



Age and longevity in fish, with consideration of the ferox trout

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Abstract

In the first part of this paper, we review the evolutionary aspects of age and longevity in fish and then summarize the theory of maturity due to Ray Beverton. This theory allows one to predict age at maturity (and thus a putative point for the onset of senescence) from information on growth rate and mortality rate. We illustrate the application of this theory with data on tilapia species and then discuss the limitations of the theory. In the second part of the paper, we develop an individual based model for the ferox trout. This is a morph of brown trout *Salmo salar* that is an exception to the common notion that caloric restriction extends lifespan, in the sense that ferox trout achieve long life by eating more, not less. The model allows one to identify the role that ecological and biochemical adaptations play in the longevity of the ferox trout. © 2001 Elsevier Science Ltd All rights reserved.

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1. Introduction

Study of aspects of longevity and aging in fish reaches back to the earliest part of the 20th century, when Kyle (1900) applied methods similar to the ones in this paper to plaice. In 1959, Alm (1959) published his classic study of brown trout in Swedish lakes and rivers and Beverton and Holt (1959) began a series (Holt, 1962, 1965; Beverton, 1963, 1987, 1992) on various species of fish. Their motivations were based on fisheries management. For example, Alm was tasked with managing trout stocks of different origins in a wide range of habitats. Beverton and Holt were seeking ways to use growth and life history parameters that were easily measured to infer natural mortality, which is both difficult to estimate and crucial for effective fisheries management (Quinn and Dersio, 1999). In the

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course of this work, they made fundamental discoveries in evolutionary ecology; these continue to be rediscovered (Roff, 1991, 1992; Stearns, 1992; Charnov, 1993; Mangel, 1996). Even so, fish have been underutilized as a model system for studies of aging (e.g. Woodhead, 1978).

Beverton (1987) concluded the following concerning the evolution of longevity in fish: Long life and (usually) large size are characteristic of living representatives of those groups that evolved early in the lineage of fishes. For example, the salmonids are 40–50 million years old (Behnke, 1992).

Short life and small size are rare outside the teleosts (which comprise about 95% of the approximately 21,000 species of fish). For example, there are many populations of three-spined stickleback *Gasterosteus aculeatus* in which the maximum age is one year (Baker, 1994), but there are other populations where the maximum age is three years and there is anecdotal evidence that in some Finnish populations the maximum age may be seven years (Nina Peuhkuri, personal communication). In saltwater, sailfin mollies (*Poecilia latipinna*) may complete their life cycles in 5 (male) to 10 (female) weeks (based on data in Travis, 1989, and Trexler and Travis, 1990). Beverton also noted that spur dogfish (*Squalus acanthias*), an elasmobranch, lives to 60 years at a size of 1 m; beluga sturgeon (*Husa husa*) up to 118 years, 5 m length; white sturgeon (*Acipenser transmontanus*) to 100 years and Icelandic–Norwegian herring (*Clupea harengus*) lives to 30 years, rarely exceeding 35 cm. Tropical clupeids, on the other hand, live 3–5 years.

The enormous speciation in later teleost evolution was accompanied by widening of the range of interspecific longevity (both extremes of life span are found in the most advanced groups); however, the high degree of intraspecific plasticity in the primitive groups (salmonids, elasmobranchs) was lost.

There is a tendency for longevity (and to some extent large size) to be associated with cold environments, and vice versa.

The mode of reproduction is weakly, if at all, related to longevity. Among long-lived species are highly fecund oviparous fish (e.g. sturgeon) or viviparous fish (e.g. *Sebastes* spp.). Both oviparity and viviparity are found among short-lived species such as killifish and mollies.

Semelparity and short life (with possible large size) was likely the primordial strategy. Replacement by iteroparity and longer life conveyed greater ecological versatility and evolutionary fitness.

This is the evolutionary starting point for the analyses that follow.

2. Beverton's growth-maturity-longevity (GML) theory of longevity

One place to begin the study of longevity and senescence is the timing of maturity because maturity is often viewed as the onset of senescence. Indeed, James Joyce (in *A Portrait of the Artist as a Young Man*) has Temple state 'Reproduction is the beginning of death' (also see Hamilton, 1996); this has been verified by a number of evolutionary analyses over the last 50 years (e.g. Williams, 1957; Hamilton, 1966; Abrams, 1991). It is thus appropriate to begin by asking if it is possible to predict the age at which organisms

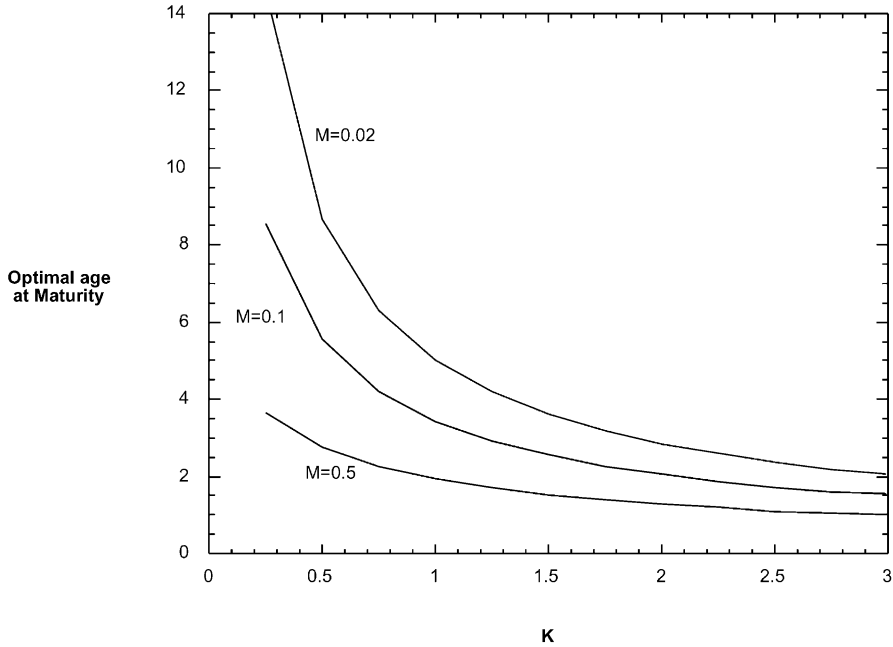


Fig. 1. Optimal age at maturity is a nonlinear function of physiological (K) and environmental (M) parameters.

will mature, given physiological and environmental parameters. Beverton's theory, which connects growth, maturity and longevity (GML), is one of the simplest approaches. We summarize it here, in a very general form.

Physiology is characterized by growth at rate K towards asymptotic size L_∞ according to a von-Bertalanffy equation

$$L(t) = L_\infty(1 - \exp(-K(t - t_0))) \quad (1)$$

where t_0 is a parameter usually negative, that is used to capture the early life history of the fish (that is, $L(t_0) = 0$). Unless one is trying to fit particular data, t_0 can be set to 0 without loss of generality. Mangel (1996) includes it in analyses similar to the ones given here. The environment affects the value of L_∞ via levels of food (see below). The size independent mortality rate is M , so that survival to age t is $\exp(-Mt)$. The natural mortality rate is connected to maximum longevity T_{\max} by an approximate proportionality

$$M = g/T_{\max} \quad (2)$$

where the parameter g is about 4 (Hoenig, 1983); we call this Hoenig's rule. Beverton (1992) estimates M and T_{\max} for a variety of *Pleuronectiformes*, *Gadiformes* and *Sebastes* species. For those data, the average value of $MT_{\max} = g$ is 4.0 and the coefficient of variation is 0.28.

If one assumes that reproductive success is related to size at maturity $L_m = L(t_m)$, where t_m is the age at maturity, by an allometric relationship of the form AL_m^B and that it is

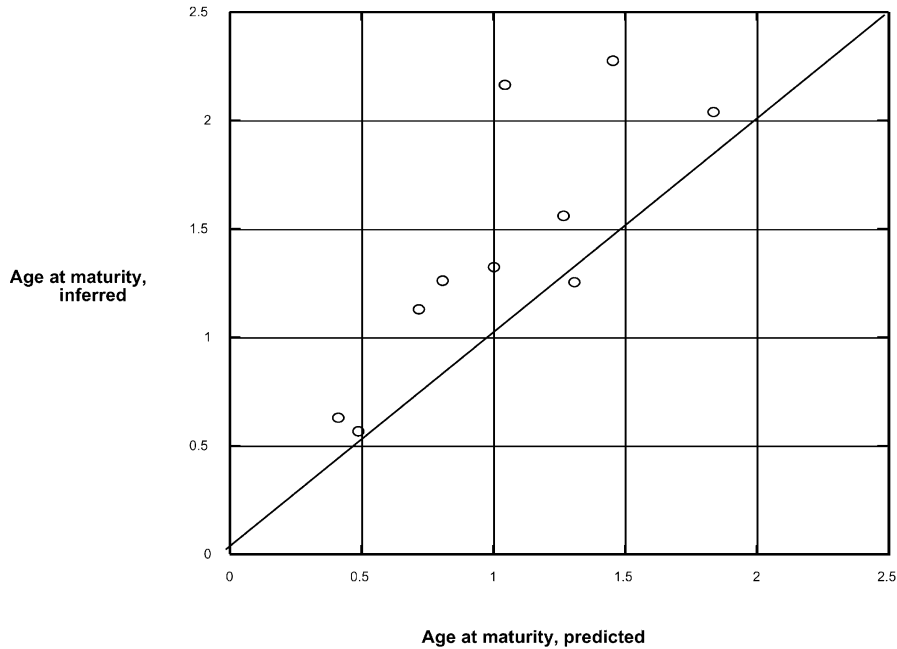


Fig. 2. Predicted and inferred age at maturity for a variety of tilapia stocks, using the GML theory and data from Lorenzen (2000).

sufficient to use expected lifetime reproductive success as a measure of fitness, then Darwinian fitness for maturity at t_m is given by

$$F(t_m) = \exp(-Mt_m)[L_\infty(1 - \exp(-Kt_m))]^B \quad (3)$$

It is then straightforward to determine the age of maturity that maximizes this measure of fitness. Note that asymptotic size will not appear in the expression (see Mangel, 1996, for an elaboration of this point). One finds

$$t_m^* = (1/K)\log[1 + (BK/M)] \quad (4)$$

Thus, optimal age at maturity is a nonlinear function of physiological (K) and environmental (M) parameters. Neither can be ignored when predicting age at maturity (Fig. 1), thus illustrating the principle that the organism is a complex adaptive system, run by a genetic program taking cues from the environment. In Fig. 2, we show predicted and inferred (estimated as the age at which 50% of the individuals of a cohort are mature) age at maturity for a variety of stocks of tilapia, using data given by Lorenzen (2000). The trend in the predicted relationship is clear, although the results suggest a bias (inferred age at maturity is either too large or predicted too small) and unaccounted variation. On the other hand, given its simplicity, this theory is remarkably successful (also see Beverton, 1987, 1992). That is, we used a typological approach that assumes that organisms are all

the same, and that life history decisions are taken once and for an average environment. However, organisms and environments vary and there is phenotypic plasticity; we treat these issues in the next section (also see Clark and Mangel, 2000).

Assuming Hoenig's rule allows one to rewrite Eq. (4) as

$$t_m^* = (1/K)\log[1 + (BKT_{\max}/g)] \quad (5)$$

so that the relative timing of age at maturity is

$$t_m^*/T_{\max} = (1/KT_{\max})\log[1 + (BKT_{\max}/g)] \quad (6)$$

depending only on the product of K and T_{\max} and the ratio B/g . This is a motivational example of what Charnov (1993) calls 'life history invariants': relative age at maturity is the same for any organism for which KT_{\max} and B/g are the same. One can compute, in a similar manner, the relative length at maturity L_m/L_{∞} and discover that it only depends on the ratio M/K .

This theory allows one to predict age at maturity and thus to estimate the onset of senescence from simple environmental and physiological parameters, and it is remarkably accurate (e.g. Beverton, 1992; also see Chadwick-Furman et al., 2000, for a recent example of age and longevity in corals). It is, of course, a bit of a simplification to call K a physiological parameter and M an environmental parameter. However, Beverton (1987) showed that food level is most influential on asymptotic size and size at maturity, whereas temperature is most influential on the rate of growth, the maximum life span and the age at maturity.

3. The ferox trout: an exception to the effects of caloric restriction

It is generally observed (especially in laboratory studies) that caloric restriction increases lifespan but decreases fecundity (Holiday, 1989; Weindruch and Walford, 1998), about which Masoro and Austad (1996) wrote:

Fitness, in the form of increased survival during unpredictable food shortages, will be enhanced in individuals with genomes that direct resources away from reproduction, thereby providing additional resources for successfully coping with environmental challenges (stressors). Thus, individuals with genomes of this sort are more likely to survive a period of food shortage and reproduce when food is once again abundant—clearly a selective advantage—than individuals with less plastic genomes (p. B387).

Finch (1990) provides examples of natural situations where caloric restriction increases longevity.

The ferox trout, a phenotypic variant (morph) of brown trout *Salmo trutta* is an exception to the notion (sensu Finch, 1990) that caloric restriction increases longevity in that long life is associated with enhanced calorie intake. The ferox trout is large (up to 100 cm) and exceptionally long-lived (sometimes more than 20 years; Plate 1). Although ferox trout have long been of interest to both scientists and fishermen (the name was coined in 1835 by Sir William Jardine (Greer, 1995) and ferox were once



Plate 1. A female ferox trout (65.5 cm, 15 + years) with two normal trout (21 cm, 3 + years; 21.5 cm, 4 + years) from Loch Veyatie, Scotland (reproduced with permission from Campbell, 1979).

considered a separate species *Salmo ferox* (Campbell, 1979) distinguished by their coloration and shape that differ from the general run of brown trout), scientific investigation was not begun until the late 1970s, when Campbell (1979) used information on about 150 ferox from 22 Scottish lochs to determine some properties of their biology and ecology. Campbell found that presence of ferox correlated well with oligotrophic waters (particularly mineral-poor lochs where the population density of normal trout is high in relation to food supply but low in relation to space), presence of charr and a large loch (over 100 ha). Campbell also found that in the first part of their lives, ferox followed the same growth pattern as normal brown trout. The point at which the rapid increase in growth rate occurred varied with individual ferox, but was a function of size, rather than age and corresponded to the onset of piscivory (Fig. 3). Thus, at the age at which most brown trout stop growing, ferox trout continue eating, growing, and living long lives. L'Abée-Lund et al. (1992) confirmed that brown trout and Arctic charr are rarely piscivorous; ferox trout are thus facultative piscivores (sensu L'Abée-Lund et al., 1992). The Scottish lochs containing ferox have glacial origins and the present fish populations are most likely remainders after the retreat of the Pleistocene ice cap about 10,000 years ago (Campbell, 1979). In addition to salmonids, Scottish lochs contain indigenous three and ten-spined sticklebacks, flounder, brook trout, river and sea lamprey and freshwater eels and introduced pike, perch and minnow (Campbell, 1979; Maitland et al., 1984). These fish provide an underlying forage base for piscivores. Ferox migrate upstream from the loch for spawning, using the stream and lochs in the same way that Atlantic salmon *Salmo salar* L. use streams and the ocean. Most offspring remain in the nursery stream for two years before descending to the loch. In 1979, although anglers caught about 100,000 brown trout, fewer than 10 notable ferox were reported (Campbell, 1979).

In addition to ferox, there are two other unique morphs of the brown trout; these are the sonaghan and gillaroo. Ferguson and colleagues (Ferguson and Mason, 1981; Hamilton et al., 1989; Ferguson and Taggart, 1991; McVeigh et al., 1995; Hynes et al., 1996) conducted genetic studies of these morphs of brown trout in lakes in Ireland and Scotland. The current best evidence is that northwest Europe experienced multiple colonization events by brown trout, of which the ferox trout are most likely the ancestral form. All of the unique morphs of brown trout diverged before northwest Europe deglaciated about 13,000 years BP.

Campbell (1979) concluded that

The presence of ferox is not essential for the success or survival of the trout population that produces them. They appear to occur by chance; for some reason a few trout succeed in living longer than the rest of their year-class, thus reaching a certain, possibly critical, length which enables them to exploit efficiently a highly nutritious and relatively abundant food source. i.e. fair size charr. The repercussions on their growth rate of this change in feeding behaviour are sudden. (p. 22).

In this paper, we explore the ecological conditions that allow ferox to achieve long life. Doing this requires a much more elaborate model for the life history than the GML theory provides.

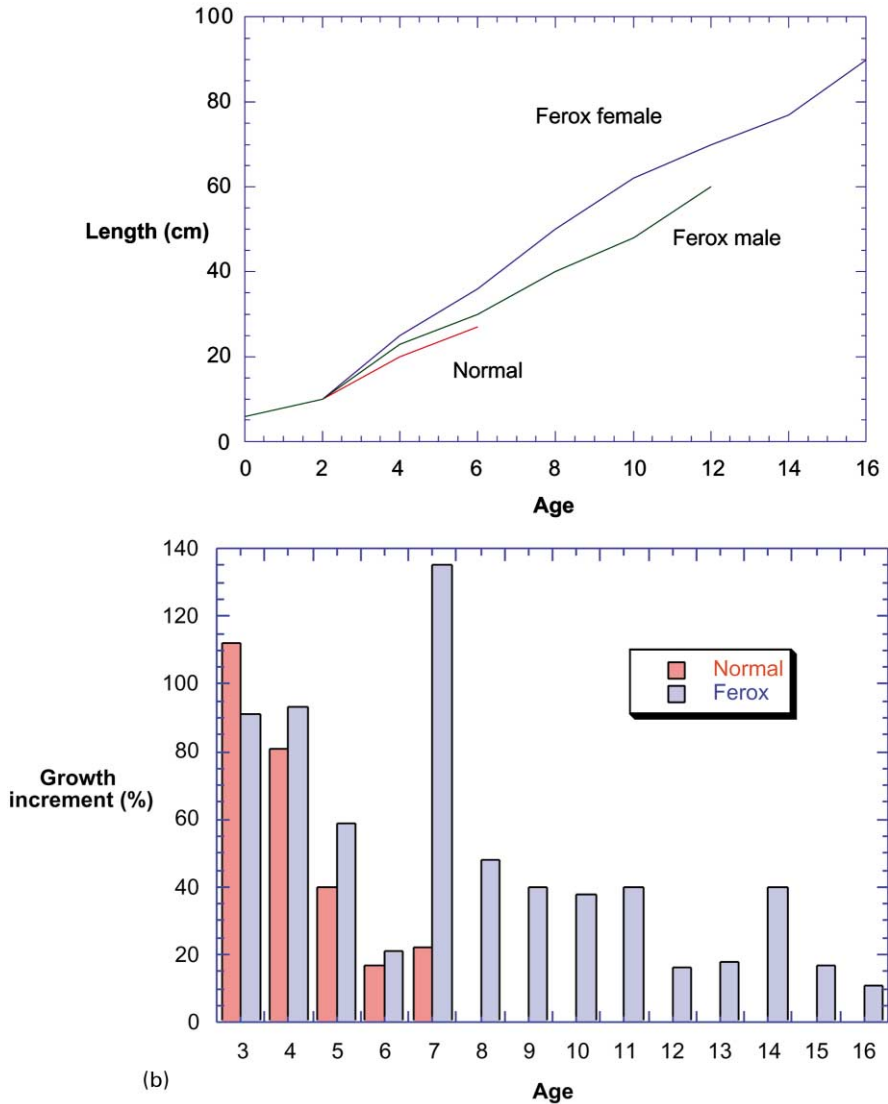


Fig. 3. (a) The growth of normal and ferox trout as a function of age; (b) the growth increments for normal and ferox trout. Based on data in Campbell (1979); also see Finch (1990).

4. An individual based model for ferox trout and charr

We use an individual based model (Cowan et al., 1996; Hinckley et al., 1996; Hermann et al., 1996; Uchmanski and Grimm, 1996; Walter et al., 1997) to understand the ecological, physiological and genetic components of the ferox life history. Our model and conclusions are very similar to those of Claessen et al. (2000) on Eurasian perch (*Perca*

Table 1
Symbols and their interpretations for the ferox trout model

Symbol	Interpretation	Value used
Environment		
T	Time within the year	Varies
$D(t)$	Daylight hours on day t	Varies
V_L	Littoral volume	Varies
V_B	Benthic volume	Varies
Fish physiology		
$W(t)$	Weight at the start of week t	Varies
$L(t)$	Length at the start of week t	$= W(t)^{1/3}$
F_0	Individual growth rate	Varies
$0, \sigma_0$	Mean and standard deviation of the log normal distribution that characterizes individual growth rate	Computed
ζ_t, ζ_t	Reduction in somatic growth after maturation for trout and charr	0.83, 0.60
T_{\min}	Minimum temperature for food gathering and assimilation	3°C for trout, -2°C for charr
T_{\max}	Maximum temperature for food gathering and assimilation	20°C for trout, 18°C for charr
T^*	Approximate optimal temperature for food gathering and assimilation	17°C for trout, 10°C for charr
ρ	The relative value of the unpreferred habitat	0.02
Ω_j	Occupied volume in habitat j ($j = L$ or B)	Varies
$H(i)$	Habitat chosen by fish i	Varies
I_{jk}	Indicator function	$= 1$ if $j = k$, $= 0$ if $j \neq k$
N_j	Number of fish in habitat j	Varies
Piscivory		
F	Relative growth of piscivore on forage fish	0.5
C_e	Flesh-to-flesh conversion	0.15
α_p	Search efficiency of the piscivore	1
L_{\max}	Maximum size fish that a piscivore can attack	
Reproduction		
R_{\max}	Maximum reproduction per year for both trout and charr	1200

fluviatilis). The parameters and their values are summarized in Table 1. For simplicity, we assume that all fish (trout and charr) are potentially long-lived, but this could be easily changed and simply requires that larger numbers of fish be simulated in the model.

The state of a fish is characterized by its age, weight, individually inherited growth rate, age at maturity and size at maturity.

4.1. Environment

The environment is characterized by latitude, which determines the number of daylight hours $D(t)$ as a function of calendar time t (measured in weeks) within the year ($t = 1$ corresponds to 1 November). We used photoperiods corresponding to 60°N latitude and

temperature profile typical for a typical Scottish loch. Temperature $T(t)$ (note that T now has a distinctly different meaning than it did in Section 2) determines the foraging capabilities and physiological costs of the fish. Lakes are characterized by littoral (roughly the shore zone where primary production is high, see Brönmark and Hansson, 1998) and benthic (roughly the bottom) volumes, V_L and V_B , respectively. In lakes in which both trout and charr are present, we assume that the trout occupy the littoral zone and the charr the epibenthic zone (Walker et al., 1988; L’Abee-Lund et al., 1992). This is a simplification. For example, Haraldstad and Jonsson (1983) found that one and two year old trout were littoral but that as fish aged (and became bigger), they shifted to the benthic and (roughly the open water) zones. Hegge et al. (1989) found that small (150–230 mm) trout and charr would co-occur in the benthic habitat, but that they were spatially segregated, with the trout occupying the first 5 m. Larger fish (>230 mm) coexisted in the pelagic zone.

We assume size-independent (e.g. disease, parasites) and size-dependent (e.g. fish, mammalian or avian predators) sources of mortality. In particular, if $m(w)$ denotes the weekly mortality of a fish of weight w ,

$$m(w) = m_0 + m_1 w^{-0.37} \quad (7)$$

The coefficients m_0 and m_1 are allowed to vary in the model (see below); the exponent -0.37 is based on the work of McGurk (1996). Unlike the Pacific salmon *Oncorhynchus* spp., ferox trout are iteroparous, so there is no catastrophic mortality after reproduction.

Other than summarizing mortality as the rate in Eq. (7), we make no specific assumptions about the cause of death.

4.2. Frequency of dependent foraging competition

Individuals can switch from one habitat (benthic or littoral) to the other; this may have profound effects on both growth and mortality (Tyler and Rose, 1997). We describe the switching rule for trout; an analogous calculation is done for charr. First, we compute the relative performance of trout in the littoral zone according to

$$r_L = \frac{V_L}{V_L + \rho V_B} \quad (8)$$

where ρ measures the relative growth in the alternative habitat. We assume that a trout goes to the littoral habitat with probability r_L and to the benthic habitat with probability $1 - r_L$. In this manner, fish i , with weight $W_i(t)$ in week t , is assigned habitat $H(i)$.

Once fish are assigned to benthic and littoral habitats, we compute the occupied foraging volume. For example, for the littoral habitat, this is

$$\Omega_L = \sum_i^N W_i(t) I_{H(i),L} \quad (9)$$

where N_L is the number of fish in the littoral zone, $W_i(t)$ is the weight of fish i and $I_{H(i),L}$ is 1 if fish i is in the littoral zone and 0 if it is in the benthic zone. A similar calculation determines Ω_B .

We assume that trout in the littoral zone are territorial. When the volume of fish in the

littoral zone does not exceed the habitat, all fish grow at a maximum rate. When fish exceed the volume, access to space in the littoral zone is assumed to be size dependent, with larger fish gaining access to territories. Fish with territories grow at their maximum rate. Fish without territories do not obtain food during that week and hence will lose weight. These fish will only be able to begin feeding once they gain access to a territory, primarily due to mortalities of other trout.

4.3. Prematuration growth dynamics

For each fish, we track age (a) and calendar time (t). However, for simplicity in what follows, we suppress the age dependence of variables. Thus, the physiology of the fish is characterized by the dynamics of weight $W(t)$ at calendar time t , with length related allometrically to weight by $L(t) = W(t)^{1/3}$. If fish i in habitat j is neither mature nor a piscivore, the growth dynamics are

$$W_i(t + 1) = W_i(t) + f_0(i)\rho_{ij}\min\left\{1, \frac{\Omega_j}{V_j}\right\}W(t)^{2/3}\frac{D(t)}{24}\Phi_i(T) - \alpha W_i(t)e^{0.071T(t)} \quad (10)$$

The various terms on the right-hand-side of Eq. (10) are explained as follows. In the anabolic term, $f_0(i)$ is the growth rate of fish i ; we assume that $\log(f_0)$ is normally distributed with mean \bar{f}_0 and standard deviation σ_0 , which we assume is 30% of the mean (Jobling, 1994, p. 178). We also assumed that the i th fish had a genetically determined age of maturity; see below for how this individual variation is used.

Trout and charr have different means of $f_0(i)$. To determine these, we computed the dynamics of weight according to Eq. (10) and measured the age at which the simulated length crossed 23 cm. Vollestad et al. (1993); Vollestad and L'Abée-Lund (1994) gave data on age and size at maturity for 28 trout stocks and 26 charr stocks (Table 2). We used the value for the mean of the growth rate to give age at maturity closest to the data. The parameter $\rho_{ij} = 1$ for trout in the littoral zone and charr in the benthic zone and $\rho_{ij} = \rho$ for trout in the benthic zone or charr in the littoral zone, $\min\{1, \Omega_j/V_j\}$ captures the frequency dependent foraging dynamics. $D(t)/24$ is the fraction of the day available for foraging. The function $\Phi(T)$, different for trout and charr, characterizes the ability of fish to assimilate food at different temperatures and is modeled by

$$\Phi(T) = c_n \left\{ \frac{T - T_{\min}}{T^* - T_{\min}} \max\left[0, 1 - \left(\frac{T}{T_{\max}}\right)^{10}\right]\right\} \quad (11)$$

In this equation, c_n is a normalization constant, chosen so that the maximum value of $\Phi(T) = 1$, T_{\min} , T^* , and T_{\max} are species-specific temperatures that characterize lethal minimum temperature, a location temperature for the optimal value of food gathering and conversion ability, and lethal maximum temperature, respectively. Eq. (11) produces a peaked function for the food gathering and assimilation ability of the fish (Elliott, 1994).

The catabolic term characterizes the standard exponential dependence of catabolic costs on temperature. The coefficient α was determined by requiring that fish of maximum size W_{\max} at an average temperature did not grow; hence the second and third terms on the right-hand-side of Eq. (10) balance.

Table 2

Age and size at maturity of trout and charr stocks (based on the data of Vollestad et al. (1993); Vollestad and L'Abbe-Lund (1994))

Species	Average (SD) length at maturity (cm)	Average (SD) age at maturity (years)
Trout	23 (5)	4.2 (1.6)
Charr	23 (7.1)	5.6 (1.7)

4.4. Postmaturation growth dynamics

After maturation, resources are diverted from somatic growth to gonadal growth. The consequence is that growth increments in $W(t)$ are reduced after maturation. We let ζ_t and ζ_c denote the reductions for trout and charr; these are, respectively, 0.83 (Elliott, 1994, p. 231) and 0.6 (Dutil, 1984). Thus, if the fish is mature, the growth dynamics are

$$W_i(t+1) = W_i(t) + \zeta_i f_0(i) \rho_{ij} W(t)^{2/3} \frac{D(t)}{24} \Phi_i(T) \min \left\{ 1, \frac{\Omega_j}{V_j} \right\} - \alpha W_i(t) e^{0.071T(t)} \quad (12)$$

We assume that fish can lose weight, but never lose length and that if a fish falls below 20% of its maximum weight to date, it starves to death (this is a very conservative condition for starvation).

4.5. Piscivory

In a study of 13 lakes in Norway, L'Abbe-Lund et al. (1992) found that piscivorous charr fed almost exclusively on three-spined sticklebacks, but that trout were much more cosmopolitan, feeding on sticklebacks, minnows, and charr. They also found little record of cannibalism by either trout or charr. However, for the latitudes that we are considering (about 55–70°), Griffiths (1994) reported cannibalism rates of charr ranging from about 5 to 40%. The median size of the cannibalistic fish was 33.5 cm. We assume that fish become piscivorous at 30 cm after which they eat forage fish and heterospecific salmonids. Thus, piscivory is characterized by a size threshold, S_{pis} . A fish for which $L_i(t) = W_i(t)^{1/3} < S_{\text{pis}}$ but $L_i(t+1) > S_{\text{pis}}$ becomes a piscivore during week t .

It is generally agreed, in many piscivores in addition to brown trout, that maximum prey size increases with predator size (e.g. L'Abbe-Lund et al., 1992; Greer, 1995). This ontogenetic increase in prey size is also consistent with the inclusion of small prey in piscivore diets, suggesting that prey selection is more passive than active (Juanes, 1994). Piscivorous fish move between the littoral and benthic zones according to the relative density of potential prey in each. Thus, for $j = L$ or B and assuming random search, the probability of encountering a prey fish when their density is N_j is $1 - \exp(-\alpha_p N_j / V_j)$, where α_p is a measure of the search efficiency of the piscivore. The expected number of prey encounters is thus $r_j = N_j (1 - \exp(-\alpha_p N_j / V_j))$. We assume that a piscivore moves to the littoral zone with a probability that is determined by its relative prey density. In this

way, we assume that the spatial distribution of predators will tend to correspond to the availability of their prey.

Once a predatory fish is in a habitat, it starts hunting. We characterize the growth of an immature fish; the modification for a mature fish is analogous to Eq. (10). The growth from forage fish is given by

$$g_{\text{forage}} = \eta f_0(i) W_i(t)^{2/3} \frac{D(t)}{24} \Phi_i(T) \quad (13)$$

where η is a measure of the level of forage fish. We assume that these are composed partially of 0 + trout and charr and partially of other fish (e.g. minnows, sticklebacks).

The success of an attack on salmonid prey is determined by the relative sizes of predator and prey. Damsgard (1995) showed that the maximum prey length that a piscivore of length L can attack is

$$L_{\text{max}} = \begin{cases} 0.268L - 0.2435 & \text{for trout} \\ 0.238L - 0.7575 & \text{for charr} \end{cases} \quad (14)$$

The probability of successful attack is computed according to the following steps. Suppose that N_j is the number of fish in habitat j . Fish number k , with length L_{kj} , is attacked with probability $(1/N_j)[1 - \exp(-\alpha_p N_j/V_j)]$ and is killed with probability $\min(1, 1.2 - L_{kj}/L_{\text{max}})$. The growth increment, g_{prey} from attacks on salmonid prey during a week is the sum of the weights of those prey successfully attacked, modified by a flesh-to-flesh conversion factor.

The weight dynamics of a piscivore are then

$$W_i(t + 1) = W_i(t) + g_{\text{forage}} + g_{\text{prey}} - \alpha W_i(t) e^{0.071T(t)} \quad (15)$$

4.6. 4.6 Reproduction

We assume that charr reproduce in littoral zone in autumn (Frost, 1965) and that trout reproduce in the streams flowing into the lake (Jonsson and Sandlund, 1979; Maitland et al., 1984). We assume that the lake can support a maximum number R_{max} of offspring per year. The maximum number of trout is $0.1R_{\text{max}}$ and the maximum number of charr is assumed to be the minimum of R_{max} and $10V_L$. Fecundity of a function of size

$$F = \begin{cases} 0.45W^{0.65} & \text{for trout} \\ 0.2308W^{0.831} & \text{for charr} \end{cases} \quad (16)$$

(see Elliott, 1984, for trout and Dempson, 1995, for charr).

A trout egg has probability 0.016 of reaching recruitment to the population; a charr egg has probability 0.01 of reaching recruitment. Upon recruitment, age 1 + trout have weight that is log-normally distributed with mean 3.22 g and standard deviation 0.05 g (Elliott, 1985) and age 0 + charr have weight that is log-normally distributed with mean 0.91 g and standard deviation 0.05 g (Fraser and Power, 1984).

We use the mean and standard deviations of size and age at maturity (Table 2) to assign reproductive characteristics to individuals, recognizing that parameters might vary in

particular lakes (Hegge et al., 1991). We also assume that growth rate, age at maturity and size at maturity have heritability $h^2 = 0.3$. Charr are recruited at age 1 and trout at age 2.

5. Sensitivity analysis

To investigate the sensitivity of this model to m_0 , m_1 , V_L , and V_B , we searched through a range of values as summarized in Table 1. We ran the model for 100 years, using only data after the first 25-year period to avoid the influence of initial transients. For any particular parameter combination, we terminated the program if a single ferox trout was produced, generating a value of 1; otherwise the model was allowed to continue until year 100, at which time a value of 0 was assigned. A value of 0 was also assigned if at any time there was a crash of the trout or the charr population. This provided us with 1039 parameter combinations and an associated binary data set, allowing us to explore the sensitivity of the model to these four parameters with logistic regression (Hosmer and Lemeshow, 1989).

6. Results

The standard parameters used in this model are $V_L = 500$ and $V_B = 1600$, $m_0 = 0.01$ and $m_1 = 0.03$. Because of fluctuations in the early period of the model, we adopted the conservative approach of only using data generated after an initial 25-year period. Under these conditions, a small proportion of the trout population becomes very large and old piscivores. Our model thus provides a mechanism underlying this phenomenon that is commonly observed in unexploited lakes containing salmoniforms (Johnson, 1976; Parker and Johnson, 1991), but see Claessen et al. (2000) for an alternative interpretation of results such as these in terms of emergent properties of complex adaptive systems. A small proportion of the charr population also achieved the size necessary to become piscivorous (i.e. a length of 30 cm). The absolute number of these fish relative to ferox trout was small, and their production was sensitive to a number of parameters (see below).

In general, relatively large benthic and littoral volumes tended to stabilize the population dynamics of trout and charr, respectively. Successive reduction in these volumes resulted in population dynamics becoming cyclic and ultimately entering an unstable chaotic state. However, the precise nature of these population dynamics interacted with background mortality rates, and we explore the statistics of these interactions below.

6.1. The existence of ferox trout

Using a stepwise multiple logistic regression, we determined that a model containing only three parameters explained 92.5% of the variation and rendered all other terms in the model non-significant (Table 3). These terms in order of their explained variation are V_L , and two interactions: $m_0 \times V_L$ and $m_1 \times V_B$. Size independent mortality exerted the greatest influence for the likely reason that some finite length of time was required for fish to achieve the size necessary to become a ferox trout. As noted below, this parameter was also very important in determining the number of ferox trout that would exist within a population.

Table 3
Multiple logistic regression describing the main parameters important in determining whether ferox trout will exist within a lake

Variable	Coefficient	S.E.	Wald	df	Sig.
V_L	0.0396	0.0051	60.1	1	< 0.0001
$m_0 \times V_L$	-0.7545	0.0982	59.0	1	< 0.0001
$m_1 \times V_B$	-0.0093	0.0042	4.9	1	0.0265

The reason that V_L exerted such a profound influence on the production of ferox trout is presumably related to territoriality and its influence upon access to food. Individuals that possessed territories would grow at a maximum rate, while those that had no territory would be unable to feed and grow. The size of the littoral zone determined the number of trout within the population that could grow at a maximal rate and hence achieve the size necessary to become a piscivore. This analysis also implies that highly irregular shorelines are conducive to the existence of ferox trout. The interaction between m_0 and V_L indicates that a combination of an increasing littoral zone (and hence population of territorial trout) and size independent mortality will influence the life expectancy of the territorial trout and hence their likelihood of crossing the size threshold into piscivory. The interaction between m_1 and V_B contributes relatively little additional explanatory power to the model.

6.2. The abundance of ferox trout

The model demonstrated that ferox trout are rare, averaging just under 6% of the total trout population for the range of parameters we tested. Size independent mortality, m_0 , affected the production of ferox trout. If m_0 was sufficiently high, no ferox trout were produced; for more moderate values of m_0 the fraction of ferox trout within the trout population increased (Fig. 4). No ferox trout are observed if the mortality rate is extremely low. A similar pattern was also observed for m_1 , although the observed change in proportion of ferox trout was not as dramatic as that observed for m_0 . The size of the littoral zone also had a significant influence on the proportion of ferox trout. Our results suggest that there is a certain probability that a lake will contain ferox trout (determined by m_0 , m_1 and V_B). Given that it does hold ferox, there is a nearly linear relationship between the volume of the littoral zone and the number of ferox trout. This result, in combination with the patterns associated with the mortality parameters, suggests that the relative abundance of ferox trout is strongly affected by the size of the littoral zone when mortality levels within a lake are low. Benthic volume, V_B , appeared to have no influence on the relative abundance of ferox trout.

To investigate interactions between our main parameters and the results of our model, we conducted a series of stepwise linear multiple regressions (Table 4). In this analysis, V_L , m_0 , and their interaction explained most of the variation associated with the size of the trout population (measured as biomass), the size of the ferox population, and the average size of ferox trout. Indeed, for both trout biomass and the size of ferox population, V_L explained most of the variation, followed by the interaction between V_L and m_0 .

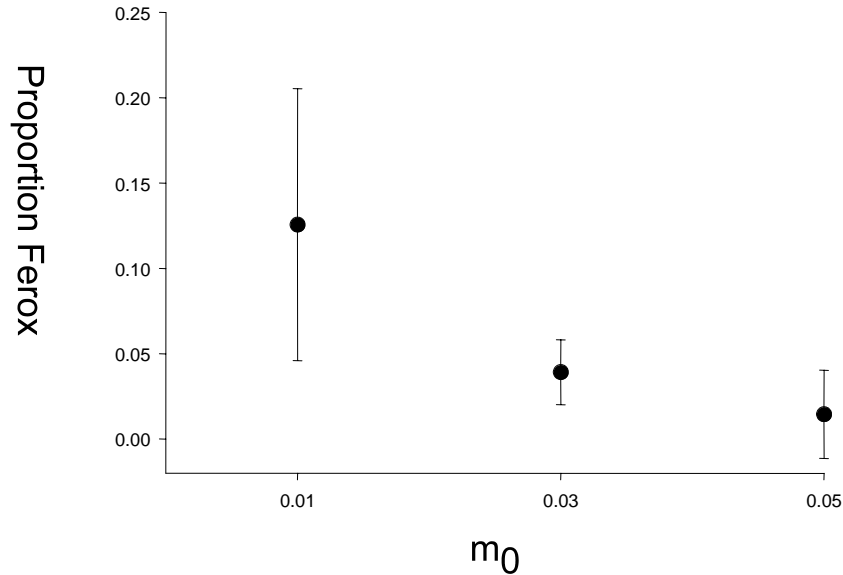


Fig. 4. The influence of size independent mortality m_0 on the proportion of ferox trout. Data presented are mean values ± 1 standard deviation.

The importance of V_L on these parameters is likely due to territorial competition. It determines the maximum number of territories that can exist within a lake. In combination with m_0 , it also determines how many trout are likely to become adults, and therefore the number that may attain the size necessary to become a piscivore, and hence a ferox trout. However, the size of these ferox trout is most affected by m_0 . This is because these fish are of a size that size-dependent mortality is no longer going to have a significant influence on their survival. With lower m_0 , animals will live longer, and achieve greater size.

The parameters affecting charr biomass and the number of piscivorous charr are not as simple (Table 4). Charr biomass is most affected by the size of the region of the lake they primarily occupy, V_B . As with the trout, there was also a significant interaction between their preferred region of the lake and m_0 . As noted above, the production of piscivorous charr was a rare event. This analysis also demonstrates it is very complicated. The parameters that explain the greatest influence on their existence is the three-way interaction between m_1 , V_L , and V_B and the four-way interaction between m_0 , m_1 , V_L , and V_B . However, the mechanism that is most likely responsible for this complicated model is the strong influence that the trout population exerts on the charr population.

When very low mortality parameters were used (i.e. $m_0 = m_1 < 0.01$), large numbers of newly recruited trout and charr persisted in the population. The influence of these low mortality rates differed between the trout and charr populations. Very low mortality rates resulted in intense intraspecific competition, and stunting of the charr population (cf. Jonsson and Hindar, 1982; Claessen et al., 2000). Individuals within this population

Table 4
Summary of multiple regression to determine the most important model parameters that influence population features of trout and charr

Variable	Model parameter	<i>t</i>	<i>p</i>
Trout biomass	m_0	-3.168	0.009
	V_L	22.184	< 0.001
	$m_0 \times V_L$	-16.753	< 0.001
Ferox abundance	m_0	2.988	0.003
	V_L	19.012	< 0.001
	$m_0 \times V_L$	-14.632	< 0.001
Ferox size	m_0	-9.544	< 0.001
	V_L	-2.274	0.024
	$m_0 \times V_L$	4.687	< 0.001
Charr biomass	m_0	18.073	< 0.001
	m_1	-2.931	0.004
	V_B	43.019	< 0.001
	$m_0 \times V_B$	-35.680	< 0.001
	$m_1 \times V_B$	12.870	< 0.001
	$V_L \times V_B$	6.922	< 0.001
	$m_0 \times m_1 \times V_B$	-14.565	< 0.001
	$m_0 \times V_L \times V_B$	-5.360	< 0.001
Pisc. Charr abundance	m_0	2.612	0.010
	$m_0 \times m_1$	-4.439	< 0.001
	$m_1 \times V_B$	6.287	< 0.001
	$m_1 \times V_L$	-8.983	< 0.001
	$m_0 \times m_1 \times V_L$	8.356	< 0.001
	$m_1 \times V_L \times V_B$	14.576	< 0.001
	$m_0 \times m_1 \times V_L \times V_B$	-14.642	< 0.001

matured due to age rather than size. Conversely, the territorial nature of the trout resulted in the failure of certain year classes because older individuals persisted in the population for a much longer period of time, providing no territories (and hence the ability to feed and grow) for new year classes. This scenario, in combination with a lake that contained a

Table 5
Linear regression parameters for the relationship between ferox trout and charr abundance

V_L	V_B	Intercept	Slope	r^2
600	800	-2.26	8.45×10^{-5}	0.913
600	1600	-2.65	2.96×10^{-5}	0.95
600	2000	-2.21	2.04×10^{-5}	0.96
1000	800	-4.79	1.8×10^{-4}	0.91
1000	1600	-6.53	6.21×10^{-5}	0.90
1000	2000	-6.3	4.31×10^{-5}	0.91
1400	800	-9.04	2.53×10^{-4}	0.84
1400	1600	-9.89	8.7×10^{-5}	0.87
1400	2000	-9.86	6.26×10^{-5}	0.90

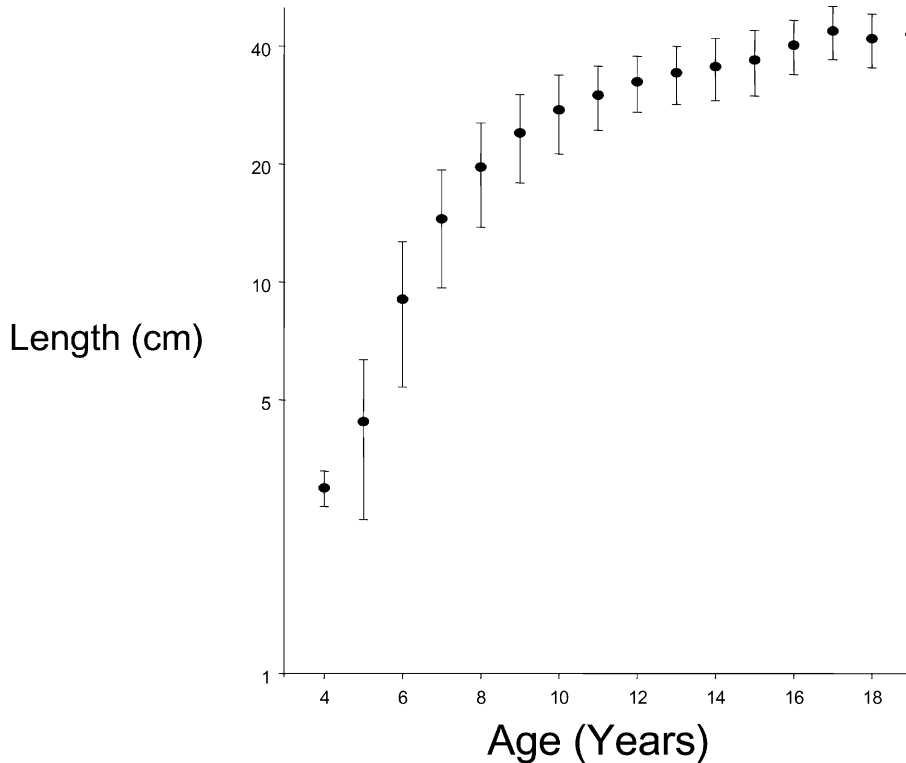


Fig. 5. The pattern of trout over their long life. The first occurs when these fish are normal brown trout. After approximately 10 years they become facultative piscivores and a new relation emerges in their rate of growth.

relatively large littoral zone, caused these populations to produce a large proportion of ferox trout.

6.3. Interactions between trout and charr

Using the default parameter combination, we examined the influence of the trout and charr populations on each other. When the lake volumes are held constant, we predict (Table 5) a nearly linear relationship between charr abundance and ferox abundance, as hypothesized by Greer (1995).

When no trout are present, there is an increase in the size of the charr population because predation pressure is reduced. As a consequence, there is more intraspecific competition, and individuals within the charr population grow more slowly, reducing the number of piscivorous charr. The charr population is relatively more dense than the trout population. Therefore, when piscivores of either species are produced, they tend to prefer the habitat containing the charr as they are relatively more abundant. The mortality

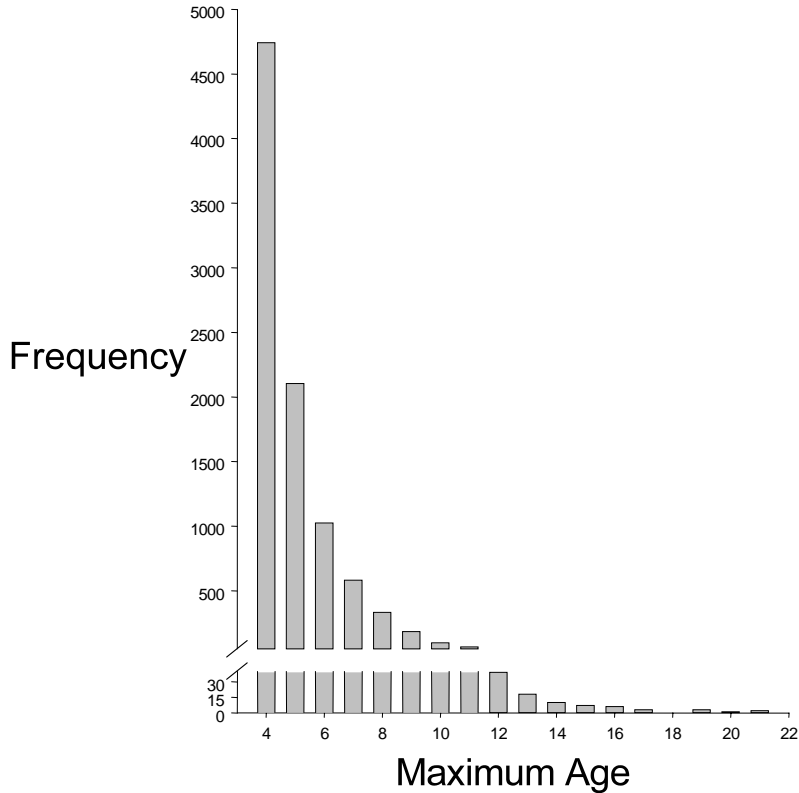


Fig. 6. A frequency histogram for the life expectancy of trout within our model.

imposed by these piscivores reduces intraspecific competition for the charr population, and increases their growth rate.

6.4. Energy, growth and longevity

To obtain detailed information on the role of caloric limitation on life expectancy, we ran our model for 500 years, but excluded data from the initial 30-year period due to early fluctuations in the model's dynamics. In addition, we lowered the mortality parameters and adjusted the lake morphology to parameters that favored the production of very large fish ($m_0 = m_1 = 0.01$, $V_L = 200$, $V_B = 800$). As illustrated in Fig. 6, the life expectancy for trout in our model follows a negative exponential relation, with the existence of the very oldest fish being an exceptionally rare event (fewer than 0.05% individuals achieved the oldest recorded age of 21 years).

Since we provided variable growth rates to all fish, we tested the hypothesis that those individuals that possessed inherently larger growth rates should have a higher probability of becoming the large piscivores within the population. Furthermore, since we allowed the growth rate of these fish to be partially heritable, we investigated whether there was any

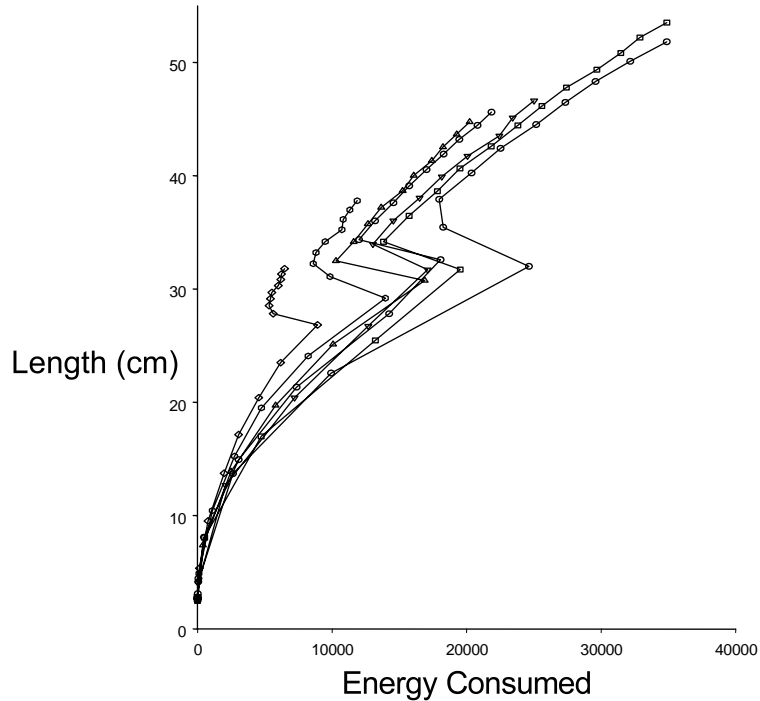
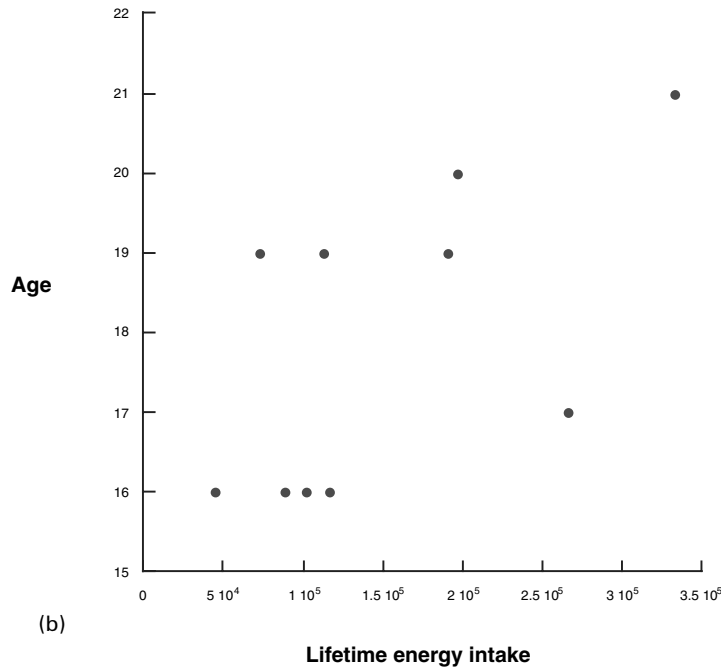
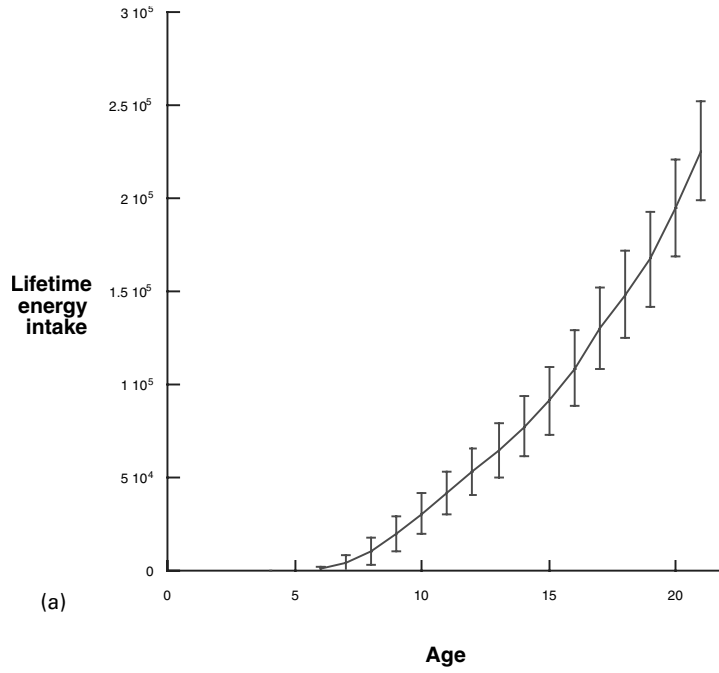


Fig. 7. The relation between gross energy intake and length for the seven largest ferox produced in our model.

evolutionary change in growth rates of the piscivorous fish over this time period. Over 500 years, there was no evidence of evolutionary change in the growth rates parameters for either trout or charr, nor any evidence of divergence within either population. We also compared the f_0 parameters of a subgroup of fish to determine whether higher f_0 values were correlated with size. Individuals that were able to live for a longer period of time attained a larger size and (because of size-dependent predation) vice versa (Fig. 5). The value of f_0 can explain more than 90% of the variation in weight for the oldest classes of fish.

The growth trajectory of the individuals within this population is illustrated in Fig. 6. These data demonstrate that through time, individuals follow two growth trajectories. The first occurs before the trout achieve the size necessary to become a piscivore (those generally 10 years and younger). After achieving the threshold size necessary to become a piscivore, the trout then follow a growth trajectory that is distinct from other trout, and one that is constant for the remainder of their life.

Fig. 8. Relationships between age and lifetime energy intake predicted by the model. (a) Average and standard deviation of cumulative energy intake to age for fish in the model; (b) the age achieved for the 10 oldest fish as a function of individual lifetime energy intake, showing a clear positive relationship between energy intake and age.



The switch to being a facultative piscivore allows these individuals to take advantage of a new niche that is more energetically rewarding than continuing within the niche occupied by smaller trout. By focusing on the oldest ferox trout produced within our simulation, it is clear that a significant cost is associated with this switch. Fig. 7 illustrates the relation between energy consumed and mass of the fish in one year increments for the seven oldest fish produced in our model. These data clearly illustrate the two distinct growth trajectories before and after becoming an obligate piscivore. Of particular interest is the cost associated with this switch. For all individuals, the point at which they switch to becoming an obligate piscivore is accompanied by an initial reduction in the amount of energy consumed. The mechanism responsible for this result is that the ability to capture other fish critically depends on the size difference between the predator and its prey. The relatively small size at the initial stage presumably has a cost due to a reduced probability of capture in these early stages. However, once this cost has been paid, these individuals reap two benefits: a higher rate of energy intake due to increased effectiveness as a piscivore, and a longer life expectancy since they achieve a size that renders them immune to cannibalistic attacks from predators.

Finally, we investigated the relationship between energy intake and age. Lifetime energy intake was an increasing function of age, with a slight nonlinearity (Fig. 8a).

Furthermore, our model shows that for the oldest individuals maximum age was an increasing function of lifetime energy intake (Fig. 8b).

7. Conclusion

It is generally understood that longevity can evolve only in situations in which background mortality rates are sufficiently low so that individuals can live to long ages without high probability of death from ‘accidental causes’. Our work with the ferox trout suggests that the situation is more complicated than this, and that a ‘window’ of background mortality rates exists and that even then, the ecological environment (in this case competition) plays an important role. Clearly, if the rates are too high, then individuals simply do not have the opportunity to develop mechanisms for longevity. On the other hand, if the rates are too low, and competitors thus sufficiently abundant, individuals will lack the opportunity to grow into size large enough to become piscivorous.

Although we focused on trout and charr, the notions that we developed in this paper are fairly general. For example, size dependent predation, one of the keys of our analysis, is observed in yellow perch (Post and Prankevicus, 1987; Post and Evans, 1989a,b), Eurasian perch (Claessen et al., 2000) and is assumed to occur throughout many aquatic ecosystems (Werner and Gilliam, 1984). We therefore believe that our results have application to most fish populations.

Within our model, we made no genetic distinction between those individuals that become ferox trout, and those that follow a more typical pattern for brown trout. Two lines of evidence suggest that this is not the case. First, ferox trout appear to have an allele (Hamilton et al., 1989; Ferguson and Mason, 1981; Ferguson and Taggart, 1991; Ferguson et al., 1995; McVeigh et al., 1995) that is not found in other brown trout. Hardy–Weinberg analysis of enzyme polymorphisms suggest reproductive isolation; this may be indicative

of multiple colonization events by the phenotypes that exhibit different lifespans (Hynes et al., 1996). Second, a recent study by Jonsson et al. (1999) showed that longevity of piscivorous brown trout was about 11 years while that of invertebrate feeders was about 10 years. Thus, the switch to piscivory itself leads to a 10% increase in lifespan, not the exceptional increases shown by ferox trout. We thus hypothesize that the ecological mechanisms described here provide the milieu in which a biochemical adaptation (represented by the unique allele) for long life occurred. Thus, the ferox trout can be understood by neither ecology/evolution alone nor cell biology alone. It is the interaction of the two that is essential. However, it is clear that they achieve long life, at least in part, through considerable additional caloric intake rather than restriction.

Our model demonstrates that ferox trout require a restrictive set of ecological conditions. These conditions are primarily affected by mortality rates and littoral volume. If the environmental mortality rates are too low, levels of intraspecific competition impair growth rates to the point that no fish will ever grow large enough to cross the size threshold necessary to become a piscivore. Conversely, if mortality rates are increased, fish may be able to grow very rapidly, but will fail to live long enough to achieve the size necessary to become a piscivore. And of course, relatively high levels of size-independent mortality mean that even if ferox are produced within a lake, they will be present for a relatively short time and therefore not achieve the age for which they are noteworthy.

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