brett 1986; Furnell and Brett 1996) in the context of recent advancements in metabolic life history theory (Brown et al. 2018; Burger et al. 2019) in order to demonstrate the practical utility and universality of the approach.

Methods

Brett compiled what he called a "Life Table of Energetics" (Brett 1983), which gives data on body mass and composition, and energy acquisition and expenditure for 33 stages of a typical four-year life cycle (distilled in Tables 1 and 2). In doing so Brett made some simplifications and assumptions:

1) He assumed that the population was in steady state with reproduction balancing mortality. In the 1970s and early 1980s the Babine Lake sockeye population was relatively stable, providing a sustainable fishery.

2) He assumed a simplified four-year life cycle, ignoring the small proportion of the population that returned to breed after three or five years.

3) He estimated average values for the population as a whole, ignoring variation among individuals and across years.

4) He used laboratory measurements, simplified models, and corrections for environmental temperature to estimate energy assimilation from feeding and energy expenditure for maintenance and activity.

5) He used additional information from models and other salmon populations to estimate parameters (e.g., growth and mortality) for the marine stages for which direct measurements for the Babine Lake population were not available.

6) He recognized that many parameters were estimated with some imprecision, so he rounded off and reported approximate average values.

We extended Brett's work and made additional changes. Most notably we used information on mortality in other papers (Brett 1986; Furnell and Brett 1996) to obtain the age structure for the 33 stages in Fig. 2. Using these values—and ignoring variation in mortality and standing stocks due to movement at sea and seasonal fluctuations in ocean temperature and productivity—we put together a MLT for the Babine Lake sockeye population in Table 1. Given the above assumptions, simplifications, and conversions, our metabolic life tables is a faithful distillation and synthesis of Brett's data.

The data on survival (number alive) come primarily from Brett (1986), which reports estimates for seven approximately yearly intervals derived from a combination of field measurements and demographic models. We interpolated between these values to estimate survival at monthly intervals.

Metabolic ecology of sockeye salmon

Natural history of the life cycle

Salmon are: 1) anadromous – breeding in fresh water and growing in the ocean, and 2) semelparous – making a single, end-of-life reproductive effort. The life cycle (Fig. 1) starts in September when the mature adults have returned to spawn in tributary streams of Babine Lake. The average female lays about 3,000 eggs, each weighing 0.013 g. Males fertilize the eggs as females deposit them in the streambed. The eggs are buried in gravel and develop over the winter. In June about 600 survivors hatch, move to the lake, and feed on plankton. After one year about 84 surviving smolts, each weighing ~5.4 g, migrate downstream and enter the ocean. During the marine phase of the life cycle, which lasts a little more than two years, juveniles move substantial distances between water masses of varying temperature and productivity, feed voraciously on zooplankton, grow rapidly, and accumulate stores of energy-rich lipids and proteins in their distinctive red flesh. In the summer of their fourth year, the maturing adults weigh about 2700 g when they return to coastal waters, stop feeding, and start their upstream migration. By September, they reach the spawning grounds, where females compete to excavate nests in the streambed and males compete to mate with spawning females. Both sexes die after spawning, leaving a clutch of eggs and depleted carcasses, having expended most of their body energy for migration and mating.

Life table: survival and reproduction

The complete MLT is presented in Table 1. The first few columns provide a traditional life table: a schedule of survival and reproduction as a function of age, stage and body mass. Each generation starts with 3,000 eggs, lasts four years, and ends with another 3,000 eggs spawned by two depleted breeders. In between the eggs hatch, the offspring grow and die as they age, and an average of two survive to breed and continue the life cycle. The dynamics of the life history as a function of age are shown in Fig. 2. Until the salmon stop feeding and enter fresh water for the return migration, cumulative assimilation, respiration and biomass increase with age; deviations from smooth monotonic curves reflect variations in energy income (assimilation from feeding) and expenditure (respiration for swimming) and associated variation in temperature (Brett 1972; 1983; Brett and Glass 1973). During the last three months of life, the returning adults use up most of their stored body energy on locomotor and reproductive activity, leaving depleted carcasses and a new clutch of eggs.

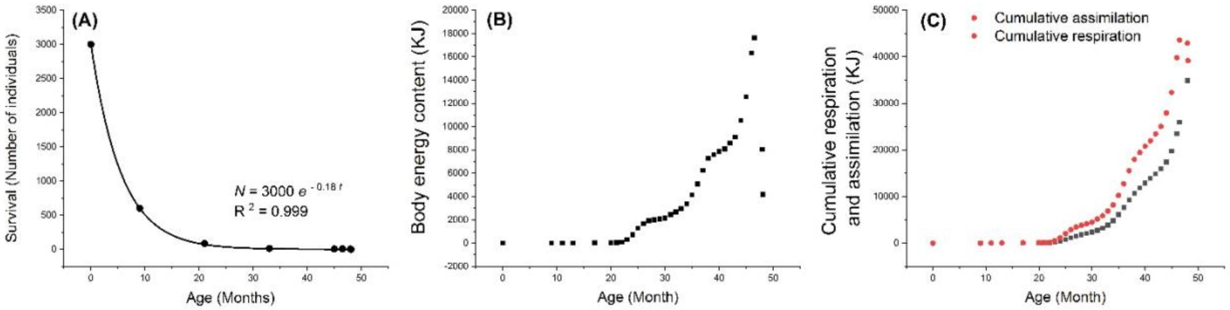

Figure 2. Dynamics of Babine Lake salmon life history and energetics: variation as a function of age. (A) Survival: number alive out of initial clutch of 3,000 eggs. Deviations from the fitted exponential relationship are too small to show on this graph. (B) Body energy content. (C) Cumulative respiration and assimilation.

Metabolism: body mass and temperature dependence of respiration, growth and assimilation.— The MLT (Table 1) documents variation in rates of respiration, growth and assimilation with age, stage, body mass and environmental temperature at monthly intervals over one generation. We compare these data to predictions from general metabolic theory (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Brown et al. 2004; Sibly et al. 2012). Whole-organism rates, B, characteristically increase with body mass, m, scaling as power laws of the form

$$B = B_0 m^{\alpha} \qquad 1$$

where $B_O$is a normalization constant, and the exponent α is characteristically close to 3/4 for respiration rate and most other whole-organism rates (e.g., Kleiber 1932; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; West et al. 1997; Brown et al. 2004; Sibly et al. 2012). In ectothermic animals, such as salmon, these rates also vary with body temperature with $Q_{10} \approx$

2.5 (increasing ~2.5 times for every 10°C increase in temperature (e.g., Gillooly et al. 2001; Huey and Kingsolver 2019)).

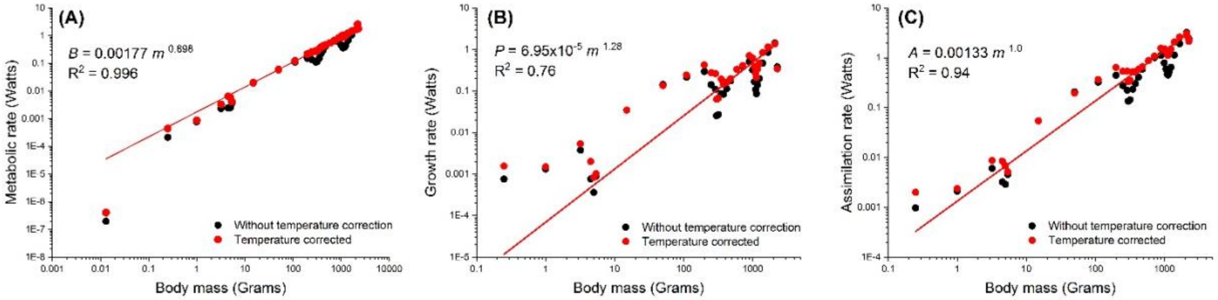

Figure 3. Plots on logarithmic axes and power-law scalings of rates of whole-organism metabolism as functions of body mass before (black symbols) and after temperature (red symbols and regression lines) correction). (A) Respiration rate (Brett's "total metabolic rate"): $B = 0.00177m^{0.898}$; $R^2 = 0.996$; B) Rate of biomass production (from Brett's "growth rate" in %/day $P = 6.95x10^5m^{1.29}$; $R^2 = 0.76$; (C) Assimilation rate (sum of the above two rates): $A = 0.00133m^{1.0}$; $R^2 = 0.94$.

Brett's data for sockeye salmon are qualitatively consistent with predictions from metabolic scaling theory, but with quantitative caveats. Brett (1983, p. 33) determined that the temperature dependence is "equivalent to a Q_{10} of about 2.3." We used this value to temperature-correct the rates of respiration, growth and assimilation, and determine their scalings with body mass (Fig. 3). The scaling relationships are sublinear ($\alpha < 1$) as has been found almost universally, but the exponents (slopes) are consistently higher than $\alpha \approx 0.75$ expected from standard metabolic theory (Brown et al. 2004) and data for most other animals (e.g., "Kleiber's rule": Kleiber 1932; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Sibly et al.

2012). We are uncertain how to interpret these deviations. On the one hand, salmon have an unusual physiology and ecology as indicated above. On the other hand, the data might be inaccurate. Brett (1983, p. 32) cautions that "More often than not when compiling energy budgets growth is measured, metabolism estimated, assimilation efficiency assumed, and excretion deduced. …The components of the balanced equation are sensitive to, and respond differently to, the chief variables of temperature, body size, and activity." Since we have no objective basis to question or correct Brett's values, we use them here with this caveat.

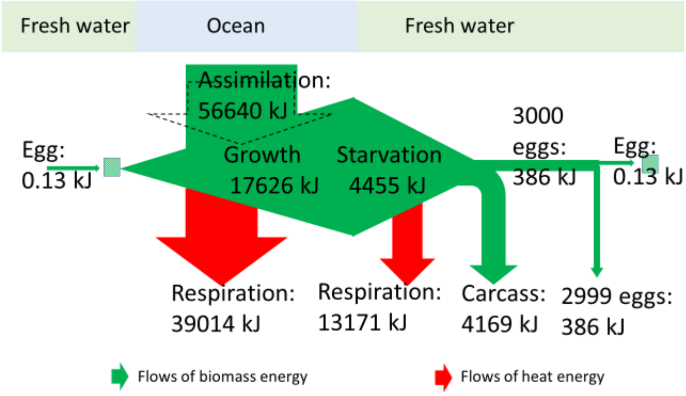

Figure 4. Energy budget for an individual female sockeye salmon surviving-to-spawning in Babine Lake. Its life cycle starts with a single egg, which hatches, assimilates food energy, respires and grows, accumulating a store of body energy over most of its 4-year life. Then it stops feeding, migrates upstream and breeds, rapidly depleting its stored body energy for respiration to fuel migration and reproduction. It dies after spawning, leaving a depleted carcass and a clutch of 3,000 eggs. The budget for a male is similar but he allocates less energy to sperm and more to respiration for courtship and mating.

Energy balance of an individual.—An energy budget for the average individual that survives to breed accounts for stocks and flows of energy over one generation (Fig. 4):

1) egg: The energy budget starts with a single fertilized egg, weighing 0.013 g and containing 0.13 kJ of energy. The egg lies inactive in the gravel, transforms from an embryo into a fry, and hatches after about nine months, having lost about one-third of its mass and energy due to respiration.

2) feeding, maintenance and growth: In the three plus years between hatching and breeding, the offspring assimilates 56,640 kJ of energy by feeding, expends 39,014 kJ (69%) on aerobic respiration, and produces 17,626 kJ (31%) in body energy reserves. More than 98% of the total lifetime assimilation and growth occurs in the ocean, where the juveniles swim and feed almost continuously.

3) migration and breeding: Once a mature salmon enters fresh water, it stops feeding and lives off its body reserves. In the last 45 days of life, an individual expends 13,071 kJ (75%) of its body energy on respiration for the energy-expensive activities of migration and spawning.

4) parental investment: A very small fraction of stored body energy is allocated to parental investment in gametes. The clutch of 3,000 eggs contains 390 kJ, only 5% of lifetime biomass production and an even smaller 0.8% of lifetime assimilation. The male invests even less energy in sperm.

5) carcass: When the spawned-out adult dies, its weight has decreased from 2,270 to 2,161 g. The carcass, depleted of nearly all fat and much of its protein, contains mostly water and only 4,169 kJ of energy. Of the 17,626 kJ stored in the body at the start of migration, 13,457 kJ has

been expended, 13,071 kJ on respiration and 386 kJ on eggs. "The energy expended in migration and the release of 3,000 ova have finally reduced the female to … not quite one-quarter of the maximum body energy achieved at the end of ocean growth" (Brett 1983, p. 50).

6) production efficiency: The efficiency of individual production, T_{ind}, is the ratio of output over input or production over assimilation:

$$T_{ind} = P_{ind}/A_{ind} \tag{2}$$

It varies with water temperature and age (Table 1), decreasing from >60% for fry and smolts in warm water to <25% for the older stages in cold ocean water. By the time a single salmon stops feeding and enters fresh water for the return migration she has accumulated 37% of assimilated energy in her body as growth. When she dies three months later, after expending more than 75% of this store on respiration for migration and spawning, her clutch of eggs and depleted body contains just 17% of the energy she assimilated over her lifetime.

Energy balance of a cohort.—At least as relevant for life history and ecology is the energy budget for the population or a representative cohort. This accounting includes intake and expenditure of all offspring produced by a pair of breeders, including those that died before reproducing. Brett (1986) called these losses the “life-cycle deficit” when he estimated the “food conversion efficiency” of the Babine Lake population.

We obtained similar results using somewhat different methods. Since the population was approximately constant during Brett’s study, we assumed steady state and used the MLT (Table 1) to compile a balanced energetic budget for a cohort (Fig. 5, Table 2):

1) juveniles in fresh water: The energy budget for the cohort starts with 3,000 fertilized eggs containing 386 kJ of energy. By the time the survivors have hatched, fed, grown, migrated

downstream, and transformed into smolts, most of the initial 3,000 offspring have died and returned 166,000 kJ of assimilated energy to the ecosystem: 2,916 carcasses containing 43,000 kJ and 123,000 kJ of respired heat energy.

2) juveniles in the ocean: The 84 surviving smolts have assimilated 9,570 kJ of food, expended 7,100 kJ on respiration, and amassed 2,470 kJ of body energy that they take with them to sea. There they feed and swim almost continuously, assimilating 68,000 kJ and expending 22,300 kJ on respiration. An additional 80 juveniles die in the ocean, leaving 267,700 kJ of assimilated energy in the ecosystem: 114,100 kJ of biomass in their carcasses and 153,600 kJ of respired heat energy.

3) migration and breeding: After two years at sea, the bodily energy of the four survivors has increased nearly 30 times, to 70,504 kJ of stored biomass that they take with them as they migrate upstream to breed. More than 99% of this energy is dissipated in fresh water: 52,600 kJ as respiration and 17,500 kJ in carcasses, leaving only 386 kJ in the new clutch of 3,000 eggs.

4) production efficiency: We estimate the efficiency of production for the cohort, T_{cohort}, of all offspring of an average female up until a given stage, S_{ref}:

$$T_{cohort} = P_{cohort}/A_{cohort}$$

and

$$P_{cohort} = \sum_{S=0}^{S=S_{ref}} N_d E_d$$

and

$$A_{cohort} = \sum_{S=0}^{S=S_{ref}} N_d A_d \tag{3}$$

and where N_d is the number of offspring dying before stage, S, and E_d and N_d are respectively, total body energy content (production) and cumulative assimilation (production plus respiration) of those offspring when they died. Production efficiencies of juveniles are high (32% in fresh water and 40% in the ocean), but most of this production is transported back into fresh water, where it is expended on respiration for migration and breeding. The overall production efficiency of the cohort over one generation is only 12%.

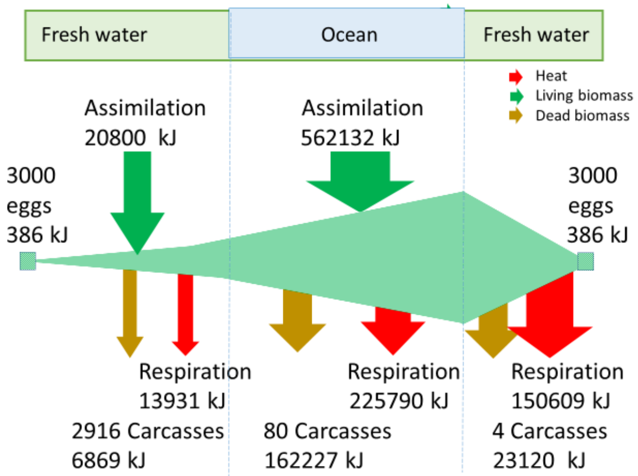

Figure 5. Balanced energy budget for a cohort of Babine Lake sockeye salmon. The accounting starts in fresh water with a clutch of 3,000 eggs. After hatching, the fry and smolts feed, grow, and suffer mortality before entering the ocean. After voracious feeding, rapid growth, and additional mortality at sea, four survivors expend most of their stored body energy migrating upstream to the breeding grounds. Two adults survive to spawn, leaving depleted carcasses and another clutch of 3,000 eggs.

Table 2 uses the energy budget of the cohort (Fig. 5) and the MLT (Table 1) to quantify the impact of salmon on freshwater and marine ecosystems. Of the food consumed and biomass produced by juveniles in fresh water, 32% is left in fresh water as heat of respiration and biomass of carcasses. Of the energy consumed and produced by juveniles in the ocean, 40% is left in the marine ecosystem due to respiration and mortality. More than half (60%) of the total energy produced by the cohort is transported from the ocean into streams and lakes in the bodies of the four adults returning to breed. The majority of this stored body energy (74%) is expended on respiration. The biomass in the carcasses consumed by scavengers and decomposers, and in eggs and sperm, is only 12% of the energy obtained in the ocean.

At steady state, the production efficiency of a cohort or species population is equivalent to the trophic transfer efficiency in ecosystem ecology

$$T_{cohort} = T_{eco} = A_2/A_1 \qquad (4)$$

the ratio of assimilation rates: A_2, the rate of energy consumption by a higher trophic level (e.g., predator or decomposer), over A_1, the rate of uptake by the next lower trophic level (e.g., prey). So T_{cohort} indexes the efficiency of converting salmon food into salmon biomass. For Babine Lake sockeye population this efficiency is ~12%, close to the 10% often taken as the rule-of-thumb average for diverse taxa and ecosystems (e.g., Lindeman 1942; Humphreys 1979; May 1979; Pauly and Christensen 1995; https://en.wikipedia.org/wiki/Ecological_pyramid).

Discussion: broader implications

The metabolic life table of *Oncorhynchus nerka* highlights a fundamental duality of life. On the one hand, each species is unique: its specialized structure and function, behavior and ecology reflect the interacting effects of ontogeny and phylogeny, genotype and environment. On the other hand, all species share attributes inherited from the single origin of life and constrained by universal scientific laws.

Comparison with dynamic energy budgets.—MLTs are similar in some respects to dynamic energy budgets (DEBs: e.g. Kooijman and Kooijman 2010; Sousa et al. 2008, 2010). Both aim to contribute to a general theory of biological metabolism. Both specify how data can be used to test theoretical predictions. Both have been applied to the empirical model of Pacific salmon (Pecquerie et al. 2011; Nisbet et al. 2012). The primary difference is that DEB focuses on how underlying processes at molecular and cellular levels contribute to metabolic homeostasis at the individual organism level, whereas MLT focuses on how metabolism at the whole-organism level affects demography of populations and energetics of ecosystems. Consequently, DEB models are usually more detailed, with more parameters to be measured or estimated, whereas MLTs incorporate just a few robust assumptions and parameters. The two frameworks offer alternative, but not mutually exclusive theories that apply biophysical laws to understand of both species-specific and universal characteristics of living things (see below).

Physiology, ecology and evolution of salmon.—Oncorhynchus nerka is a an exemplar of how natural selection has created a unique suite of physiological, behavioral and ecological traits (Quinn 2018). These special features beg for explanation in terms of phylogenetic history and natural selection playing out in temporally and spatially varying environments. The MLT provides such an explanation from the perspective of energetics. It combines the demography of a traditional life table with the physiological ecology of a balanced energy budget. By analyzing the wealth of data on this well-studied and economically valuable fish in the context of recent advances in metabolic theory, the MLT provides a formal structure that integrates and synthesizes many aspects of population biology, physiological ecology, and ecosystem energetics.

Energetics of migration.—Several features of the MLT reflect the central role of migration. Very little energy, 1,092 kJ, is produced by the fresh water stages, even though these account for most of the individuals and about half of the four-year life cycle. Despite the large clutch of eggs spawned, the freshwater stages produce very little biomass because of small size and high mortality. Nearly all of the biomass energy produced over the life cycle (98% for a surviving breeder and 96% for an entire cohort) is acquired by the voracious feeding and rapid growth of the marine stages. The vast majority of this production, stored as body energy and transported into fresh water by returning adults, is expended on the respiration for migration and breeding. By the time they spawn, adults have expended 74% of their body energy, leaving only 24% in depleted carcasses and 2% in gametes.

Sockeye and kokanee.—Comparisons between closely related populations provide additional insights. As indicated by fossil history and shared traits associated with reproduction in fresh water, the ancestral salmonids lived in streams and lakes (Hoar 1976). Multiple lineages subsequently evolved independent life histories in which juveniles migrate to sea, grow to maturity, and migrate back to fresh water to breed (McCormick and Saunders 1987). A consequence is a diversity of salmonid lifestyles, with closely related migratory and sedentary, anadromous and “land-locked” populations.

Oncorhynchus nerka is a good example. Sea run sockeye are widely distributed, with marine stages in the North Pacific and freshwater stages in coastal drainages. Another morpho-ecotype, known as kokanee, spends its entire life cycle in fresh water, with native populations in lakes scattered throughout the range and introduced populations more broadly distributed (Quinn 2018). Kokanee and sockeye represent alternative yet evolutionary stable strategies: different combinations of traits that confer equal fitness. Landlocked kokanee of the same age are smaller and less fecund (~700 g and ~800 eggs) than sea-run sockeye (~2,700 g and ~3,000 eggs; USDA Forest Service 2015). These and many other differences originated when populations diverged from freshwater ancestors and evolved an anadromous lifestyle: by migrating to sea and feeding on the abundant plankton, ocean-run salmon were able to grow larger, produce more offspring, and occupy a distinctively different ecological niche. Despite the initial advantages that selected for the derived ocean-run ecomorphotype, however, kokanee and sockeye are now equally fit (Brown et al. 2018), as evidenced by the fact that in some locations the two populations coexist in alternative stable states and breed together but rarely hybridize. Compilation of a MLT for a population of kokanee would show quantitatively how the life history and energetics evolved in successful adaptation to its landlocked existence and reveal the tradeoffs that result in equal fitness between kokanee and anadromous salmon.

Ecosystem energetics.—Another consequence of the anadromous lifestyle is that the enormous numbers of migrating salmon transport large quantities of energy and materials from marine to freshwater and surrounding terrestrial ecosystems (Juday et al. 1932) originally suggested, also Krokhin 1967, Donaldson 1967; long ago Cederholm et al. 1999; Gende 2002; Naiman 2002; Schindler et al. 2003, 2005; Quinn et al. 2018). Inorganic compounds in the bodies of salmon are major sources of nutrients for freshwater algae and land plants. Large quantities of the biomass energy are also transported into fresh water. Most of the lipids and proteins and some of the carbohydrates are catabolized in aerobic respiration, generating ATP and releasing carbon dioxide, water and heat into the environment. A smaller but substantial quantity of salmon biomass is consumed by predators, scavengers and decomposers in freshwater and surrounding terrestrial ecosystems.

The ecological impact of this input is substantial because of the large body size and sheer numbers of migrants. When Brett did his studies in the late 1970s and early 1980s, the Skeena River sockeye was in approximate steady state and the annual runs of returning adults averaged about 3 million (Larkin and McDonald 1968; http://waves-vagues.dfo-mpo.gc.ca/Library/342179.pdf). Multiplying this by the 17,626 kJ of body energy per individual leaving the ocean gives about 53,000 megajoules of ocean production (or 1,500 tonnes of organic carbon) transported to freshwater and terrestrial ecosystems of the Skeena River basin. For reference, this annual energy subsidy is equal to the annual net primary production of approximately 6,000 ha of taiga forest: ~25 gC/m^2 (https://daac.ornl.gov/NPP/guides/NPP_BOREAL.html). See Burger et al. (2012) for similar energetic analysis for sockeye and sustainability of the Bristol Bay fishery in Alaska. As the number of returning salmon have decreased due to human activities (see below), the reduced marine subsidies of energy and nutrients have caused substantial changes in freshwater, marine and terrestrial ecosystems (Cederholm et al. 1999; Gende 2002; Naiman 2002; Schindler et al. 2003, 2005; Burger et al. 2012; Quinn et al. 2018).

Use of wild salmon by humans.—Few wild animals have been as important to humans as salmon. For thousands of years native fishers captured returning breeders in nets and traps at the mouths of rivers, preserved their flesh by drying and smoking, and budgeted the stored food to last through the lean months and years between good runs. Since the arrival of Europeans, populations have declined precipitously due to overfishing of juveniles at sea, overharvesting of migrating adults as they come inshore, damming and pollution of rivers, and changes in ocean temperature and productivity. Ironically, one of the seriously depleted stocks is the Skeena River population that Brett studied. Annual returns fluctuated around 3 million until the late 1990s, then dipped to all-time lows. Harvests by commercial, recreational and Native American fishers are now severely restricted (https://waves-vagues.dfo-mpo.gc.ca/Library/342179.pdf; http://vancouversun.com/business/local-business/skeena-river-sockeye-returns-forecast-at-all-time-low-sports-fishing-closed).

Aquaculture and artificial selection.—Over the last 50 years as harvests of wild stocks have decreased, production of farmed Pacific salmon has increased rapidly (https://en.wikipedia.org/wiki/Aquaculture_of_salmonids). The semelparous life history, efficient biomass production, flesh rich in lipids and proteins, and other traits make salmon especially well-suited for aquaculture. Artificial selection, technological applications to husbandry, and massive inputs of fossil fuel energy have increased production with consequent reduction in swimming speed and endurance, and territorial, reproductive, and antipredator behaviors that were adaptive in the wild. Results have been spectacular, achieving production efficiencies (P/A: flesh output over food input) of 25-50% for factory-farmed fish (https://en.wikipedia.org/wiki/Aquaculture_of_salmonids). Comparison with wild stocks is complicated, however, by withholding of proprietary information and difficulties in compiling complete energy budgets that account for the large subsidies of additional energy, mostly from fossil fuels, to create specially formulated diets enriched in digestible carbohydrates, fish oils, and carotenoids, minimize losses due to predators and pathogens, and artificially breed, house, and move fish between freshwater and marine environments (Naylor et al. 1998; https://en.wikipedia.org/wiki/Aquaculture_of_salmonids).

Impacts of climate change.—Recently Huey and Kingsolver (2019) used Brett's (1970, 1971; Brett et al. 1969) early studies on "fingerling" sockeye (smolts: < 5 g body weight, <20 months old, in fresh water) to "develop a basic bioenergetic model that examines how the combined effects of climate warming, T_b (body temperature), and food intake alter the energetics and thermoregulatory strategies of ectotherms." The model predicts that "warming plus the associated food restriction could potentially amplify negative effects of climate warming, effectively lead to a "metabolic meltdown," and thereby accentuate any negative energetic consequences of warming" (see also Thomas et al. 2017). Important for such prediction, however, is the effect of climate change not only on intrinsic metabolic physiology (i.e., rates of assimilation, respiration and growth: Figs. 2-3), but also on extrinsic environmental conditions, especially food supply. Capture and assimilation of food depends largely on encounter rate, which in turn depends on density of the prey and swimming speed of the predator, any or all of which may be altered by climate change (e.g., Grady et al. 2019). To the extent that these extrinsic environmental factors can be predicted, the MLT provides a basis for incorporating the marine and returning adult stages to model the effects of climate change on the entire life cycle of sockeye.

Universal laws of life.—The MLT constructed and analyzed here from Brett's detailed data not only provides an empirical "life table of energetics" for a single model species, it also offers quantitative examples of universal characteristics of living things. These include the exponential decrease in survival with age and the scalings of the metabolic rates of assimilation, respiration and production with body size and temperature. More generally, the MLT indicates how variation in physiological, life history and ecological traits is constrained by two biophysical laws that apply to all organisms at steady state (Brown et al. 2018; Burger et al. 2019):

1) *a demographic constraint* dictates that in all sexually reproducing organisms, regardless of the number and size of offspring hatched or born, only two survive on average to maturity and reproduce to replace their parents; and

2) *an energy balance constraint* dictates the relationships between uptake and expenditure, the tradeoff between offspring growth and parental investment, and the scalings of production and generation time with body size and temperature.

Together, these laws dictate the relationship between the life history – the schedule of survival and reproduction – and the energy budget – the balance of energy uptake from the environment and allocation to metabolism. These constraints are absolute; there can be no exceptions. At steady state a population of sockeye salmon – and any other species – must conform to demographic equilibrium and energy balance. It is far from trivial, however, to predict the particular combinations of life history and metabolic traits that allow a species to persist. It is even more difficult to predict how these traits will be affected by departures from steady state, such as when a population grows or declines, or is subject to natural or artificial selection or human harvest. Two such applied questions are:

1) How much "take" for human consumption or increase in mortality due to dams, pollution, climate change and other human impacts can a wild salmon population sustain without collapsing? Many sockeye stocks have declined precipitously to some small fraction of their historic value, but in 2018 humans still harvested an estimated 79% (49.8 million of the 63.0

million mature sockeye returning to Bristol Bay, Alaska https://www.adfg.alaska.gov/FedAidPDFs/FMR19-12.pdf)

2) How do life history and energetic traits affect biomass production efficiency and economic profitability of sockeye in aquaculture? The MLT for the wild Babine Lake population highlights likely targets for husbandry and selection. These include: i) changing rearing conditions to reduce mortality of immature stages due to starvation, competition, predation and disease; ii) feeding diets that enhance growth rates; iii) genetic modification and artificial selection so that less assimilated energy is expended on respiration and more on growth; and iv) implementation of technologies that use exogenous energy from fossil fuels to substitute for biological energy sources (i.e., moving stocks to substitute for natural migration and feeding diets that do not require continuous swimming to forage). These technologies are currently being applied, but they are regarded as trade secrets in competition for markets, so there is limited information on their effects on metabolic and economic efficiency of salmon aquaculture.

In conclusion, the MLT framework that Brett pioneered decades ago to synthesize information on life history, demography, energetics and physiology of sockeye salmon is widely applicable to contemporary metabolic ecology. We encourage data compilation in an MLT framework for additional species to evaluate universalities from emerging metabolic life history theories (e.g., Brown et al. 2018; Burger et al. 2019). Doing so will have additional practical applications for sustainable resource management, biodiversity conservation and predicting global change impacts on demography and populations of species.

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Table 1. Metabolic life table (MLT) for sockeye salmon in Babine Lake, based on data in Brett (1983, 1986). The definitions of stages and traits follow Brett, although we have transformed his data into modern units and calculated additional parameters. Green rows represent stages in freshwater and blue rows marine.

Individual values

Date	Temp.	Stage	Age	Wet weight	Number alive	(dry/wet)	Energy density	Body energy content	Production rate	Whole-organism respiration rate	Assimilation rate	Energy† expended	Production efficiency	Cumulative energy expended
(mo/day)	(oC)		(months)	(g)	number	decimal	(kJ/g)	(kJ)	(watts)	(watts)	(watts)	(kJ)	decimal	(kJ)
15-Sep	6	Egg	0	0.013	3000	0.41	9.90	0.13	0.0000	0.0000002	0.0000000	0.00	0.00	0.00
15-Jun	6.0	Fry (spring)	9.0	0.25	600	0.20	4.60	1.15	0.00	0.0002144	0.0009733	0.08	0.78	2.09
15-Aug	11.0	Fry (summer)	11.0	1.00	367	0.22	4.97	4.97	0.00	0.00078	0.0021052	2.09	0.63	9.21
15-Oct	9.0	Fry (fall)	13.0	3.20	224	0.23	5.23	16.73	0.00	0.00233	0.0060826	7.12	0.62	34.74
15-Feb	4.0	Fry (winter)	17.0	4.50	137	0.23	5.22	23.51	0.00	0.00246	0.0032261	25.53	0.24	54.00
15-May	5.0	Smolt yearling	20.0	5.00	84	0.23	5.20	26.00	0.00	0.00254	0.0029052	19.26	0.12	62.37
15-Jun	11.0	Smolt yearling	21.0	5.40	75	0.24	5.44	29.39	0.00	0.00366	0.0045643	8.37	0.20	84.56
15-Jul	12.0	Smolt yearling	22.0	15.00	66	0.25	5.76	86.34	0.03	0.02006	0.0547624	22.19	0.63	179.16
15-Aug	12.5	Smolt yearling	23.0	50.00	59	0.26	6.09	304.74	0.14	0.06203	0.2060148	94.60	0.70	400.60
15-Sep	11.0	Smolt yearling	24.0	110.00	53	0.27	6.44	708.65	0.22	0.10927	0.3250237	221.44	0.66	733.39
15-Oct	9.0	Smolt yearling	25.0	200.00	47	0.27	6.44	1288.45	0.30	0.15216	0.4489740	332.79	0.66	1117.24
15-Nov	6.5	Smolt yearling	26.0	250.00	42	0.28	6.68	1670.21	0.14	0.13447	0.2775480	383.86	0.52	1438.31
15-Dec	4.8	Smolt yearling	27.0	290.00	37	0.28	6.68	1937.45	0.11	0.11523	0.2251318	321.07	0.49	1740.54
15-Jan	4.5	Smolt yearling	28.0	300.00	33	0.28	6.68	2004.26	0.03	0.10903	0.1345524	302.23	0.19	2037.33
15-Feb	4.5	Smolt yearling	29.0	310.00	29	0.28	6.68	2071.07	0.03	0.11266	0.1390374	296.79	0.19	2314.44
15-Mar	4.5	Smolt yearling	30.0	320.00	26	0.28	6.68	2137.87	0.03	0.11630	0.1435225	277.11	0.19	2666.48
15-Apr	5.3	Smolt yearling	31.0	350.00	23	0.29	6.95	2433.74	0.09	0.14925	0.2352539	352.04	0.37	3134.06
15-May	7.3	Smolt yearling	32.0	380.00	21	0.29	7.03	2670.67	0.08	0.21913	0.3026008	467.58	0.28	3813.86
15-Jun	9.0	2 yr immature	33.0	420.00	18	0.29	7.05	2962.01	0.11	0.29511	0.4082625	679.81	0.28	4715.95
15-Jul	11.0	2 yr immature	34.0	480.00	16	0.29	7.03	3374.75	0.18	0.41170	0.5874999	902.08	0.30	5986.40

15-Aug	12.0	2 yr immature	35.0	590.00	15	0.29	7.04	4151.67	0.33	0.54893	0.8805507	1270.45	0.38	6142.54
15-Sep	11.5	2 yr immature	36.0	720.00	13	0.29	7.05	5074.27	0.39	0.62453	1.0122159	1562.63	0.38	7731.96
15-Oct	9.3	2 yr immature	37.0	890.00	11	0.29	7.04	6263.93	0.51	0.60379	1.1186258	1589.42	0.46	9151.43
15-Nov	6.5	2 yr immature	38.0	1000.00	10	0.30	7.28	7283.64	0.32	0.46520	0.7883632	1419.47	0.41	10315.56
15-Dec	5.0	2 yr immature	39.0	1060.00	9	0.30	7.16	7587.54	0.17	0.43147	0.5983565	1164.13	0.28	11380.48
15-Jan	4.5	2 yr immature	40.0	1100.00	8	0.30	7.16	7873.87	0.11	0.36247	0.4718452	1064.92	0.23	12349.96
15-Feb	4.5	2 yr immature	41.0	1130.00	7	0.30	7.16	8088.61	0.09	0.36688	0.4526258	969.48	0.19	13257.06
15-Mar	4.5	2 yr immature	42.0	1180.00	6	0.30	7.28	8594.70	0.14	0.38311	0.5224005	907.11	0.27	14376.40
15-Apr	5.0	2 yr immature	43.0	1250.00	6	0.30	7.28	9104.55	0.20	0.44824	0.6484892	1119.34	0.31	15805.08
15-May	7.0	3 yr maturing	44.0	1400.00	5	0.31	7.53	10537.00	0.46	0.67841	1.1419302	1428.68	0.41	18086.03
15-Jun	9.5	4 yr maturing	45.0	1670.00	4	0.31	7.53	12576.42	0.86	1.07630	1.9352652	2281.79	0.44	21685.61
15-Jul	12.5	Adult-mature	46.0	2100.00	4	0.32	7.77	16315.35	1.44	1.80118	3.2365951	3598.70	0.44	26813.00
1-Aug	13.0	Adult-mature	46.5	2270.00	4	0.32	7.76	17626.41	0.38	2.02399	2.4081649	5127.43	0.16	29435.53
15-Sep	12.0	Adult-mature	48.0	2200.00	2	0.21	3.63	4455.00	0.00	2.55858	2.5585824	2622.53	0.00	39013.52
16-Sep	12.0	Carcass	48.1	2161.00	0	0.20	1.93	4169.00	0.00	0.00000	0.0000000	5345.52	0.00	39013.52

Table 1 continued
Cohort values

Date (mo/day)	Temp. (oC)	Stage	Standing stock of biomass (kJ)	Cohort production lost to mortality kJ	Cohort respiration before dying kJ	Cohort assimilation beore dying kJ
15-Sep	6	Egg	386.03	0.00	0.00	0.00
15-Jun	6.0	Fry (spring)	690.69	1535.79	2511.6	4047.39
15-Aug	11.0	Fry (summer)	1825.15	713.42	1316.623794	2030.04
15-Oct	9.0	Fry (fall)	3755.26	1546.30	3131.982487	4678.29
15-Feb	4.0	Fry (winter)	3228.30	1753.78	3868.102532	5621.89
15-May	5.0	Smolt yearling	2183.59	1319.87	3102.698087	4422.57
15-Jun	11.0	Smolt yearling	2195.64	257.02	681.9018036	938.93
15-Jul	12.0	Smolt yearling	5738.04	477.72	1088.681233	1566.40
15-Aug	12.5	Smolt yearling	18015.50	1436.05	2128.900796	3564.95
15-Sep	11.0	Smolt yearling	37264.19	3310.00	3703.907398	7013.91
15-Oct	9.0	Smolt yearling	60266.29	5802.26	5376.71596	11178.97
15-Nov	6.5	Smolt yearling	69490.30	7646.08	6604.313975	14250.39
15-Dec	4.8	Smolt yearling	71701.40	8293.05	7307.319567	15600.37
15-Jan	4.5	Smolt yearling	65977.58	8059.68	7724.674396	15784.36
15-Feb	4.5	Smolt yearling	60643.22	7412.10	7914.886782	15326.98
15-Mar	4.5	Smolt yearling	55682.15	6809.22	8058.131768	14867.35
15-Apr	5.3	Smolt yearling	56383.71	6578.69	8347.156985	14925.85
15-May	7.3	Smolt yearling	55035.73	6533.73	8893.456575	15427.18
15-Jun	9.0	2 yr immature	54294.69	6413.22	9711.818069	16125.04
15-Jul	11.0	2 yr immature	55024.72	6417.62	10838.90796	17256.53
15-Aug	12.0	2 yr immature	60212.21	6780.18	10926.33887	17706.51
15-Sep	11.5	2 yr immature	65460.64	7392.79	11117.6938	18510.48

15-Oct	9.3	2 yr immature	71878.52	8081.41	12033.79686	20115.20
15-Nov	6.5	2 yr immature	74344.03	8589.14	12342.04889	20931.19
15-Dec	5.0	2 yr immature	68888.12	8386.47	12235.29054	20621.76
15-Jan	4.5	2 yr immature	63588.21	7755.83	11903.78294	19659.62
15-Feb	4.5	2 yr immature	58104.24	7122.38	11425.72549	18548.10
15-Mar	4.5	2 yr immature	54917.40	6621.44	10967.44636	17588.88
15-Apr	5.0	2 yr immature	51746.79	6248.42	10655.06793	16903.49
15-May	7.0	3 yr maturing	53270.57	6167.89	10642.58165	16810.48
15-Jun	9.5	4 yr maturing	56555.24	6456.11	11109.1341	17565.24
15-Jul	12.5	Adult-mature	65261.62	7178.38	12049.84547	19228.22

1-Aug	13.0	Adult-mature	70505.64	8485.44	14062.13445	22547.58
15-Sep	12.0	Adult-mature	8910.00	6682.50	58520.28	65202.78
16-Sep	12.0	Carcass	0.00	8338.00	78027.04	86365.04

Table 2. Impact of a cohort of Babine Lake sockeye salmon on fresh water and marine ecosystems. This accounting uses the MLT (Table 1) to quantify the input of food energy from assimilation (green) and its allocation to biomass production: growth and gametes (blue) and respiration (red).

Ecosystem	Fresh water			Marine			Fresh water		Net flow
	Dead	Alive	Total	Dead	Alive	Total	Total		
Assimilation	20800	7423	28223	388016	185818	573834	0		602057
Respiration	13931	5239	19170	225790	117496	343286	52284		414740
Production	6869	2184	9053	162227	68322	230549	0		239602
Imported biomass						2184	70506		70506
Carcasses							17834		17834
Clutch							386		386
Net flow	13738	4367	18106	324454	136644	461098	0		0
Production efficiency	0.33	0.29	0.32	0.42	0.37	0.40	0.00		0.12