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Modeling fish population dynamics

Thomas G. Hallam[a,*], Ray R. Lassiter[b], Shandelle M. Henson[c]

[a] *Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA*
[b] *US Environmental Research Laboratory, US Environmental Protection Agency, Athens GA 30613-7799, USA*
[c] *Department of Mathematics, College of William and Mary, Williamsburg, VA 23187, USA*

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1. Introduction

Prediction of population dynamics in natural or laboratory systems is difficult because of the multitude of physiological, genetical, and environmental processes and interactions that influence each individual in the population. Development of a cognitative capability for the major dynamic aspects of a population rests on our ability to determine a finite, measurable and representable set of foundational processes. We focus on modeling one aspect of individual organism characteristics, the role of physiological processes in population dynamics. An underlying motivation for employing individual-based approaches to study higher ecological organizational levels is that this is the level where the most biological information exists. The modeling approach that we have used to investigate complex individual-based models first requires formulation of the individual organism model and, then, formulation of the population model. The analysis stage of the modeling involves performing simulations to investigate dynamics and sensitivity studies to determine relationships and changes in the dynamics. The model validation stage initiates at the individual model level where biological phenonmena are mimicked and checked; subsequently, we develop aggregated models that incorporate the governing features identified in the analysis phase. These more rudimentary models hopefully will yield to analytical study to validate the conclusions of the simulations.

The individual-based approach for studying ecological systems is an important technique for determining roles of structure and function in ecology; see DeAngelis and

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[*] Corresponding author.

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Gross [12] for an overview. The generic approach is illustrated by investigating fish population dynamics that is acceptable for, and motivated by, ecological risk assessment purposes. Here, we apply individual-based modeling to explore the role of individual life history in determining fish population dynamics under the influence of chemical stressors. We indicate fish biology relevant to the development of the individual model, which is a coupled system of ordinary differential equations. Then, by use of a system of hyperbolic partial differential equations, the density of the population is generated and used to perform analysis of the dynamics.

Papers which explore energetics and model growth in fish populations include Stewart et al. [65], and Kitchell et al. [40,41]. Age-structured models for fish have also been developed [10,13,14]. An individual-based approach to looking at smallmouth bass populations has been developed by DeAngelis et al. [11]. Kooijman and Metz [44], Kooijman [42], and Hallam et al. [29,30] have developed model formulations for *Daphnia* that employ a philosophy similar to the one presented here. Physiological processes and energetics representations are fundamental to this approach utilizing individual growth characteristics. However, the specifics of the individual (and subsequently, the population model) are different from the representation used in the *Daphnia* population model.

There have been many efforts to model the growth of fish (see the review of Moreau [51] for models of individuals that relate to generalized von Bertalanffy equations) but there are few articles on fish models which include a storage compartment. Kooijman [43] explores many of the roles of storage materials and concludes that it is not possible to understand dynamics of populations without referencing a storage compartment at the individual level. An interesting approach at the biochemical level that does look at the dynamics of lipid, protein and carbohydrates is that of Machiels and Henken [48,49]. Our model includes a lipid compartment, but focuses on the physiological level, not on the related biochemistry as do Machiels and Henken.

1.1. Roles of physiology in fish life history

Physiological processes that influence the dynamics of an individual fish are well documented in the literature (see books in the series edited by Hoar and Randall [34]). Because of availability of abundant data at the individual level, it is convenient and possible to develop detailed representations of physiological processes connected with fish life history.

The phenology of lipid, protein, and carbohydrate is fundamental to individual fish growth [34] and, ultimately, to fish population demography. Shul'man [61] lists variables important for the determination of population dynamics including dynamics of fat and moisture in individuals; composition of lipid fractions; dynamics of glycogen content and certain elements of carbohydrate and phosphorus metabolism; protein growth and nitrogen balance; oxygen uptake and utilizations of fat and protein in energy metabolism as well as several others. Because of the large numbers of individuals required to adequately represent a population, from a population modelling perspective it is prudent to be parsimonious without ignoring crucial physiological processes. To this end, we will focus on the dynamics of lipid and structure (nonlipid dry material consisting mostly of proteins and carbohydrates) in our individual fish model and base our approach on energetics of an individual organism.

Lipid is essential for fish; it functions as the major source of energy for most fish [61], as a regulator of certain metabolic functions, as a threshold trigger and an essential component of reproduction [72], as a thermoinsulator, and is of major importance in hydrostatic and hydrodynamic factors [61].

From a toxicological perspective, lipid apparently serves as a buffer against toxic stress due to exposure to hydrophobic organic chemicals [47]. Geyer et al. [24] have demonstrated that the median lethal concentrations (LC50) of γ hexachlorocyclohexane (Lindane) in 14 different fish species are increasing (i.e., the toxicity is decreasing) with increasing lipid content; see Lassiter and Hallam [47] for theoretical developments that provide motivation for the concept "survival of the fattest". Lipid also plays a fundamental role in chemical depuration of adults via reproductive processes [45].

Fat content of fish is variable both among individuals and species. Brockway [7] in the laboratory, and James Clark (work done at EPA Gulf Breeze; personal communication) in the field, found that the lipid content of fish of similar appearance and size can cover a spectrum of concentrations. Different species also can have extremely different ranges of lipid content; e.g., Eschmeyer and Phillips [17] (see also Phillips [56]) found mature and apparently healthy lake trout with 89% fat dry weight whereas trout lipid is often closer to 20–33% of dry weight (e.g. for rainbow trout see [64]). Shul'man [61] presents an excellent discussion on the dynamics of lipid in many North Sea fishes. For detailed reviews on lipid metabolism in fish, see Greene and Selivonchick [25] and for lipid composition and biochemistry in fishes, see Henderson and Tocher [32].

The role of protein in fish nutrition is also fundamental to population dynamics; indeed, most structured modeling efforts tend to emphasize size or weight, each is often an approximate surrogate for body structural protein. Protein requirements change with advancement in the fish's life cycle with additional amounts needed in developmental stages. Protein can serve as a source of energy but it is an inefficient one [56].

Phillips [56] has delineated the role of carbohydrate in energetics of fish, concluding that trout are physiologically unable to utilize high levels of dietary carbohydrates. Carbohydrates exhibit different digestibility levels. The diets of many fishes including trout contain only small amounts of carbohydrate that can be converted into lipid. There is a sparing action of carbohydrate on protein metabolism although some studies report side effects such as liver damage from high carbohydrate diets. For trout and salmon there is evidence that carbohydrates are used immediately for energy [56]. With this as motivation we have incorporated carbohydrate and protein into a structure component for our model development and assume that no synthesis of fat can occur from carbohydrates and proteins of the resource. For some species of fish, this is not a valid hypothesis as indicated by Shul'man [61] for anchovies; see also Hochachka [35] for trout.

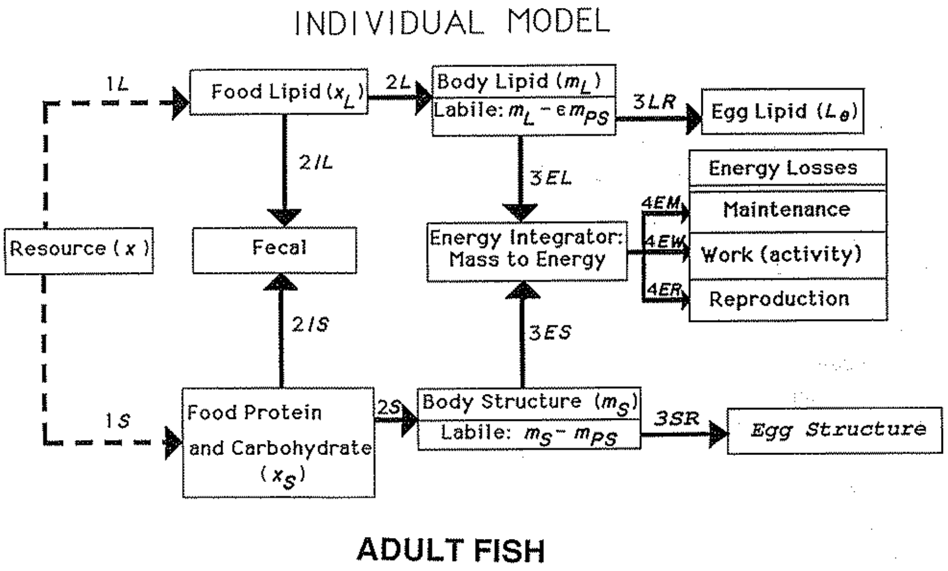

Fig. 1. The energy flow diagram for a conceptual model of an adult fish.

2. The blending of individual model concepts and of fish life history

Fig. 1 presents the conceptual model recording associated compartments and the flow chart for an adult female fish. The model features two major components, one called lipid and the other structure, a surrogate for protein and other nonlipids, each consisting of a labile and a nonlabile portion. The dynamics of an individual fish are determined by the rates of change of the storage and structure components expressed as ordinary differential equations. These rates are the difference in inputs (measured by the growth of the lipid compartment and the growth of the structure compartment) and the outputs (the totality of the losses from the compartments). These losses represent lipid and structural matter allocation to egg production, and energy allocation to maintenance, work (activity) and reproduction. We assume that losses due to maintenance and activity occur on a continuous time scale and that the reproductive losses occur periodically on a discrete time scale.

In our simulations, the ingested food of the model fish is assumed to be given in the same compartmental proportions as *Daphnia* and the available resource upon consumption is instantaneously partitioned to compartments, with the proportions of food assimilated dependent upon the assimilation efficiency. The lipid and structure composition of *Daphnia* can be quite variable over time. For this particular presentation, we employ an average value for the input densities although our model can readily accommodate variable food densities as inputs. Our fat to structure input ratio of 20% (see Table 1) is close to Phillips et al. [57] who indicate that the diet of trout in natural conditions feeding upon five species of insect larvae, *Gammarus* and *Helodrilus*, was composed of fat-to-protein ratios ranging from 11 to 34% with an average of 19%.

Table 1
Nominal model parameter values

Symbol	Interpretation	Value	Unit	Source
x	Density of resource	5.0002×10^{-7}	$\mathrm{g\,cm^{-3}}$	Created
x_L	Density of resource lipid	1×10^{-7}	$\mathrm{g\,cm^{-3}}$	Created
x_S	Density of resource structure	4.0002×10^{-7}	$\mathrm{g\,cm^{-3}}$	Created
M_p	Mass of the prey	2.7×10^{-4}	g	[42]
L_p	Length of the prey	0.34	cm	[42]
ε	Nonlabile lipid/nonlabile structure	0.12	Nondimensional	[15] (brown trout)
ρ	Structure per egg	2.38×10^{-2}	g	[31, 62]
B_2	Decay constant for structure	1.38×10^{-3}	$\mathrm{d^{-1}}$	[31, 62]
s_p	Body lengths/second for prey	0.3	$\mathrm{s^{-1}}$	[22, 59]
s_h	Body lengths/second for hunting fish	0.36	$\mathrm{s^{-1}}$	[4, 70]
s_c	Body lengths/second for fish in pursuit	10	$\mathrm{s^{-1}}$	[4, 70]
k_0	Constant in gut clearance	16.5	$\mathrm{g^{0.7}d^{-1}}$	[26, 64]
k_1	Loss rate constant in gut clearance	0.7	Nondimensional	[26]
k_2	Fraction food undigested	0.283	Nondimensional	[4, 20, 64]
β_1	Allometric constant in mass-length relationship	1.7×10^{-3}	$\mathrm{g\,cm^{-3}}$	[15, 64, 71]
β_2	Allometric constant in surface area-length relationship	0.4	Nondimensional	[71]
α	Proportionality constant in structure-protected structure	0.71	Nondimensional	[64]
bdensp	Dry weight body density of prey	0.052	$\mathrm{g\,cm^{-3}}$	Kooijman (personal)
ε_m	Minimum lipid per egg	3.2×10^{-3}	g	[31, 32, 63]
ε_M	Maximum lipid per egg	1.02×10^{-2}	g	[31, 32, 63]
σ	Slope of egg equation	67.2	$\mathrm{cm^{-1}}$	[9]
η	Length intercept of egg equation	17.4	$\mathrm{cm^{-1}}$	[9]
q	Swimming efficiency	6.2	Nondimensional	[22]
a	Slope constant in reactive distance	7.5	$\mathrm{cm^{-0.5}}$	[5, 66, 67]
b	Intercept in reactive distance	5.2	$\mathrm{cm^{0.5}}$	[5, 66, 67]
c	Proportionality constant for gut volume	0.864	$\mathrm{cm^3\,g^{-1}}$	[26, 64]
P	Reproductive period	365	d	[60]
Y	Length of embryonic period	51	d	[60, 63]
A_{0L}	Lipid assimilation efficiency	0.85	Nondimensional	[3, 19, 20]
A_{0S}	Structure assimilation efficiency	0.684	Nondimensional	[3, 19, 20, 64]
A_3	Labile lipid mobilization rate	5×10^{-3}	$\mathrm{d^{-1}}$	Created
A_4	Labile structure mobilization rate	1.1×10^{-2}	$\mathrm{d^{-1}}$	Created
A_7	Energy to maintain lipid	3.25×10^{1}	$\mathrm{J\,g^{-1}\,d^{-1}}$	[6]
A_8	Energy to maintain structure	3.25×10^{1}	$\mathrm{J\,g^{-1}\,d^{-1}}$	[6]
A_9	Half saturation constant modulated by E_S	3.0×10^{-4}	g/egg	Created
A_{10}	Energy to mobilize labile structure for eggs	2.0×10^{2}	$\mathrm{J\,g^{-1}}$	Created
A_{11}	Energy to mobilize labile lipid for eggs	2.0×10^{2}	$\mathrm{J\,g^{-1}}$	Created

The density of the resource is denoted by x and we assume that $x = x_L + x_S$ where x_L and x_S are the storage (lipid) and structural portions of the resource density, respectively. In our computations, the prey density is fixed for a subpopulation called an ecotype. It is assumed that the inputs to the lipid and structure compartments are obtained from the lipid and structure of the food; there is no synthesis of either structure or lipid within the organism. This implies that the structural and storage components of the resource are also constant in our computations. This is not a necessary requirement of our approach but is used to achieve our objective, to illustrate the role of physiological processes in population dynamics. Indeed, we have investigated effects of chemicals on a *Daphnia*-fish community where the dynamics of the fish resource, the *Daphnia* are allowed to be temporally varying [36].

2.1. Structure compartment

The structure component primarily represents protein and is composed of both labile and nonlabile portions of protein and carbohydrate. The nonlabile portion is structure bound as somatic tissue and is designated in the model by m_{PS} (mass of protected structure; g). The variable m_{PS} is assumed to be nondecreasing with age after the organism attains reproductive size and is computed as a fraction αm_{S} of the structural mass. To prevent the length of the organism from decreasing when allocation of mass and energy occurs to a discrete sink such as reproduction, our model for length is based on m_{PS}.

The labile portion of the component is measured by $m_{\mathrm{S}} - m_{\mathrm{PS}}$, where m_{S} (g) designates the mass of the structure pool.

2.2. Lipid compartment

The principal site of lipid storage is dependent upon the fish; even representatives of the same genus may have quite different fat depots. For example, fat is most heavily concentrated in the musculature of *Salmo salar* and in the abdominal cavity of *Salmo trutta* [18,32,61].

As in the structure compartment, a proportion of the storage pool is assumed to be labile and another nonlabile. The nonlabile lipid, represented in the model by $\varepsilon m_{\mathrm{PS}}$ (ε is nondimensional: mass lipid/mass structure), is a portion of the storage compartment that is associated with protein in cellular membranes and other fine subcellular structure and is not available to the organism even under conditions of starvation. The labile storage is represented by the variable $m_{\mathrm{L}} - \varepsilon m_{\mathrm{PS}}$ where m_{L}(g) designates the mass of the individual's lipid pool.

2.3. Life history description

We describe the life history of a female fish mathematically by the following sequence of events. At age 0 the egg with size

$$m_{\mathrm{S}}(0) = m_{\mathrm{S0}}, \qquad m_{\mathrm{L}}(0) = m_{\mathrm{L0}} \tag{1}$$

grams is deposited and fertilized. Brown [8] indicates that a rainbow trout egg of weight 100 mg contains about 26 mg structure and about 7 mg lipid. Rainbow trout eggs hatch 34–36 d after fertilization at 10°C [63], the yolk sac is depleted 3–7 d later, and the fry begin feeding about 15 d after hatching [60]. The developing sacfry juvenile does not feed and the decrease in size due to costs of differentiation is assumed proportional to the size of the component and is modeled by the differential equations

$$\frac{\mathrm{d}m_{\mathrm{L}}}{\mathrm{d}t} = -B_1 m_{\mathrm{L}}, \tag{2}$$

$$\frac{\mathrm{d}m_{\mathrm{S}}}{\mathrm{d}t} = -B_2 m_{\mathrm{S}} \tag{3}$$

with initial condition (1). The compartmental rate coefficients B_i, $i = 1,2$ can be determined by consideration of the difference between the size of an egg when laid versus the size of an individual fry immediately following yolk sac absorbtion and the beginning of feeding.

The discrete loss of chorion structure which occurs at hatching is modeled smoothly by the differential equation, making it necessary to use size after hatching for the determination of B_2. The individual depletes the yolk sac and begins to feed Y days after fertilization. The dynamics of the organism of age at least Y are now described by the ordinary differential equations representing changes in lipid and structure components:

$$\begin{aligned} \frac{\mathrm{d}m_{\mathrm{l}}}{\mathrm{d}t} &= g_{\mathrm{l}}(m_{\mathrm{l}}, m_{\mathrm{s}}, X) = \frac{a_{0\mathrm{l}} X_{\mathrm{l}}}{X} F - a_1 (m_{\mathrm{l}} - \varepsilon m_{\mathrm{ps}}) \frac{D}{E}, \\ \frac{\mathrm{d}m_{\mathrm{s}}}{\mathrm{d}t} &= g_{\mathrm{s}}(m_{\mathrm{l}}, m_{\mathrm{s}}, X) = \frac{a_{0\mathrm{s}} X_{\mathrm{s}}}{X} F - a_2 (m_{\mathrm{s}} - m_{\mathrm{ps}}) \frac{D}{E}. \end{aligned} \tag{4}$$

Here D denotes the total energy demand and E denotes the available energy. The expression for available energy is

$$E = 3.768 \times 10^4 A_3 (m_{\mathrm{L}} - \varepsilon m_{\mathrm{PS}}) + 1.675 \times 10^4 A_4 (m_{\mathrm{S}} - m_{\mathrm{PS}})$$

and the total energy demand is activity energy expressed here using work of Gerritsen [22]; see the appendix for details of the nonlinear representation and maintenance. The remainder of the symbols in Eqs. (3) and (4) are discussed in the section entitled feeding. Information on the representations of the individual model have been relegated to the appendix primarily when the details of the formulations are not significantly different from those presented in our individual daphnid model [30]. The main differences are related to feeding and gut clearance with those changes indicated subsequent to this chronology.

Note that from a mathematical perspective, the feeding term of the model should be proportional to mass to some power less than one at high resource levels. Otherwise, because the loss term in the individual model is basically proportional to mass, the individual fish could grow without bound when given increasing levels of food.

The initial conditions for the model described by Eqs. (3) and (4) are taken as the terminal conditions $m_{\mathrm{S}}(Y)$ and $m_{\mathrm{L}}(Y)$ obtained from Eqs. (1) and (2). The organism

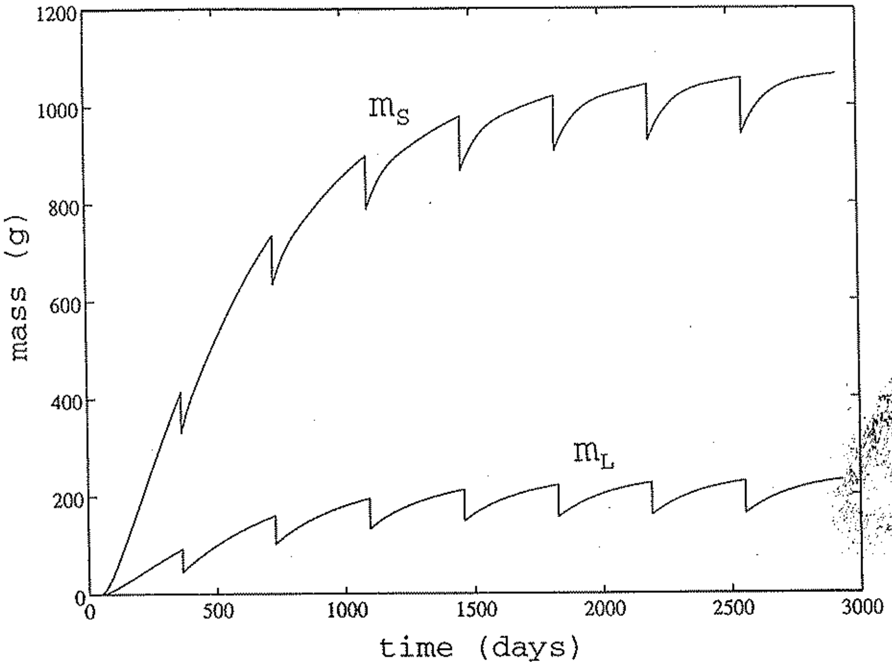

Fig. 2. The graph of a numerical solution of the individual fish model; the upper curve represents the dynamics of the structure component as a function of age and the bottom curve represents the dynamics of the lipid component. The discrete jumps occur due to allocation to reproduction at the birthing event.

grows according to the differential equations in (3) and (4) until reproduction occurs at the first reproductive window after it reaches maturation size.

The assumption that this maturation size is a species-dependent parameter appears valid for some salmonids [8]; it is not true for some other fish such as *Tilapia*. All losses associated with reproduction are computed at the age A when reproduction occurs. At this time the values of m_S and m_L are reset to account for the losses of labile lipid and labile structure that go to reproduction. For age larger than A but less than $A+P$, where P is the periodic reproductive time interval (P is taken as 365 d in our illustrations; Brown [8] indicates that marked seasonal periodicity in egg production is characteristic of many fish species), the fish again grows according to (3) and (4) with initial conditions as the reset values. The reset process occurs again at $A+P$ when the fish reproduces provided it has sufficient storages to do so. The entire process is repeated periodically with reproduction occurring with period P until the individual dies at the prescribed maximum age.

Fig. 2 presents dynamic numerical solutions of the individual fish model.

We now return to Eqs. (3) and (4) to describe the components of the differential equation in additional detail.

2.4. Feeding flows 2L and 2S of Fig. 1

The growth rate of a fish depends upon exogenous factors such as resource density and quality as well as other environmental conditions such as pH and temperature [16,26]. Endogenous factors such as morphometric attributes and metabolic capabilities are also important for growth. The inputs to the individual model are determined by exogenous factors with control also exerted by internal constraints.

The following assumptions imposed on the internal constraint of the feeding process of fish lead to the representations in Eqs. (3) and (4). The entire gastrointestinal tract is considered to be a single compartment, the *gut*. Fish, as most organsms, attempt to feed when hungry [16,26]. Perhaps the simplest way to represent hunger controlled feeding is to require the probability of feeding to be proportional to the emptiness of the gut: prob(feeding) $=g$ (gut capacity $-$ gut content), where g is a constant. Hence, on the average over time, an individual will feed the same proportion of time as the ratio of its gut emptiness to its gut capacity. This hypothesis goes back at least as far as Rashevsky [58] and has been utilized frequently in the literature [46]. Feeding in proportion to gut emptiness serves two functions. First, it requires that consumption equals clearing (over time, the food intake flux must equal the gut clearing flux). Second, this assumption permits dynamic energy expense computations for activity. The work of Jobling [37,38] relates gastric emptying to consumption in terms of the volume of food in the stomach.

We will use the gut clearance model

$$\frac{\mathrm{d}m_{\mathrm{g}}}{\mathrm{d}t} = -km_{\mathrm{g}},$$

where m_{g} (g) is the mass of the food in the gut at time t, and k has units of (1/d). For a given meal size, gut clearing time, and hence k, depends on several factors. The most significant of these are fish size and temperature [26]. k should not be considered a constant in the individual fish model since k varies as much with fish size as with fish species.

Because

$$-\frac{1}{t}\ln\frac{m_{\mathrm{g}}}{m_{\mathrm{g}0}} = k,$$

k is proportional to (gut clearance time)$^{-1}$, where “gut clearance time” is defined as the time required to clear a prescribed percentage of the gut.

In general, gut clearance time is proportional to (fish mass)^{k_1}, and so $k = k_0 m_{\mathrm{PS}}^{-k_1}$ (1/d), where k_1 is a nondimensional constant, and k_0 is a constant with units g^{k_1}/d. For rainbow trout, $k_1 = 0.7$ [26]; for the dab *Limanda limanda*, $k_1 = 0.386$ [39]; for young yellow perch *Perca flavescens*, $k_1 = 0.33$ [50].

The fish searches for food at a velocity characteristic of its species and body size. It pursues food organisms at a characteristic velocity that is usually different than the velocity employed while searching, and it captures all food pursued. From a modeling perspective, the assumptions made to implement this are that a predator searches at a velocity that is directly proportional to its length and pursues at another velocity – generally different from the search velocity – that is also directly proportional to its length. Webb [71] indicates that the maximum swimming velocity of small salmonids is proportional to length. This assumption may not be valid for the larger individuals of a given species; Ware [68] states that optimal foraging and cruising speeds of pelagic fish vary directly with (fish length)$^{0.4}$.

An equation given by Lassiter [46] Eq. (64) for the feeding of pursuit predators is derived by imposing the nonspecific assumption that, at equilibrium over time, food intake and gut clearance rate must balance. The assumption made here is merely a description about how this equalization occurs. Therefore, the Eqs. (64) and (66) of Lassiter may be used in this setting.

Modification of Lassiter's Eq. (64) is required if the predator and the prey do not swim at equal speeds. For a single predator feeding upon a single population of prey the expression for feeding, F, may be written as

$$F = \frac{x}{[a_{\mathrm{d}}]^{-1} + [s_{\mathrm{d}}/M_{\mathrm{p}}\delta v + [kM_{\mathrm{g}}]^{-1}]x} \tag{5}$$

(g/d).

In (5), x is the density of the prey population. The quantity a_{d} is the encounter rate coefficient (cm^3/d) obtained from Gerritsen and Strickler [23] and is given by

$$a_{\mathrm{d}} = 8.64 \times 10^4 \pi s_{\mathrm{d}}^2 (v_{\mathrm{p}}^2 + 3v_{\mathrm{h}}^2)/3v_{\mathrm{h}}.$$

s_{d} is defined as the reactive distance (cm) of the fish [5] and is given by $s_{\mathrm{d}} = [a(L_{\mathrm{p}}) + b]L_{\mathrm{f}}^{1/2}$, where L_{f} and L_{p} denote the lengths of the fish and prey in cm, and a and b are constants with units cm$^{-0.5}$ and cm$^{0.5}$, respectively. v_{p} is the velocity of the prey (cm/s) and is given by $v_{\mathrm{p}} = s_{\mathrm{p}}L_{\mathrm{p}}$ where s_{p} denotes the body lengths per second of the prey; and v_{h} is the velocity of the fish (cm/s) while hunting for prey defined by $s_{\mathrm{h}}L_{\mathrm{f}}$ where s_{h} denotes the body lengths per second of the fish while hunting. The symbol M_{p} represents the mass of the prey (g dry wt); δv is the difference in the pursuit velocity v_{c} of the fish and the escape velocity of its prey: $\delta v = (v_{\mathrm{c}} - v_{\mathrm{p}})8.64 \times 10^4$ cm/d, where $v_{\mathrm{c}} = s_{\mathrm{c}}L_{\mathrm{f}}$ cm/s; k is the gut emptying rate coefficient $(1/d)$; M_{g} is the mass capacity of the fish's gut (g), and is calculated from the volume V_{g} of the fish's gut and the body density of the prey. V_{g} (cm^3) is a linear function of fish mass [26] given by $V_{\mathrm{g}} = c(m_{\mathrm{PS}})$. The constant c has units of cm^3/g. m_{PS} is used in this representation so that the volume of the gut is nondecreasing.

If it is assumed that a constant proportion $A_{0\mathrm{L}}$ of resource lipid and a constant proportion $A_{0\mathrm{S}}$ of resource structure are assimilated, then inputs to the lipid and structure compartments can be represented as

$$\frac{A_{0\mathrm{L}}x_{\mathrm{L}}}{x}F, \qquad \frac{A_{0\mathrm{S}}x_{\mathrm{S}}}{x}F,$$

respectively. These are then the growth rate representations for the inputs to the storage and structure compartments. The value of $A_{0\mathrm{S}}$ may be difficult to find in the literature since structure includes all nonlipid dry material. If k_2 is the proportion of the food passed through the gut undigested, and if A_{T} is the overall assimilation efficiency, then $A_{\mathrm{T}}(\textit{food consumed}) = A_{0\mathrm{L}}(\textit{lipid consumed}) + A_{0\mathrm{S}}(\textit{structure consumed})$, so $A_{\mathrm{T}} + k_2 = A_{0\mathrm{L}}(x_{\mathrm{L}}/x) + A_{0\mathrm{S}}(x_{\mathrm{S}}/x) + k_2 = 1$. Furthermore, $x_{\mathrm{S}}/x = 1 - x_{\mathrm{L}}/x$. Thus, three values out of the four parameters $A_{\mathrm{T}}, A_{0\mathrm{L}}, A_{0\mathrm{S}}$, and x_{L}/x, are sufficient to compute the remaining one from these relationships. Flows 1L and 1S (Fig. 1), which represent decoupling of the resource components, translate into Flows 2L and 2S as given by the above representations. The remainders of the Flows 2IL and 2IS, consist of indigestible and nonassimilated resource.

There are other useful ways to describe the feeding rate. It is convenient to view each individual term of the denominator in the feeding rate F in (5) as a characteristic time for a process. This perspective will assist in the determination of the particular component of predation limiting the feeding rate, and consequently the growth rate, of the fish. The terms in the denominator relate to characteristic times (d/g) for encounter, pursuit, and digestion of prey respectively. If N_p is the numbers of prey encountered per unit volume,

$$\begin{aligned} T_e &= 1/(a_d N_p M_p), (\text{d/g } \textit{encountered}),\\ T_p &= s_d/(\delta v M_p), (\text{d/g } \textit{captured}),\\ T_d &= 1/(k M_g), (\text{d/g } \textit{cleared}). \end{aligned} \tag{6}$$

With these interpretations the feeding rate can be written as $F=(T_e+T_p+T_d)^{-1}$. The feeding rate can also be viewed as a saturation process in terms of resource density. We can write F as a hyperbolic function $F=x/(A_1+A_2x)$ where A_1 and A_2 are given by the first term and the coefficient of x in the last two terms in the denominator in (6), respectively. Hence, the encountering process as represented by A_1 is relatively more important when resource densities are low and the pursuit and digestion processes are dominant when there are abundant resources. At other resource densities, each of these processes are relevant.

When formulated in terms of N_p, the above form of the feeding rate may also be written as a hyperbolic function of numbers of prey:

$$F = \frac{N_p}{[a_d M_p]^{-1} + [s_d/M_p\delta v + [kM_g]^{-1}]N_p}.$$

The energetic losses for maintenance and work (activity) are distributed on a continuous time scale. The discussion about the energy integrator compartment that controls these processes is given in the appendix because the details, while distinct in content, do not differ in character from our previous efforts. Mass and energetic losses for reproduction are assessed on a discrete timetable. At the periodic times of reproduction, the losses to reproduction result in an instantaneous change in quantity of structure and lipid. This translation is determined by bulk allocation of lipid and structural material to egg formation and the energy required for these processes.

3. The dynamic population model

The basis of our approach to model population dynamics is a system of equations of extended McKendrick–von Foerster type [2]. This partial differential equation operates on a continuous time scale, allows incorporation of individual dynamics into a dynamic population formulation, contains explicit representation of physiological variables and tracks population through a population density function. Hence, if

$$\rho = \rho(t, a, m_{\mathrm{L}}, m_{\mathrm{S}})(numbers\ age^{-1}\ mass^{-1}\ mass^{-1}\ volume^{-1})$$

is the population density function ρ which depends upon time and the physiological variables a, representing age (d); m_{L}, representing the mass of the lipid (g); and m_{S}, representing the mass of the structure compartment (g); and g_{L} and g_{S} are the growth rates (g/d) of the lipid and structural components of an individual respectively, then an equation that incorporates these physiological variables into a population scheme is

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} + \frac{\partial(\rho g_{\mathrm{L}})}{\partial m_{\mathrm{L}}} + \frac{(\partial \rho g_{\mathrm{S}})}{\partial m_{\mathrm{S}}} = -\mu\rho. \tag{7}$$

The birth process for the population is represented by a boundary condition while the mortality rate is given explicitly in the differential equation as μ (d^{-1}). For physiologically structured models, the particular form of the birth process may be written in several equivalent representations. One of these forms is

$$\rho(t, 0, m_{\mathrm{L}_0}, m_{\mathrm{S}_0}) = \int_0^{\infty} \int_{m_{\mathrm{S}_0}}^{\infty} \int_{m_{\mathrm{L}_0}}^{\infty} \beta(t, a, m_{\mathrm{L}_0}, m_{\mathrm{S}_0}, m_{\mathrm{L}}, m_{\mathrm{S}}) \rho(t, a, m_{\mathrm{L}}, m_{\mathrm{S}})\, \mathrm{d}m_{\mathrm{L}}\, \mathrm{d}m_{\mathrm{S}}\, \mathrm{d}a,$$

where m_{L_0} is the mass of the lipid; m_{S_0} is the mass of the structure at age $= 0$; and β is the birth function which represents the number of eggs with lipid content m_{L_0} and structure content m_{S_0} born to an individual of age a with lipid content m_{L} and structure content m_{S} at time t. This form can be used because there is a one-to-one correspondence between lipid mass, structure mass and age for fixed m_{L_0} for a given individual.

Several different types of mortality are represented in our numerical model formulation including piecewise linear formulations for age-dependent mortality, size-dependent mortality, and total biomass dependent mortality [29]. Age-dependent mortality is assessed uniformly for cohorts whereas the total biomass-dependent mortality is assessed uniformly across the population. Total biomass-dependent mortality contains an optimal biomass density as indicated in [8] for *Salmo trutta* that results in a biomass carrying capacity for the population. Size-dependent mortality is viewed as caused by predation and is determined by weight of the individual. The population model is, in general, nonlinear with the nonlinearity appearing in the total biomass-dependent mortality term.

Specific forms of these mortalities are generic and can be structured to test processes and stresses.

This population model is a first order hyperbolic partial differential equation that may be represented in an equivalent manner by the method of characteristics, a method that reduces the partial differential equation to a set of ordinary differential equations valid along special curves called characteristics. For this model, an equivalent representation for the partial differential equation is the following system of five ordinary differential equations:

$$\frac{\mathrm{d}a}{\mathrm{d}\lambda} = 1, \quad \frac{\mathrm{d}t}{\mathrm{d}\lambda} = 1, \quad \frac{\mathrm{d}m_{\mathrm{L}}}{\mathrm{d}\lambda} = g_{\mathrm{L}}, \quad \frac{\mathrm{d}m_{\mathrm{S}}}{\mathrm{d}\lambda} = g_{\mathrm{S}}, \quad \frac{\mathrm{d}\rho}{\mathrm{d}\lambda} = -(\mu + (g_{\mathrm{L}})_{m_{\mathrm{L}}} + (g_{\mathrm{S}})_{m_{\mathrm{S}}}\rho),$$

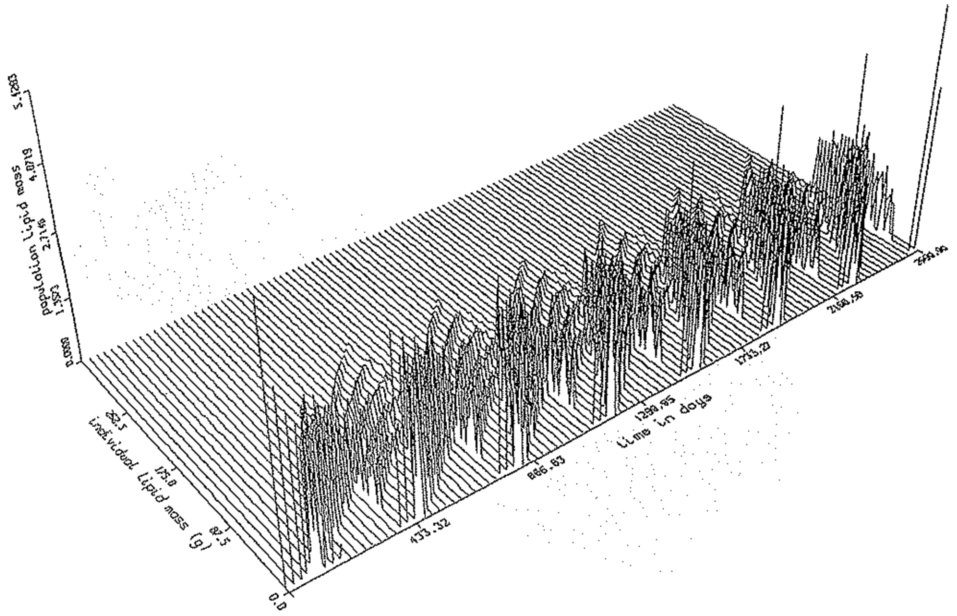

Fig. 3. The dynamic distribution of lipid in the fish population as a function of time. The right horizontal axis is the time axis. The left horizontal axis is the individual lipid mass. The vertical axis is a scaled lipid density; the number of individuals with a given lipid mass multiplied by the lipid mass. This last scaling factor keeps the figure from being completely dominated by smaller lipid classes. The structure in the population is obtained by utilizing a set of nominal parameter values and additional ecotypes generated by the percentage changes in the values of x, x_L/x and k_0.

where λ is the characteristic parameter. Our simulation approach solves this system of ordinary differential equations numerically [29]. The three parameters employed to portray the population was determined by sensitivity of the individual model and are described below; other parameters could also be used to structure the population. The parameters we employ in the simulation relate to rainbow trout although several involving the energy integrator department were unavailable to us and required estimation. An environmental reference range for parameters must be prescribed; our nominal parameter values for rainbow trout have been chosen within a temperature range of 11–15°C. Our specific parameter choices allow the individual model to generate the spectrum of all known feasible trout sizes. For example, in the structured population whose parameters are given by Table 1 and whose dynamics are presented in Figs. 3–5, the highest resource level is the least one at which the trout grow to largest possible size during their lifetimes. The lowest resource level corresponds to the least one at which the trout can still reproduce in their lifetimes. The intermediate resource level listed in Table 1 is the average of the highest and lowest levels.

Any number of individual ecotypes can be employed in the population model representation. The population structure utilized here is based upon 27 different types of individuals. These particular individual ecotypes (morphs) are determined by the

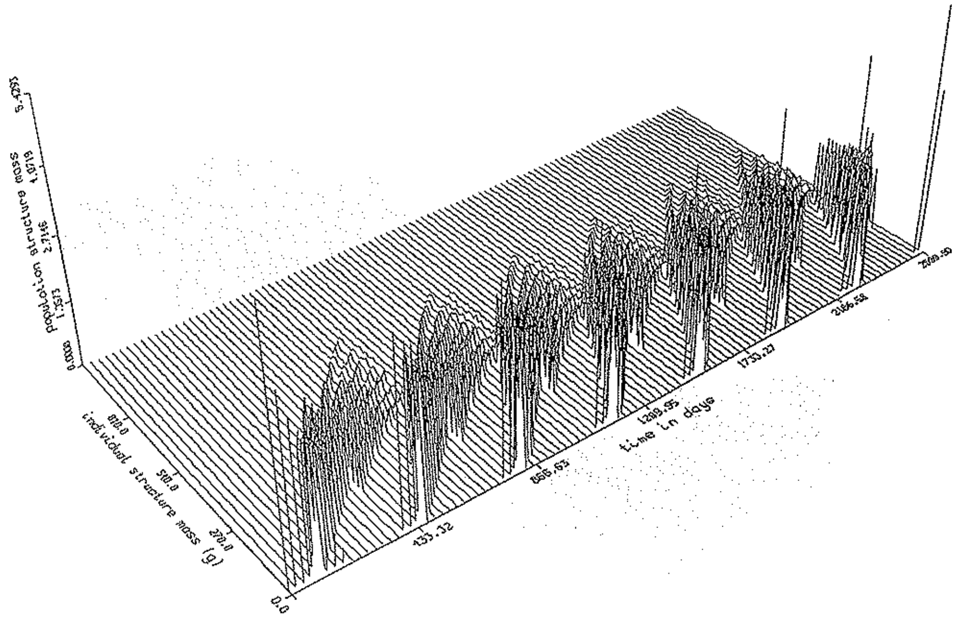

Fig. 4. The distribution of structure in the fish population as a function of time. The right horizontal axis is the time axis. The left horizontal axis is the individual structure mass. The vertical axis is scaled structure density; the number of individuals with a given structure mass multiplied by the structure mass. The structure in the population is obtained by utilizing a set of nominal parameter values and additional ecotypes generated by the percentage changes in the values of x, x_L/x and k_0.

constant level of resource at which they feed, the quality of that resource as indicated by its lipid content, and the gut clearance rate of the organism with each of these three individual characteristics ranging through three levels for the total of 27. We employ 27 because the diversity generated is sufficient to cover a spectrum of individuals with different physiological characteristics at different ages.

The population model records the dynamics of cohorts of individuals in the population essentially through a family tree, assesses mortality in these cohorts, and indicates births. We have addressed a population containing only a single sex and organisms are assumed to be clones of their female parent. If a model employs only a single partial differential equation of the McKendrick–von Foerster type indicated above in Eq. (7), there will be no physiological variation amongst individuals of the same age independent of the number of physiological variables utilized. Additional variation can be obtained by the introduction of ecotypes of individuals which differ from population individuals by genetic or environmental parameters. To track this variation in the population, these different individual types need their own descriptor, a partial differential equation, that accounts for the family tree associated with this new type of individual. The population model studied here then consists of 27 partial differential equations of the form of Eq. (7).

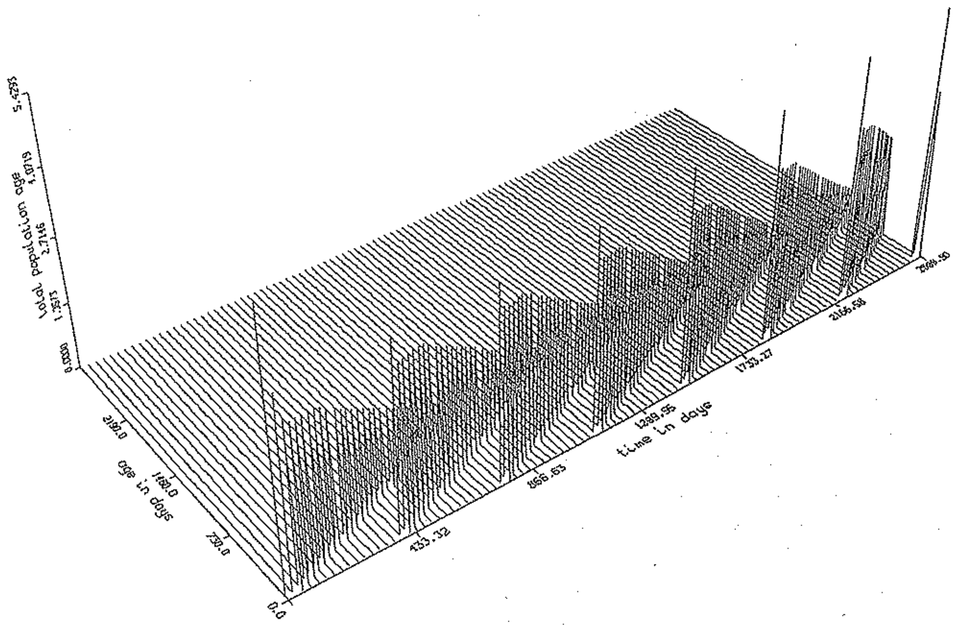

Fig. 5. The distribution of age in the fish population as a function of time. The right horizontal axis is the time axis. The left horizontal axis is the age of the individual. The vertical axis is the scaled age density; the number of individuals with a given age multiplied by the age. The structure in the population is obtained by utilizing a set of nominal parameter values and additional ecotypes generated by the percentage changes in the values of x, x_L/x and k_0.

4. Results

Simulations demonstrated that dynamic characteristics of our population model are determined by physiological characteristics of individuals and by the periodic reproductive period. Examples of graphical representations of the numerical solutions are given in Figs. 3–5 where the densities of lipid, structure, and age variables for the population are presented. (We will provide the nominal set of parameters used in the simulations upon request.) The numerical simulations as well as frequency analysis, illustrate that, in general, the composition of the population in age, lipid and organismal structure is oscillatory on several scales. There are oscillations on the time scale of the reproductive times of the species. Recall that the reproductive times were required to be periodic after reaching maturity; consequently, this component of the behavior is predictable because the length of the juvenile period is a population level parameter assumed to hold for all individuals in the population. There are longer-term oscillations present in the population dynamics that are germane to the rate at which the fish grow, or more specifically, to the physiology of the ecotypes and are not due to the dynamics of the constant density resource levels. In particular, this long-term fluctuation is not a typical predator–prey oscillation where both predator and prey have oscillatory behavior. Oscillatory behavior of a consumer when the resource is at a relatively constant level is characteristic of some aquatic populations [52]. The cause of the longer-term fluctuations is intrinsic to the population, not a result of the assumed density-dependent regulation because oscillations still arise when the density dependence mortality is set to zero in the model. The folklore in rudimentary non-structured models indicates that oscillations can be caused by inclusion of density dependence (cf. [27]). These fluctuations are due to the structural variation present in the population and can be varied by changing the physiological parameters of the individual.

Our simulation analysis of the population model shows that the model does exhibit "survival of the fittest" in that the population is ultimately dominated by a single individual type, a fact confirmed by analytical investigations [33]. In the absence of a chemical stressor, this fittest individual ecotype is the organism that produces the maximal number of eggs, grows the fastest and is ultimately the largest. The fittest individual in the population, according to this definition of fitness, need not always be the surviving dominant ecotype. If the population is stressed and mortality depends on physiological factors other than age, size and density, then other ecotypes can emerge as the dominant. If the population is acutely stressed by a lipophilic chemical so that mortality can depend upon fat content of the individual, then the fattest individual ecotype can survive [47]. Other toxicant exposure scenarios can lead to other ecotypes as ultimate dominants of the population dynamics (e.g. [29]).

We have also examined the spectral frequencies of model output for a related population model under conditions where the growth rate is changed by a chemical stressor and found that it is difficult to relate the dynamics for different stress scenarios by observing the dominant oscillatory frequencies present in a simulation and the corresponding physiology [28].

Analytical analysis of this class of population models delineating determinants of the dynamics and specific attractors for these fluctuating systems has recently been successful and will be the subject of forthcoming papers. This forthcoming work demonstrates that the length of the juvenile period and the periodic reproduction time completely determines the dynamics of a population composed of a single ecotype of individuals. Hence, changes in the environment that affect physiological parameters that, in turn, affect either the length of the juvenile period or the adult period of reproduction and, subsequently, impact population dynamics.

5. Discussion

We have developed a representation of physiological processes of individual fish that seems appropriate for population ecology and for the study of effects of chemicals on fish populations. One novel aspect of the individual model is inclusion of a representation of the dynamics of two storage compartments, lipid, and structure (protein). It is argued that lipid inclusion is necessary for both ecological (lipid is necessary for reproduction) and toxicological (lipid is a buffer for hydrophobic chemicals) reasons. A second contribution to the fish individual model is the inclusion of a pursuit term together with the ingestion and digestion terms in the uptake terms of the individual model. A third is the refinement that represents the gut clearance rate as a function of the volume of the fish. A weakness of this individual model from the physiological perspective is that lipogenesis is not present.

Aside from our modeling contributions, our main contribution is the demonstration via simulations that behavioral characteristics of a population may be determined by physiological characteristics. Biological processes influence population fluctuations on at least two time scales: one related to reproduction and one determined by physiological processes related to individual growth and determination of the length of the juvenile period.

Our simulations, performed for a population structured to encompass a variety of ecotypes that span a diversity of combinations of ages and physiological characteristics, illustrate strengths of the approach, particularly, the flexibility of this methodology to structure the population. The parameter values employed are representative of rainbow trout but this species was chosen only for demonstration purposes. If simulation of a particular population is desired, parameter selection at the individual level should be made to best mimic the physiological processes of the specific fish species and the spectrum of fish characteristics found in assays of the population.

At this stage of development, this model is a qualitative, but quantitatively based, population model grounded in physiology. The variability within the population will only be as diverse as the initial set of individuals and model output should provide an indication of the dynamic structure of a population only if sufficient physiological structure is included at the individual level. Some assumptions of this modeling effort are also restrictive. These include a relatively constant resource density with the ability of individuals to partition the resource to unequal extents; environmental factors deviation from nominal are relatively unimportant; and interspecific interactions do not have a strong influence on population dynamics.

An initial goal in our ecological risk assessment project was to develop a generic formulation of a population that was based upon physiological processes and could be utilized across species and in settings other than the ecotoxicological environment that provided our initial motivation. The extension to model fish populations helps demonstrate the utility and generality of the procedure.

We have not seriously attempted to correlate our model output with fish population data for several reasons. Fish populations are not governed by physiology alone; a point we are making is that physiology is fundamental because it helps to regulate birth processes and ultimately population dynamics. Another reservation lies in the lack of the existence of a suitable dynamic lipid data set for a fish population; obtaining an appropriate lipid data set requires a nondestructive lipid bioassay which does not exist at the present time. It is easy by proper choice of parameters to obtain caricatures of lipid and structure dynamics like those found in [61].

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Appendix. Additional details on the individual fish model

The inputs to the lipid and structure compartments and the subsequent formulation of feeding have been discussed above. The focus of this appendix is on the representations of the loss terms in (3) and (4).

A.1. Energy integrator compartment and flows

We assume that both labile structure and labile storage can be used to support the energetic demands of the individual. The energy integrator compartment functions as a processor that takes the mass input from both lipid and structure, converts it to energy and supplies the energy sinks (work, maintenance, and reproduction) of the individual. The energy integrator functions as a constrained modulator that, under high-energy requirements for physiological processes, releases the maximum energy that can be supplied. When demand is not at maximum, it supplies only what is required by the organism for physiological needs. The input flow to the energy integrator is a mass flow; the output flow is in terms of energy.

The energy integrator constrains and prioritizes organismal function with limits imposed by process and by supply. A priority allocation scheme is operative when energy demand exceeds supply. The allocation is modelled in the order maintenance, activity and reproduction when demand exceeds supply.

The energy integrator compartment has input flows $3LE$ and $3SE$. The maximal available energy supply (E; power) is a function of labile structure and labile storage: $E = 3.768 \times 10^4 A_3(m_{\mathrm{L}} - \varepsilon m_{\mathrm{PS}}) + 1.675 \times 10^4 A_4(m_{\mathrm{S}} - m_{\mathrm{PS}})$. The energy conversion factors, 3.768×10^4 and 1.675×10^4, are measured in units of joules per gram lipid and joules per gram protein and carbohydrate, respectively [54]. The lipid and structure mobilization rates A_3 and A_4 are measured in units of 1/d. A novel feature of the energy integrator is its switching control mechanism. If the total energy demand, D (power), as represented by the sum of the demand flows $4EM$, $4EW$, and $4ER$, to the reproduction, maintenance, and work sinks, exceeds the available energy, E, then the supply flows from the storage and the structural pools will be exhaustive in that the flow $3LE$ will be $A_3(m_{\mathrm{L}} \varepsilon m_{\mathrm{PS}})$, the fraction mobilized daily from labile storage, and the flow $3SE$ will be $A_4(m_{\mathrm{S}} - m_{\mathrm{PS}})$, a similar fraction of labile structure tissue. If, however, E exceeds D then only a fraction of the possible contribution from structure and storage pools is utilized. This is accomplished via supply flows that are apportioned by the fraction D/E. Specifically, the flow $3LE$ becomes $A_3(m_{\mathrm{L}} - \varepsilon m_{\mathrm{PS}})D/E$ and flow $3SE$ becomes $A_4(m_{\mathrm{S}} - m_{\mathrm{PS}})D/E$. The total power supply is, in energetic equivalents, just D.

A.2. Energy and mass sinks

Energetic demands of the organism include the sinks of maintenance, reproduction, and work. Maintenance is the energetic cost of transporting nutrients and metabolic products to and from cells – that is, respiration and the costs, net materials, and energy of cellular repair and reconstruction. Work is individual activity such as movement. There is a loss of energy associated with reproductive activities. The allocation of mass of lipid and structure for egg production must also be accounted for in the model representations.

Sinks with continuous representation (*Maintenance and work*). The losses associated with the individual fish model include energetic needs associated with maintenance and activity. The representation for work and maintenance are dependent upon both m_L and m_S because both lipid and protein must be maintained and transported.

Maintenance Flow 4*EM*. Objectives of the maintenance demand flow include allocation of the energy necessary for cell maintenance and repair. Because each living cell in an organism must be maintained, the model formulation postulates the demand in energetic equivalents by $A_7 m_L$ and $A_8 m_S$, where A_7 ($\mathrm{J\,g\,d^{-1}}$) and A_8 ($\mathrm{J\,g\,d^{-1}}$) are constants. For fish, basal metabolism is measured as *standard metabolism*, which is the minimum observed metabolism for fish at rest [6]. It may not be possible to find separate maintenance values for lipid and structure. Brett and Groves [6] estimate the standard metabolism of rainbow trout to be 100 mg O_2/kg/h, and list the respiratory energy equivalent for fish as 3.25 cal/mgO_2. This gives a standard metabolism of 32.5 J/g/d. Thus, the energy allocated by rainbow trout for maintenance is $32.5(m_S + m_L) = A_7 m_L + A_8 m_S$, and so we can choose $A_7 = 32.5$ and $A_8 = 32.5$.

Other investigators have imposed requirements similar to ours for maintenance. Most formulations for maintenance in the literature are of the form gW^h for constants g and h (e.g. [53,55]). When these forms are employed, often no additional sinks such as activity are modeled. Differentiation and development in the yolk sac are treated in our model framework by assuming that the only loss is proportional to m_L and to m_S. The proportionality constants can be different from those utilized in the adult maintenance requirements.

Work (*Flow* 4*EW*): The activities of an individual in performing life functions are often difficult to quantify because they depend upon many variables including food availability, health of the individual, and behavioral aspects of the species. Behavioral mechanisms are important for fish although in the present model we do not relate any behavioral aspects to fish physiology. Energy expenditure on work is a relatively major portion of the energy budget for many fish. Work activities are modelled here according to Gerritsen [22] who states the relationship for power consumed by a swimming fish as

$$P = 0.275 S v^{2.5} L_f^{-0.5} q^{-1} \quad (\mathrm{erg\ s^{-1}}),$$

where S is wetted surface area and is given by $\beta_2 L_f^2$, v is swimming velocity (part of the time hunting, part of the time chasing and is given as the appropriate product of body lengths per second and L_f), and q is swimming efficiency (nondimensional; 0.2 according to Gerritsen). Thus, substituting for S and v and after converting from erg per second to joules per day (1 joule $= 10^7$ erg), we obtain

$$P = 1.188 \times 10^{-2}(\text{bls})^{5/2} L_f^4 \beta_2$$

joules/d, where (bls) represents an average body lengths per second. The active time is the time spent finding and capturing the daily ration, F. Hence, $T_p F$ is the time in days per daily ration captured and is nondimensional. Likewise, the days per daily ration encountered is $T_e F$. The total active time per day of the fish is $(T_p + T_e)F$. Hence the energy expense for the fish due to swimming is

$$P = 1.188 \times 10^{-2} L_f^4 \beta_2 (s_h^{5/2} T_e F + s_c^{5/2} T_p F) \text{ (joules d}^{-1}\text{)}.$$

L_f is the length of the fish in cm and is given by the allometric relationship $L_f = \sqrt[3]{m_{PS}/\beta_1}$. Our computations will be referenced as dry weight with allometric weight measured by protected structure m_{PS}.

Discrete losses: We now discuss the losses that are assessed in the model at discrete times of reproduction.

Reproduction Flows 4LR, 4SR and 4ER: All losses associated with reproduction are assessed at discrete times as opposed to the continuous time allocations to maintenance and work. Reproduction is also required to occur in a time window to represent seasonal aspects of reproduction. This reproductive interval is utilized to set the birthing times for the specific species and, because we do not indicate hormone triggers such as photoperiod or temperature related phenomena, it is a nonmechanistic aspect of our model. It is clear that the process of allocation of bulk mass to eggs occurs over a continuous time frame rather than the discrete allocations we employ. Because there is little specific information on the time scales of this process and it is short relative to population time scales we treat them as discrete events. The reproductive losses include bulk allocation to eggs and the energy required to deposit this mass in the eggs. These operations, as well as the mechanism employed to determine the number of eggs produced, are now described.

There are numerous aspects to reproduction. In addition to the hormonal switches, which are modelled here by a periodic function, there are mass flows of lipid (storage) and protein (structure) for egg formation as well as the energy utilized to accomplish this mass transfer. To describe each of the flows 3RL, 3RS and 4ER, we indicate the technique used to determine the number of eggs produced; in general, reproduction will be constrained by thresholds of both lipid and structure.

Lipid constraints to reproduction are now indicated. Variability in egg size, assumed here to be determined by lipid, is probably controlled by many factors. The governing factors for allocation of lipid to eggs are assumed to be labile lipid, $m_L - \varepsilon m_{PS}$, and a counteractive coupling with structure. Because structure per egg is assumed to be constant, the interplay between protein, carbohydrate, and lipid in eggs is accomplished by utilizing a variable E_S, the maximum number of eggs for available labile structure. The lipid allocated to each egg is defined by

$$\frac{(e_M - e_m)(m_L - \varepsilon m_{PS})}{A_9 E_S + (m_L - \varepsilon m_{PS})} + e_m.$$

This hyperbolic function in $m_L - \varepsilon m_{PS}$ spans the range from a minimum lipid content per egg, e_m, to a maximum lipid content per egg, e_M. Although this function assumes values in the interval $[e_{\mathrm{m}}, e_{\mathrm{M}})$, the maximum e_{M} is only attained asymptotically as labile lipid is large. The regulation of this function by E_{S} is achieved by noting that as E_{S} increases, lipid per egg decreases for fixed labile lipid. The constant A_9 (g/egg) determines, in some sense, the relative importance the female places on lipid in eggs and consequently initial size at birth. The maximum number of eggs for available lipid is the total labile lipid, $m_{\mathrm{L}} - \varepsilon m_{\mathrm{PS}}$, divided by the lipid per egg.

Structure constraints to reproduction are also needed. A constraint to set E_{S}, the maximum number of eggs that can be made from labile structure, is also needed. Weatherley [69], using data from Allen [1], found that the number of eggs laid by trout in the Horokiwi stream can be determined, at least in a restricted range, as a linear function of body length. This provides motivation to define the maximum number of eggs produced per available protein and carbohydrate as

$$\min\{\max[0, \sigma[(\sqrt[3]{m_{\mathrm{PS}}/\beta_1}) - \eta]], \ (m_{\mathrm{S}} - m_{\mathrm{PS}})/\rho\}.$$

The first expression in this formulation relates a linear function of organismal length to maximum number of eggs per clutch: $\sigma[\sqrt[3]{m_{\mathrm{PS}}/\beta_1} - \eta]$ (see [69]). The slope, σ, is generally a function of resource level; however, in our setting with the resource density fixed, σ is constant. The expression $\sqrt[3]{m_{\mathrm{PS}}/\beta_1}$ is an allometric equivalent of length. The difference between organism length and a positive number η (length), chosen less than the length at which the organism first reproduces, results in a positive number of eggs produced.

The length at onset of reproduction is $\eta + 0.5$ so that the number of eggs per clutch is at least $\sigma/2$.

The second expression is the structural material available for reproduction, $m_{\mathrm{S}} - m_{\mathrm{PS}}$, divided by a prescribed amount of structure, ρ, in each egg. Weatherley [69] argues that the size at reproduction is a governing factor for reproduction. We have imposed the size constraint for reproduction and also require that there be sufficient lipid and structure to make eggs.

The method of finding the total number of eggs per female is obtained from the two constraints above. The number of eggs is the minimum of the maximum number of eggs producible from available lipid and from available structural material. The egg composition, assumed to be a fixed amount of structural material and a variable amount of lipid, fluctuates according to labile lipid reserves of the female.

The energy required to support the mass transfer of lipid and structure to reproduction is indicated in the flow diagram by Flow 4ER, and is modelled by $A_{10}S_{\mathrm{e}} + A_{11}L_{\mathrm{e}}$, where S_{e} is the total structure in eggs and L_{e} is the total lipid in eggs. This formulation is much like the one for allocation to maintenance, so no additional discussion is given here.

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