

Models of alternative life-history strategies, population structure and potential speciation in salmonid fish stocks

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Summary

1. High Arctic landlocked Arctic charr, *Salvelinus alpinus* L., are used as a reference system to examine the theory of alternative life history strategies in Salmonids and their implication for population structure and potential speciation. In these closed, autonomous systems, Arctic charr are the only fish species present and alternative life history strategies are represented by two distinct size modes, commonly known as ‘dwarf’ and ‘normal’ charr.

2. Simple mathematical models are used to caricature the density-dependent interactions within and between the dwarf and normal components of these bimodal populations. Two different assumptions concerning the genetic relationship between the two alternative life history strategies are investigated: complete reproductive isolation, or a single stock which chooses between the alternative strategies facultatively.

3. In constant environmental conditions, the evolutionarily stable strategy (ESS) is not affected by the assumed genetic relationship, and the ESS proportions of dwarfs and normals are shown to depend on environmental parameters. The ESS proportions vary with these parameters along an evolutionarily stable continuum (ESC) and, in particular, a high proportion of normals is associated with high growth rate as a juvenile, and a ‘stunted’ or unimodal population with low growth rate. The predicted ESC for selection of the normal strategy is similar to that observed experimentally in the analogous case of smolting in Atlantic salmon, *Salmo salar* L.

4. A difference in the ratio of fecundity to mortality rate between dwarf and normal sub-populations is shown to be essential to maintaining bimodal populations, and it is argued that cannibalism is one mechanism which could achieve this difference.

5. The model is extended to ask what ecological conditions would favour evolution toward the speciated or reproductively isolated state. It is concluded that short-term environmental fluctuations select against speciation and it is speculated that most natural bimodal Arctic charr stocks will achieve maximum individual fitness within a ‘semispeciated’ configuration which is maintained by incomplete assortative mating.

Key-words: evolutionarily stable strategies (ESS), population dynamics, size-structured populations, sympatric speciation.

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Introduction

Some of the most-studied examples of alternative life history strategies in nature involve members of the Salmonid family of fishes. The typical Salmonid life cycle includes parr, smolt and anadromous stages and, in most examples, alternatives are represented by male

maturation occurring either as parr or as anadromous individuals (e.g. Hutchings & Myers 1994). Alternative life history strategies in Salmonids can even coexist in non-anadromous species, a situation well exemplified by the landlocked, single-species, Arctic charr populations of the High Arctic. Even in these systems, however, many features of their presumed ancestral life history remain, and Klemetsen *et al.* (1989) propose a relict anadromous life cycle as a model for landlocked charr in Norway.

An important characteristic of the fish samples obtained from these undisturbed autonomous Arctic

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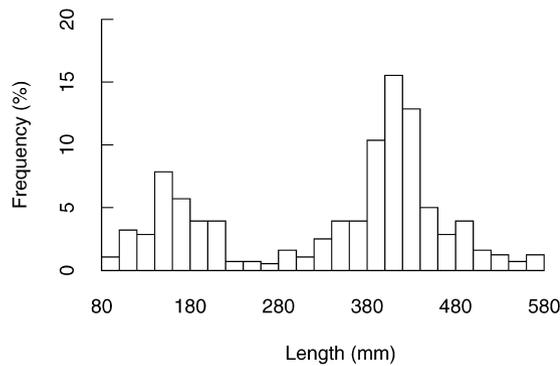


Fig. 1. A typical bimodal length–frequency distribution of a landlocked Arctic charr population in the High Arctic. The smaller mode consists of dwarfs, the larger of normals. From Parker & Johnson (1991).

lakes is that the size or weight distributions may be unimodal, bimodal (Fig. 1), or even multimodal. When more than one mode exists, each is associated with an alternative life history strategy. Both males and females can exhibit bimodality, unimodal populations remain common at all latitudes, and modal size may vary. Individuals associated with the smaller mode may or may not be reproductively competent, and sexual dimorphism is observed in both size and reproductive strategies. In order to retain consistency with the literature, this paper labels the members of the smaller mode ‘dwarfs’ and the larger fish ‘normals’ (e.g. Klemetsen & Grottnes 1980). This convention is not liked by the current authors. A more appropriate nomenclature might be ‘parr-type’ and ‘smolt-type’ to relate these forms to the hypothesized relict anadromous life cycle.

This bimodality is of both ecological and evolutionary interest. Ecologically, each of the size modes is normally associated with a different habitat and interactions within and between individuals from the different size modes have important population dynamics implications which are studied in this paper.

Evolutionary thought focuses on whether the bimodal size–structure is determined by genetic differences between individuals adopting each strategy, or conditional responses to the environment. In the former case, the alternative life history strategies imply some isolation of their respective gene pools and hence potential speciation. In the latter, the representatives of each alternative life history strategy share gene pools. Thus, alternative life history strategies may lie anywhere on a spectrum between full speciation and a phenotypically determined reaction norm. For landlocked charr populations, the evidence is inconclusive. Morphological differences between members of different size modes, for example in gill raker counts, are commonly observed (e.g. Parker & Johnson 1991), indicating, perhaps, some genetic component. Similarly, some experiments with laboratory-reared progeny of the two morphs suggest that the observed differences in behaviour and life history are genetically based (Skulason *et al.* 1993, 1996). On the other hand, the majority

of studies designed to test for genetic divergence, predominantly using molecular techniques (e.g. Hindar, Ryman & Stahl 1986; Snorrason *et al.* 1989; Danzmann *et al.* 1991; Hartley *et al.* 1992), detect, at best, only slight genetic divergence.

There is also strong experimental evidence for a conditional response. Thorpe *et al.* (1989) showed in Atlantic salmon that the percentage of smolts at age 1 year was correlated with an ‘index of growth opportunity’, an environmental stimulus. Transplantation experiments between dwarf, normal and anadromous charr from different locations also confirm that there is both a genetic and an environmental component (Nordeng 1983; Nordeng, Bratland & Skurdal 1989).

Populations of Arctic charr at the northern extreme of their range offer a unique system for studying these ecological and evolutionary processes. Not only is the researcher presented with simple, undisturbed ecosystems of low complexity but the severity of the resource limitation in these habitats results in an exceptionally long developmental period, followed by a single spawning event. This means that seasonally driven variation in reproductive strategies can be ignored for modelling purposes. Instead, it can be assumed that the alternative life history strategies are a response to long-term average resource density, which may vary between populations.

Modelling of these High Arctic systems is used in this paper to supplement field observations and laboratory experiments conducted elsewhere. By using models, the interactions within and between the various elements of the population can be studied where important parameters, such as mortality and recruitment rates, can neither be measured nor accurately manipulated in the field or the laboratory.

The models are subsequently used as measures of fitness whereby individuals adopting different strategies compete within the same model and individuals adopting suboptimal strategies are driven to simulated extinction. This allows prediction of the evolutionarily stable strategy (ESS) for the proportion of dwarfs and normals in a population subject to given environmental conditions. Changes to these environmental parameters are then used to determine the evolutionarily stable continuum (ESC) (Hutchings & Myers 1994).

The mechanism of selection of the alternative life history strategies is then investigated by assuming, in turn, either of two extreme possible assumptions. The first assumption is that an individual adopts the strategy of its parents; that is, that dwarfs and normals are genetically distinct. The second assumption is that the offspring of an individual consist of some combination of dwarfs and normals, i.e. a mixed strategy. Competition between the two types within a single simulated population is then used to determine which achieves the greatest fitness. By paying particular attention to the effects of environmental fluctuation, we then ask under what circumstances a selective advantage might occur if the competing life history strategies evolve towards speciation.

Models

POPULATION DYNAMICS AND STRUCTURE

Our key hypothesis is that the variability in population structure is the result of adaptations to energy limitation. Existing theory of ontogenetic niche shifts in fish (e.g. Werner & Gilliam 1984) typically assumes two distinct habitats, each with different size-specific growth and mortality rates. Individuals behaving optimally make the transition from one habitat to the other on achieving a critical size at which the ratio of growth and mortality rates has an equal value in the two habitats. While there is much evidence for correlations between size and habitat use in charr (e.g. Parker & Johnson 1991), the energetic/mortality basis of this is not well established, although Forseth, Ugedal & Jonsson (1994) document a shift from benthic to pelagic feeding associated with a reduced cost of feeding for larger fish in the pelagic habitat.

Energetics also affect reproductive strategies. If energy limitation is sufficiently strong, an individual which reproduces while still small may never achieve the critical size for transition to the next habitat associated with larger size. In this case, it is possible that a second strategy becomes viable in which juveniles opt for a different growth trajectory, thereby gaining access to the second habitat where they can subsequently reproduce. Parker (1995, 1997) confirmed theoretically that, in the absence of seasonal effects, trade-offs between growth, reproduction and mortality would lead to optimization of fitness for these two strategies at different growth rates.

While there is considerable existing work (e.g. Stearns & Crandall 1984) that shows that fish are capable of optimizing age and size at maturity within habitats, much less work has been conducted on the equally fundamental ability to select an alternative life history strategy where alternatives arise. Some work has, however, been conducted in amphibians (Kaplan & Cooper 1984), whereby individuals adopting different life history strategies maximized their fitness by 'bet-hedging' against future environmental uncertainty. This was achieved via a postulated 'weighted coin' which optimized the proportion of their offspring which adopted each of two strategies. The term 'weighted coin' is also used in the same sense in this paper as shorthand for the switch which 'decides' which of two life history strategies an individual will adopt in the mixed strategy case.

Our models assume that the population is size-structured and that all juvenile fish share a single habitat. Dwarfs reproduce in this habitat whereas normals shift to a new habitat at some size threshold and continue to grow prior to reproduction. Thus a lake containing two habitats, H1 and H2, is modelled with dwarfs and juvenile normals in H1 and adult normals in H2. Recruitment to both habitats is limited by the density of individuals already in the habitat, an assumption intended to provide a crude representation

of factors as diverse as territorial behaviour or avoidance of cannibalism whereby 'residents' repel 'immigrants', an assumption previously proposed for Arctic charr in the (verbal) model of Johnson (1976).

Three variations on this basic size-structured model are studied:

(A) *Separate stocks model*. Dwarfs and normals are different species.

(B) *Single stock model*. Dwarfs and normals are recruited from a single gene pool, with a 'weighted coin' allocating individuals to each life history strategy at birth, i.e. simultaneously with entry to habitat H1.

(C) *Speciation model*. There are three 'species': pure dwarfs, pure normals, and 'mixed strategists' (individuals equipped with the weighted coin from model B).

The structure of the models is illustrated in Fig. 2; the model parameters and equations are listed in Tables 1 and 2.

The models assume the well-established phenomenon that age and size at maturity have been optimized within each habitat. This is represented by the fecundity rates, r_d and r_n , since, owing to the relationship between size and fecundity, these are a function of the size at spawning and the time (since recruitment) that they take to reach that size. The relative values of these parameters can therefore be estimated from field data (see Appendix I). It is also supposed, but not an assumption of the model, that the normal strategy is part-optimized by achieving recruitment to H2 with minimum possible mortality risk. This is represented by the recruitment factor, G , which cannot be estimated from field data since it requires knowledge of the accumulated chance of mortality experienced by an individual as it grows from the egg to recruitment as a normal. This kind of information is practically impossible to obtain from a natural system. The modelling approach nevertheless allows this parameter to be varied over a wide range of values in order to examine its influence on the system.

Despite not being able to estimate G from a natural system, it can be related in general terms to observable environmental conditions. A high value of G implies that environmental conditions favour recruitment to H2. In a size-structured population, this means that G is closely associated with the growth rate in H1. Taking the situation where seasonal effects are negligible, it would be expected that a high growth rate would reduce the time needed to reach threshold size and hence the cumulative mortality experienced. In this case high G would be associated with high average growth rate in H1. In situations where seasonal effects are more relevant, a situation not covered by this model, this may not necessarily be the case, and further comment on this subject is deferred to the Discussion. For now, G should merely be viewed abstractly as a description of the gradient of different environmental parameters which affect recruitment to H2.

Three terms of the model simulate aspects of competition. The Ricker-like terms, $\exp(-(D + J)/K_d)$

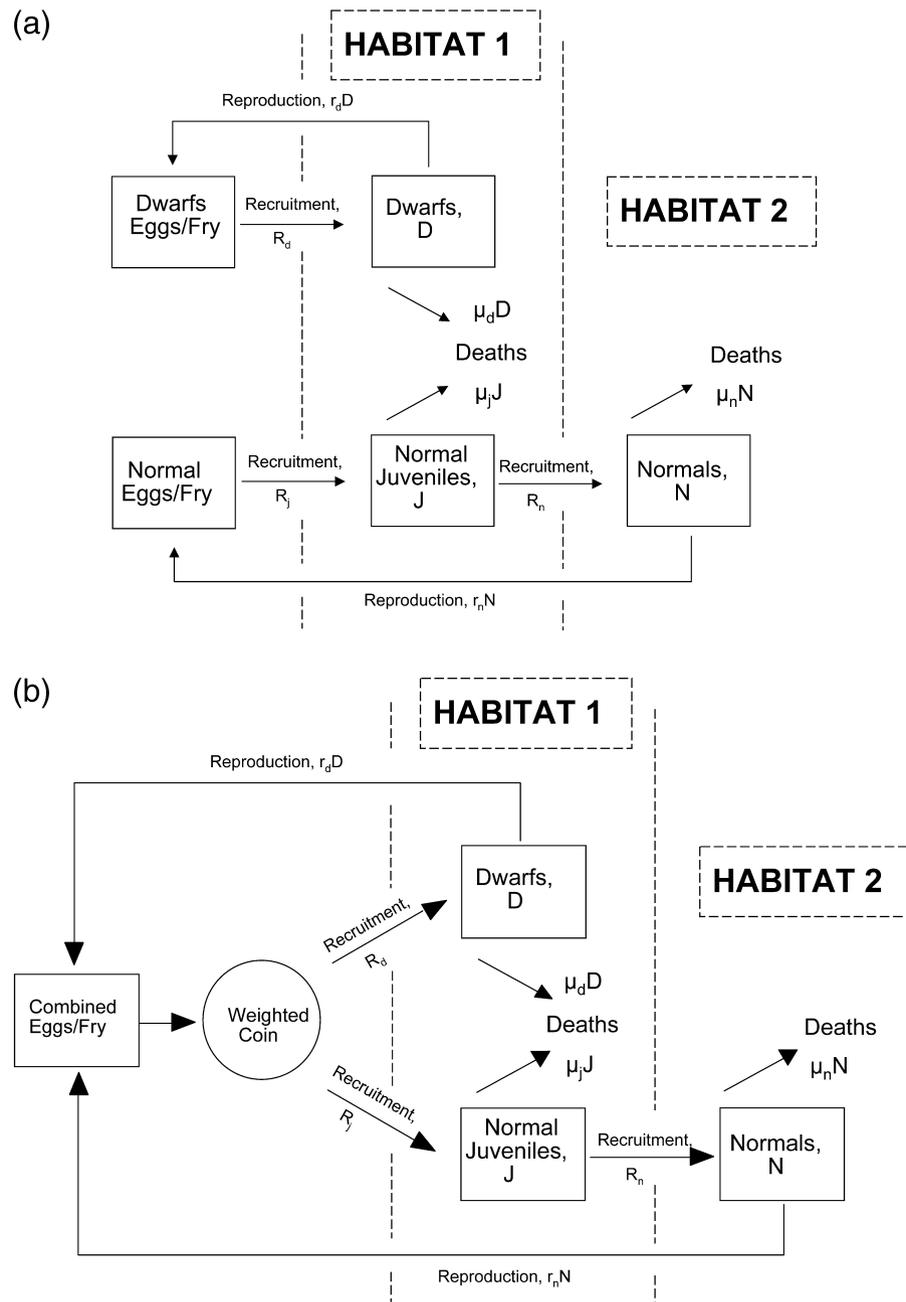


Fig. 2. (a) Model of two reproductively isolated stocks of Arctic charr coexisting within the same lake (model A). Density-limited recruitment occurs between each habitat and no individual is capable of spawning in more than one habitat. (b) Single stock model where individuals are subject to the same constraints as separate stocks model but contribute to the same gene pool (model B). Choice of life history strategy is determined by a phenotypic weighted coin.

and $\exp(-N/K_n)$, mimic the decrease in fecundities and growth rates at high population densities. They are, however, also intended to be a crude representation of the negative frequency-dependent success of alternative reproductive strategies due to behavioural interactions on spawning grounds (Gross 1984; Hutchings & Myers 1994), as well as another behavioural interaction whereby recruitment to both habitats is limited by the density of individuals already in it (Johnson's (1976) 'filter'). Alternative density-dependent functions were also tried and found to have no substantial effect on the behaviour of the models.

The third competition term is $J/(D + J + D_o)$ which models the competition between the strategies in H1. Density-dependence is envisaged to limit growth rate and, hence, the presence of dwarfs in H1 will reduce the ability of juvenile normals to reach critical size and recruit to H2. The term can also be seen as the proportion of H1 which is available to the juvenile normals. D_o is small relative to the equilibrium values of D and J and limits recruitment to biologically sensible finite limits at low values of $D + J$.

The output of the model is in terms of sub-population numbers, D , J and N . The related changes in body size

Table 1. Variables and parameters used in the ordinary differential equation models

	Symbol	Default value	Units	Description
Variables	D		Individuals	Mature dwarfs
	J		Individuals	Juvenile normals in dwarf habitat
	N		Individuals	Mature normals
	P_d		Dimensionless	Probability of selection of dwarf life history strategy
	P_n		Dimensionless	Probability of selection of normal life history strategy
Parameters	r_d	1.5	Time ⁻¹	Dwarf fecundity rate
	r_n	6.0	Time ⁻¹	Normal fecundity rate
	μ_d	0.125	Time ⁻¹	Dwarf mortality rate
	μ_j	0.125	Time ⁻¹	Juvenile normal mortality rate
	μ_n	0.125	Time ⁻¹	Normal mortality rate
	K_d	10	Individuals	Dwarf habitat carrying capacity
	K_n	10	Individuals	Normal habitat carrying capacity
	G	1.7	Individs./time	Recruitment factor
	D_o	0.01	Individuals	Recruitment restriction term

Table 2. Formulation of the ordinary differential equations used in the bimodal population models

	Symbol	Separate stocks	Single stock
Recruitment rates	$R_d =$	$r_d D \exp(-(D+J)/K_d)$	$(r_d D + r_n N) P_d \exp(-(D+J)/K_d)$
	$R_j =$	$r_n N \exp(-(D+J)/K_d)$	$(r_d D + r_n N) P_n \exp(-(D+J)/K_d)$
	$R_n =$	$\frac{GJ}{J+D+D_o} \exp(-N/K_n)$	
Balance equations	$\frac{dD}{dt} =$	$R_d(t) - \mu_d D_o$	
	$\frac{dJ}{dt} =$	$R_j(t) - \mu_j J - R_n(t)$	
	$\frac{dN}{dt} =$	$R_n(t) - \mu_n N$	

are implied within the fecundity rates, r_d and r_n , and density dependent terms. Similarly, environmental changes are also only implied within the model by varying the carrying capacities, K_d and K_n , and the recruitment factor, G .

The models discussed so far use ordinary differential equations as the simplest representation of the structure and dynamics of these populations. This type of model ignores time delays in that it assumes that dwarfs are reproductively mature at birth, the per capita rate of transition from juvenile to adult normal is constant, and normals are reproductively mature upon recruitment from the juvenile stage. To test the robustness of our results against relaxation of these clearly unrealistic assumptions, we developed a model which explicitly includes the time delays inherent in transitions between stages.

We modelled populations with developmental delays using delay-differential equations (Nisbet 1997 and many references therein). In the models, transitions between stages occur after fixed times. During these time delays, mortality occurs as in the simpler models, either at a constant per capita rate or through density-dependent terms. The sub-populations from the simpler model are divided further into stages based on their reproductive status. Within the dwarf class,

individuals are born into an immature stage, and recruit to the mature stage only after a fixed developmental delay. The normal sub-population is divided similarly; however, in this case we have added a pre-recruit stage, during which density dependence in the transition from juvenile to adult normal habitat occurs. The parameters and equations for these models are listed in Tables 3 and 4, respectively.

EVOLUTIONARILY STABLE STRATEGIES

In this paper, population dynamic models are used to obtain measures of fitness because individuals are affected by the other members of the population through the mechanism of competition. An evolutionarily stable strategy (ESS) is defined as a strategy such that, if most members of the population adopt it, there is no mutant strategy that can invade the resident population at its equilibrium (Maynard Smith & Price 1973). The possible strategies are pure dwarf, pure normal, or the proportion of each in a mixed strategy.

A three-stage approach is taken to the analysis of ESSs. First, it is supposed that the population consists entirely of pure strategists (model A: Separate Stocks) and the ESS is determined by the numbers of pure

Table 3. Variables and parameters used in the delay-differential equation models

	Symbol	Default value	Description
Variables	D_i		Immature dwarfs
	D_m		Mature dwarfs
	N_j		Juvenile normals in dwarf habitat
	N_p		Normal prerecruits waiting for 'space' in normal habitat
	N_i		Immature normals in normal habitat
	N_m		Mature normals
	Tot_d Tot_n		$= D_i + D_m + N_j + N_p =$ occupants of dwarf habitat $= N_i + N_m =$ occupants of normal habitat
Parameters	T_{dim}	8 years	Age at maturity for dwarfs
	T_{njp}	8 years	Time to dwarf/normal recruitment
	T_{nim}	8 years	Age post-recruitment for maturity as a normal
	G'	10	Recruitment factor

Table 4. Formulation of the delay-differential equations used in the bimodal population models

	Symbol	Separate stocks	Single stock
Recruitment rates	$R_{dei}(t) =$	$r_d D_m \exp(-Tot_d/K_d)$	$(r_d D_m + r_n N_m) P_d \exp(-Tot_d/K_d)$
	$R_{nej}(t) =$	$r_n N_m \exp(-Tot_d/K_d)$	$(r_d D_m + r_n N_m) P_n \exp(-Tot_d/K_d)$
	$R_{dim}(t) =$	$R_{dei}(t - T_{dim}) \exp(-\mu_{di} T_{dim})$	
	$R_{njp}(t) =$	$R_{nej}(t - T_{njp}) \exp(-\mu_{nj} T_{njp})$	
	$R_{npi}(t) =$	$\frac{GN_p}{Tot_d + D_o} \exp(Tot_n/K_n)$	
	$R_{nim}(t) =$	$R_{npi}(t - T_{nim}) \exp(-\mu_{ni} T_{nim})$	
Balance equations	$\frac{dD_i}{dt} =$	$R_{dei}(t) - \mu_{di} D_i - R_{dim}(t)$	
	$\frac{dD_m}{dt} =$	$R_{dim}(t) - \mu_{dm} D_m$	
	$\frac{dN_j}{dt} =$	$R_{nej}(t) - \mu_{nj} N_j - R_{njp}(t)$	
	$\frac{dN_p}{dt} =$	$R_{njp}(t) - \mu_{np} N_p - R_{npi}(t)$	
	$\frac{dN_i}{dt} =$	$R_{npi}(t) - \mu_{ni} N_i - R_{nim}(t)$	
	$\frac{dN_m}{dt} =$	$R_{nim}(t) - \mu_{nm} N_m$	

dwarfs and pure normals when the model is at equilibrium. An evolutionarily stable continuum (ESC) (Hutchings & Myers 1994) is then found by varying the recruitment factor, G . This provides insight into the conditions necessary for both sub-populations to occur.

The second stage (model B: Single Stock) is to note that, at equilibrium, the sub-population numbers are independent of the mechanism by which the alternative life history strategy is determined. That is to say that it is irrelevant whether the ESS consists of a given proportion of pure dwarfs and pure normals or of a population of mixed strategists which 'play' dwarf or normal in the equivalent proportion. This gives the form of the 'weighted coin' which mixed strategists must adopt if they are not to be driven to extinction.

The final stage (model C: Speciation Model) is to combine model A and model B such that pure and

mixed strategists compete within the same environment. By examining the non-equilibrium conditions, it is possible to determine the impact of environmental fluctuation upon the relative success of the different strategies.

The model equations were solved using standard numerical techniques and the software package SOLVER (<http://www.stams.strath.ac.uk/ecodyn>).

Results

EQUILIBRIUM CONDITIONS VS. RECRUITMENT FACTOR, G (MODEL A)

According to the theory of mixed strategies (see above), the same ESS is achieved regardless of whether the individuals are pure strategists (model A), mixed

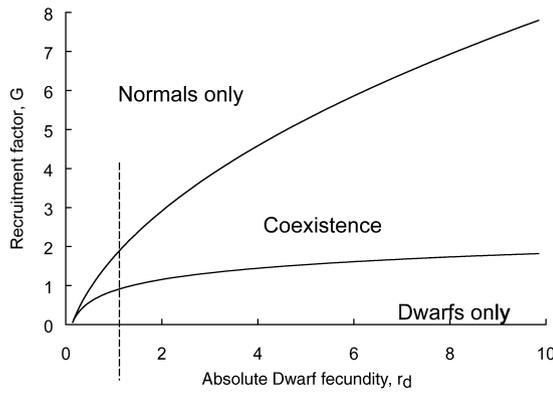


Fig. 3. Result of the analysis showing conditions for existence of dwarfs and normals at equilibrium as environmental conditions change. There are regimes of dwarfs only, coexistence, and normals only as absolute values of fecundity r_d and r_n are varied. The ratio of dwarf to normal fecundity is maintained constant at 1 : 4 to reflect observation (see Appendix I). The vertical line represents the parameters analysed in more detail in Fig. 4.

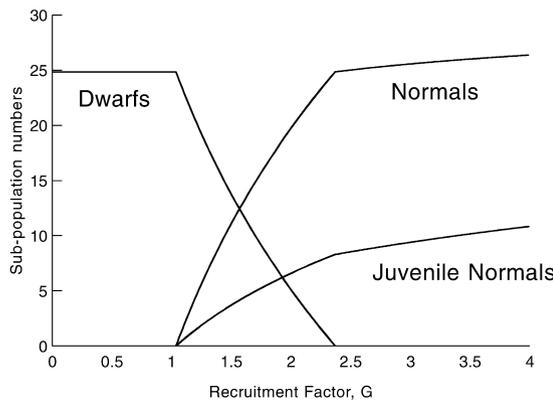


Fig. 4. Actual sub-population equilibria as the recruitment factor, G , is varied while other parameters remain at default values (Table 1). This diagram provides the detail for those parameters marked with the vertical line in Fig. 3.

strategists (model B), or represent some compromise between the two. Mathematically, model A is simpler than model B, and it is thus possible to use model A to conduct an analysis of equilibrium conditions without knowledge of the weighted coin. Figure 3 illustrates the different equilibrium regimes, which are calculated as the absolute value of the fecundity terms, r , and are varied in the observed ratio of 1 : 4 while other parameters remain at default settings (Table 1). Figure 4 shows the actual variation in sub-population numbers through a ‘cross-section’ of Fig. 3 as the recruitment factor, G , is varied. There are regimes of dwarfs only, coexistence, and normals only.

In dwarf/normal systems where seasonal effects are negligible, it was previously argued that large G is associated with high growth rate in H1. If this claim is valid, the figures make three predictions which are consistent with field observations. First, all-dwarf populations are associated with low G and this compares with the slow growth that gives stunted populations their name. Secondly, high G , and hence good growth conditions,

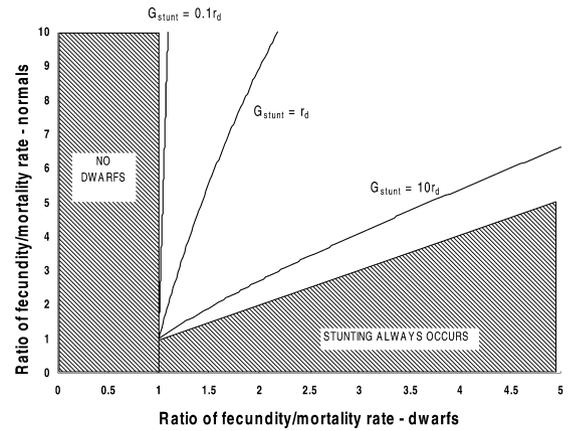


Fig. 5. Conditions for stunting as a function of differences in the ratio of fecundity to mortality rate between dwarfs and normals.

is associated with large numbers of normals. Thirdly, the frequencies which define the mixed strategy ESS equilibrium vary with environmental conditions. This represents the evolutionarily stable continuum (ESC) described by Hutchings & Myers (1994) for alternative mating strategies in Atlantic salmon.

CONDITIONS FOR STUNTING

Transition between model regimes for the separate stocks model occurs at analytically calculable critical values of G . The boundary between the region of parameter space with dwarfs only and coexistence has

$$G_{dc} = \frac{r_d \mu_j \mu_n K_d \ln(r_d / \mu_d)}{r_n \mu_d - r_d \mu_n}$$

The boundary between coexistence and normals only is:

$$G_{cn} = \frac{\mu_n N^*}{\exp(-N^*/K_n)}$$

where

$$N^* = \frac{r_d \mu_j J^*}{r_n \mu_d - r_d \mu_n}$$

and

$$J^* = K_d \ln(r_d / \mu_d)$$

Stunting occurs if the value of G falls below G_{dc} . If the further assumption is made that $\mu_j = \mu_d$, then this boundary can be rewritten as

$$G_{stunt} = \frac{r_d K_d \ln(r_d / \mu_d)}{\frac{r_n}{\mu_n} - \frac{r_d}{\mu_d}}$$

Figure 5 illustrates how G_{stunt} might vary as the ratios of r/μ for the two habitats are varied against each other. From this figure it is apparent that the greater the difference between r/μ , the greater the numbers of normal fish. r_n/μ_n must be greater than r_d/μ_d , and if they ever become equal stunting will always occur.

THE EVOLUTIONARILY STABLE FORM OF THE WEIGHTED COIN (MODEL B)

If it is assumed for the single stock model (model B) that the weighted coin is itself subject to natural selection, an analysis can be made in which individuals adopting different weighted coins compete within the same lake. The ESS will be represented by the individuals which adopt the weighted coin which outcompetes all the other possibilities.

Suppose that the lake is occupied by two competing single stock populations (model B's) in which one consists of dwarfs, juvenile normals, and adult normals labelled D , J and N , while the other is labelled X , Y and Z . By analogy with Table 2, and without presenting all the equations, the situation is illustrated by:

$$\frac{dD}{dt} = P_d(r_d D + r_n N) \exp(-(D + J + X + Y)/K_d) - \mu_d D \quad \text{eqn 1}$$

$$\frac{dX}{dt} = P_x(r_d X + r_n Z) \exp(-(D + J + X + Y)/K_d) - \mu_d X \quad \text{eqn 2}$$

etc. At equilibrium,

$$\frac{dD}{dt} = \frac{dJ}{dt} = \frac{dN}{dt} = \frac{dX}{dt} = \frac{dY}{dt} = \frac{dZ}{dt} = 0$$

Recall that the ESS for the single stock model will be identical to the equilibrium for the separate stocks model. Therefore, we expect the ESS value of the weighted coin to be that value for which the single stock model reaches the same equilibrium as the separate stocks model. From Table 2, we see that this condition implies that

$$P_d = \frac{r_d D^*}{r_d D^* + r_n N^*}$$

and

$$P_n = (1 - P_d) = \frac{r_n N^*}{r_d D^* + r_n N^*}$$

where D^* and N^* are the equilibrium values calculated from the separate stocks model.

Substitution of P_d into eqn 1 and further simple substitutions into the remaining equations give the following cases which can satisfy the six simultaneous differential equations at equilibrium:

Case I: $P_x = \frac{r_d X^*}{r_d X^* + r_n Z^*}$ X, Y, Z identical to D, J, N

Case II: $X^* = Y^* = Z^* = 0$ X, Y, Z extinct.

Case III: $P_x = 1$ and $Y^* = Z^* = 0$ Some pure dwarf strategists can coexist with the mixed strategist.

Case IV: $P_x = 0$ and $X^* = 0$ Some pure normal strategists can coexist with the mixed strategist.

In words, if an individual adopts a mixed strategy, i.e. Case I, then the ESS value of the weighted coin is $P_d = r_d D^*/(r_d D^* + r_n N^*)$. Any other value for the weighted coin leads to extinction of the genotype adopting it (Case II). A further possibility is the

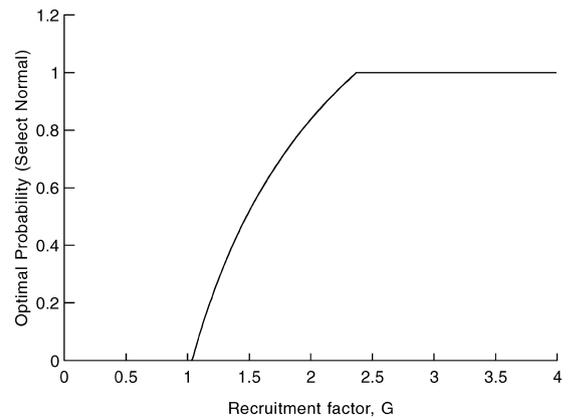


Fig. 6. The evolutionarily stable value of P_n for the single stock model, model B, as a function of the recruitment factor, G .

combination of Case III and Case IV. In this situation, the population will consist of an undefined mixture of dwarf and normal pure strategists in addition to some mixed strategists. In this way, the single stock model (model B) can coexist with the separate stocks model (model A) provided that the model assumptions of a stable environment, equal fecundities, r , and equal death rates, μ , hold. These conclusions are supported by substitution of relevant trial values for the weighted coin into the model.

It was shown previously how the equilibria of model A varied as a function of G . It is thus a simple matter to calculate the ESS value of P_n over all values of G . This calculation is illustrated in Fig. 6. The coin is characterized by a threshold followed by an almost linear rise to complete selection of the normal strategy.

Unfortunately, little work on life history responses to growth stimuli has been reported for Arctic charr, but experiments with smolting in Atlantic salmon provide a good comparison. Thorpe *et al.* (1989) showed that the percentage of smolts at age 1 was correlated with an 'index of growth opportunity' during the July post-hatching. This index is analogous to the recruitment factor, G . The Thorpe *et al.* (1989) data show a threshold growth opportunity necessary before any individuals opt for smolting in year 1. This is followed by an approximately linear relationship between greater probability of smolting and further growth opportunity. Comparison of the results of Thorpe *et al.* (1989) and Fig. 6 reveal that they are similar functions. Thorpe's growth opportunity threshold may therefore be a result of selection due to the low likelihood of immediate success of the smolting strategy at low growth rates.

SPECIATION MODEL (MODEL C)

In order to tackle the unresolved question of the genetic relationships between life history strategies, both the separate stocks and single stock populations are set into competition within the same habitats. This

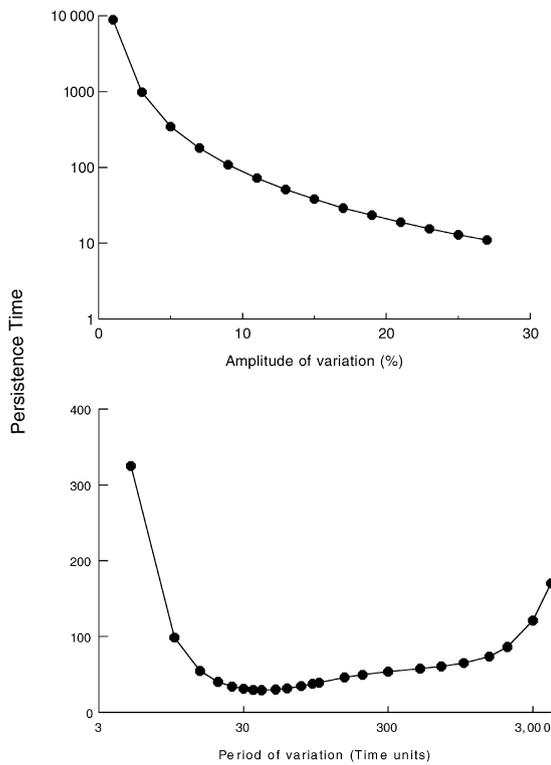


Fig. 7. Persistence times for the separate stocks model (model A) in competition with the single stock model (model B) when subject to sinusoidal fluctuation in the recruitment factor, G . The upper diagram shows persistence as the amplitude of the fluctuations is varied with period fixed at 40 time units. The lower diagram shows persistence as the period is varied with the amplitude set at 10%. Persistence time is defined as the time for both dwarf and normal separate stocks to fall below a fixed low population size. Both diagrams were calculated using default parameters (Table 1).

is best visualized by imagining that Fig 2a and 2b have been combined into one model in order to find which strategy is the ESS (this replicates the process of finding the ESS weighted coin by competing two different mixed strategies). In a static environment, with fecundity and mortality rates equal, both models coexist neutrally.

The imposition of environmental fluctuations onto the population, implemented by driving one or more of the parameters K_d , K_n and G over a range of sinusoidal frequencies, changes the above result. Variation in G illustrates this difference most clearly. In contrast to the steady state, the separate stocks are driven extinct under a wide range of circumstances. Figure 7a and 7b illustrate the persistence times of the separate stocks model in competition with the single stock model assuming both types have the same fecundities. Trial experiments using step changes in K_d , K_n and G were also conducted without affecting the end result of the model runs. This shows that, despite the non-linearities, the response to sinusoidal fluctuations is a fair indication of the model behaviour under the majority of conditions.

Mathematically, the reason for this result is that the response time near equilibrium is much faster for the single stock model than for the separate stocks model.

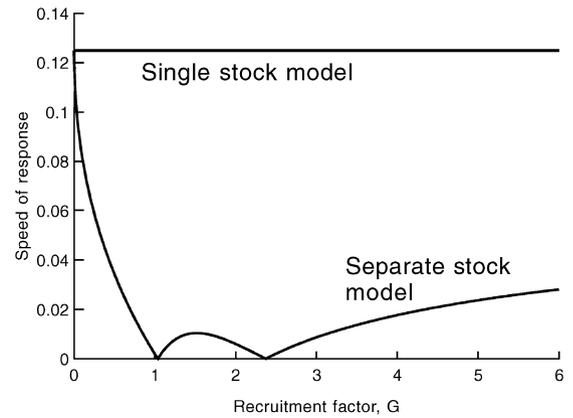


Fig. 8. Speed of response diagram. The y-axis is the negative real part of the dominant eigenvalue of the linearized stability matrix at equilibrium.

Figure 8 shows that if the steady state population is perturbed, the single stock model will return to equilibrium more quickly than the separate stocks model, whatever the value of G . This means that, in a variable environment, the single stock model will always be the ESS even though the value of G is not known.

Biologically, the reason for this result is that, in a fluctuating environment, it is a better strategy for the individual to ‘bet-hedge’ by having some offspring of each type. This is illustrated by the extreme case where, for instance, the dwarfs become extinct. With the single stock present, the dwarf strategy can be resurrected from normal offspring. In the separate stocks case, there is no means for the strategy to be re-established.

INCORPORATION OF DEVELOPMENTAL TIME DELAYS

Analysis of the delay-differential equation model shows that the qualitative results derived from the simpler model remain valid. In particular, for a given set of environmental parameters K_d , K_n and G , both models equilibrate at identical values of dwarfs, juvenile normals and adult normals. Therefore, the conclusions from the equilibrium analysis and the general results about stunting remain valid. Furthermore, the differences in response times are even more apparent in this model. This result indicates that the argument concerning dynamic characteristics is strengthened when developmental delays are taken into consideration. We confirmed that the single stock model drives the separate stocks model to extinction relatively more quickly using sample runs of the delay-differential equation model.

Discussion

GROWTH RATE, RECRUITMENT, AND MATURATION

Conflict between immediate and future reproduction is a critical issue in any study of alternative life history

strategies. In this paper it creates difficulty in interpreting the recruitment factor, G . This is because, in the size-structured population modelled, a high growth rate is required to reach a threshold size but, as a general rule, high growth rate is also associated with early maturation (Alm 1959). Thus both maturation and recruitment are, in some way, related to growth rate.

Alm (1959) was careful to qualify the rule that faster-growing fish mature first as applying only to the same species or form. This shows that he recognized that the presence of alternative life history strategies might disrupt this finding, and there are many examples (some within Alm's paper) of where this qualification is necessary. In the Arctic charr systems of Parker & Johnson (1991), slow growth was associated with relatively early maturity. In a rearing experiment, Svedang (1991) found a significant negative correlation between maturation rate and growth rate in male Arctic charr; a relationship which was also reflected in females but not with statistical significance. Similar evidence is provided by analogy with smolting in Arctic charr (Svenning, Smith-Nilsen & Jobling 1992), Atlantic salmon, *Salmo salar* (e.g. Huntingford *et al.* 1992; Metcalf & Thorpe 1992) and Masu salmon, *Oncorhynchus masou* Brevoort (Hirata, Goto & Yamazaki 1988).

There are also cases, however, where Alm's rule has not been reversed by the presence of alternative life history strategies since many populations of Atlantic salmon (e.g. Hutchings & Myers 1994) exhibit early maturity as parr by young, fast-growing males. We hypothesize that this inconsistency is due largely to seasonal effects. In a strongly seasonal environment, both strategies suffer high mortality as well as low growth during the winter. Seasonality may thereby alter the trade-off between growth rate and survival such that selection favours early reproduction by fast-growing parr. The common feature of all these examples is that the dwarf and normal strategies, or their equivalents in other systems, tend to be optimized at different growth rates. Thus, the concept that the recruitment factor, G , is related to growth rate remains valid but, in the general case, it will depend on local conditions as to whether the correlation is positive or negative.

POPULATION STRUCTURE

Our models predict that a high proportion of normals is associated with high growth rate as a juvenile, and a stunted, or unimodal, population with low growth rate. The predicted weighted coin for determining the life history strategy of an individual is similar to that observed experimentally for smolting in Atlantic salmon (Thorpe *et al.* 1989).

Furthermore, we showed that a difference in the ratio of fecundity to mortality rate (r/μ) between dwarf and normal sub-populations is essential to maintaining bimodal populations. Experimental evidence mainly in other species (e.g. Werner *et al.* 1983; Gilliam & Fraser 1987; but see also Damsgard 1993) suggests

that cannibalism by normals upon dwarfs could have this effect. Specifically, cannibalism, or the threat of cannibalism, could invoke a behavioural response amongst dwarfs which would reduce their growth rate, and provide an alternative food source for normals which would increase their growth rate. Cannibalism would increase the mortality rate of dwarfs, and potentially decrease that of normals. Given that fecundity is closely related to size, growth rate and fecundity are also related. Hence, cannibalism will increase the ratio of r/μ for normals while reducing it for dwarfs.

Although cannibalism is not the only mechanism that can maintain bimodality in populations (Huston & DeAngelis 1987), the findings on population structure discussed above suggest that there are good theoretical reasons for why cannibalism might be suspected in this case. This has been speculated upon previously (e.g. Amundsen 1989), but not on theoretical grounds.

The practical importance of this result, if maintenance of bimodality is considered desirable, is that management practice must be aimed at preserving or increasing the difference in the r/μ ratio. This could be achieved in a number of ways: (a) in a sport fishery, by placing a catch limit on large fish, thereby reducing μ_n ; (b) by reducing the spawning area, thus reducing r_d relative to r_n through size-specific competition for spawning sites; and (c) by selective fishing on small fish, thus increasing μ_d relative to μ_n . Of these means of managing the r/μ ratio (a) is becoming common practice, although probably for unrelated reasons; (b) is speculative in that no case is known in which it has been attempted; and (c) has been conducted in Takvatn, Norway (Amundsen 1989). In this experiment, funnel traps, which select for small fish, were used to remove 13.1 kg/ha of fish from this typical stunted population between 1984 and 1986. A considerable increase in growth rate and number of large charr has been observed since.

POTENTIAL SPECIATION

The speciation model (model C) illustrates that individuals which in all cases adopt the same life history strategy as their parents can be driven to extinction by individuals making the decision facultatively if there is enough environmental variation at adequately high frequency. The long-term result does not appear to be affected by the magnitude of the perturbations, indicating that over evolutionary time only slight fluctuations are adequate to maintain the mixed strategy as the ESS. Without modification to the model, this indicates that there is no selective advantage to speciation.

Considerations of speciation become more revealing, however, if it is supposed that the common gene pool of the single stock model limits the degree of adaptation which can be achieved within each of the habitats, and that reproductive isolation might lead to greater adaptation through specialization to one or other of the habitats. In this case, the single stock model would

represent individuals adopting a generalist strategy, whereas the separate stocks model would represent individuals adopting a specialist strategy.

The increased habitat-specific adaptation associated with specialization can be modelled as a slight increase in r/μ for the specialists relative to the generalists. In the steady state, with no simulation of environmental variation, this assumption leads to total extinction of the generalists. If environmental variation is added, however, there is a situation where the dynamic characteristics of the model (Figs 7 and 8) cancel the tendency in the steady state for specialists to exclude generalists. This leads to the conclusion that a compromise occurs at some point between these two strategies which achieves maximum individual fitness. In this state of 'semispeciation', some adaptive advantage can be achieved as a specialist without totally excluding the ability to 'play' the other strategy, albeit to some small disadvantage, if circumstances require.

The argument that there is some evolutionary advantage to a state of semispeciation presupposed that there is a mechanism available for maintaining it, and a considerable body of theoretical work of a general nature (e.g. Levene 1953; Maynard Smith & Hoekstra 1980; Hoekstra, Bijlsma & Dolman 1985; Hedrick 1986) asks whether genetic polymorphism can be achieved in a random mating population. The results of this work indicate that the conditions for achieving a genetic polymorphism within a random mating population are tight and unlikely to be realized in a charr system without the relaxation of 'habitat selection', whereby offspring utilize the maternal patch type rather than being randomly distributed; or 'mating within a patch', with different degrees of assortative mating (Maynard Smith 1989, p. 75). It can be speculated that both these relaxations occur. Large fish lay larger eggs, which is correlated with faster initial growth (Wallace & Aasjord 1984; Sargent, Taylor & Gross 1987) and more normals, thus achieving habitat selection. Similarly, incomplete assortative mating is a common feature of most salmonid populations (e.g. Jonsson & Hindar 1982).

The results of this analysis have some impact on the 'charr problem' and the two main hypotheses which exist as to potential mechanisms for genetic divergence (Klemetsen & Grotnes 1980). The first of these mechanisms is allopatric speciation via successive reinvasion of the systems from different glacial refugia after the Pleistocene. The second is the mechanism of sympatric speciation, the credibility of which has recently been greatly strengthened by both theoretical work and experiments (e.g. Kondrashov & Mina 1986; Rice & Salt 1990; Rice & Hostert 1993; Bush 1994; Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999).

Here, we have shown that there is an evolutionary significance to 'semispeciation' within a bimodal population. Under stable environmental conditions, there is a selective advantage in habitat specialization, giving a tendency towards speciation. Under unpredictable

environmental conditions, however, the faster recovery time of the single stock model illustrates that an individual would be at a selective disadvantage if speciation had occurred. This same faster response time, however, also allows the equilibrium conditions which favour speciation to be re-established more quickly. There is therefore a link between the genetic structure of the population and the population dynamics which implies that there is a dynamic equilibrium whereby sympatric speciation is arrested before it becomes complete.

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References

- Alm, G. (1959) Connection between maturity, size and age in fishes. *Report of the Institute of Freshwater Research, Drottningholm*, **40**, 5–145.
- Amundsen, P.-A. (1989) Effects of intensive fishing on food consumption and growth of stunted Arctic charr (*Salvelinus alpinus* L.) in Takvatn, Northern Norway. *Biology of Charrs and Masu Salmon* (eds H. Kawanabe, F. Yamazaki & D.L.G. Noakes), pp. 265–278. Kyoto University, Japan.
- Bush, G.L. (1994) Sympatric speciation in animals: new wine in old bottles. *Trends in Ecology and Evolution*, **9**, 285–286.
- Damsgard, B. (1993) *Biomaniipulation with piscivorous fish. An experimental study of prey selection, food consumption and growth of piscivorous brown trout, Salmo trutta (L.), and Arctic charr, Salvelinus alpinus (L.)*. PhD Thesis, Norwegian College of Fishery Science, University of Tromsø, Tromsø.
- Danzmann, R.G., Ferguson, M.M., Skulason, S.S. & Noakes, D.L.G. (1991) Mitochondrial DNA diversity among four sympatric morphs of Arctic charr, *Salvelinus alpinus* L., from Thingvallavatn, Iceland. *Journal of Fish Biology*, **39**, 649–659.
- Dieckmann, U. & Doebeli, M. (1999) On the origin of species by sympatric speciation. *Nature*, **400**, 354–357.
- Forseth, T., Ugedal, O. & Jonsson, B. (1994) The energy budget, niche shift, reproduction and growth in a population of Arctic charr, *Salvelinus alpinus*. *Journal of Animal Ecology*, **63**, 116–126.
- Gilliam, J.F. & Fraser, D.F. (1987) Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, **68**, 1856–1862.
- Gross, M.R. (1984) Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. *Fish Reproduction: strategies and tactics* (eds G.W. Potts & R.J. Wootton), pp. 55–75. Academic Press, London.
- Hartley, S.E., McGowan, C., Greer, R.B. & Walker, A.F. (1992) The genetics of sympatric Arctic charr [*Salvelinus alpinus*

- (L.)] populations from Loch Rannoch, Scotland. *Journal of Fish Biology*, **41**, 1021–1031.
- Hedrick, P.W. (1986) Genetic polymorphism in heterogeneous environments: a decade later. *Annual Review of Ecology and Systematics*, **17**, 535–566.
- Hindar, K., Ryman, N. & Stahl, G. (1986) Genetic differentiation among local populations and morphotypes of Arctic charr, *Salvelinus alpinus*. *Biological Journal of the Linnean Society*, **27**, 269–285.
- Hirata, T., Goto, A. & Yamazaki, F. (1988) Individual growth and smoltification of juvenile masu salmon, *Oncorhynchus masou* Brevoort, under rearing conditions. *Journal of Fish Biology*, **32**, 77–84.
- Hoekstra, R.F., Bijlsma, R. & Dolman, A.J. (1985) Polymorphism from environmental heterogeneity: models are only robust if the heterozygote is close in fitness to the favoured homozygote in each environment. *Genetic Research*, **45**, 299–314.
- Huntingford, F.A., Thorpe, J.E., de Garcia Leaniz, C. & Hay, D.W. (1992) Patterns of growth and smolting in autumn migrants from a Scottish population of Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology Supplement B*, **41**, 43–51.
- Huston, M.A. & DeAngelis, D.L. (1987) Size bimodality in monospecific populations: a critical review of potential mechanisms. *American Naturalist*, **129**, 678–707.
- Hutchings, J.A. & Myers, R.A. (1994) The evolution of alternative mating strategies in variable environments. *Evolutionary Ecology*, **8**, 256–268.
- Johnson, L. (1976) The ecology of Arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic charr, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. *Journal of the Fisheries Research Board of Canada*, **33**, 2459–2488.
- Jonsson, B. & Hindar, K. (1982) Reproductive strategy of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, Western Norway. *Canadian Journal of Fisheries and Aquatic Science*, **39**, 1404–1413.
- Kaplan, R.H. & Cooper, W.S. (1984) The evolution of developmental plasticity in reproductive characteristics: an application of the ‘adaptive coin-flipping’ principle. *American Naturalist*, **123**, 393–410.
- Klemetsen, A., Amundsen, P.-A., Muledal, H., Rubach, S. & Solbakken, J.I. (1989) Habitat shifts in a dense resident Arctic charr, *Salvelinus alpinus*, population. *Biology of Charrs and Masu Salmon* (eds H. Kawanabe, F. Yamazaki & D.L.G. Noakes), pp. 187–200. Kyoto University, Japan.
- Klemetsen, A. & Grotnes, P. (1980) Coexistence and immigration of two sympatric Arctic charr. *Charrs: salmonid fishes of the genus Salvelinus* (ed. E.K. Balon), pp. 757–763. Dr W. Junk, The Hague.
- Kondrashov, A.S. & Kondrashov, F.A. (1999) Interactions among quantitative traits in the course of sympatric speciation. *Nature*, **400**, 351–354.
- Kondrashov, A.S. & Mina, M.V. (1986) Sympatric speciation: when is it possible? *Biological Journal of the Linnean Society*, **27**, 201–223.
- Levene, H. (1953) Genetic equilibrium when more than one ecological niche is available. *American Naturalist*, **87**, 331–333.
- Maynard Smith, J. (1989) *Evolutionary Genetics*. Oxford University Press, New York.
- Maynard Smith, J. & Hoekstra, R. (1980) Polymorphism in a varied environment: how robust are the models? *Genetic Research*, **35**, 45–57.
- Maynard Smith, J. & Price, G.R. (1973) The logic of animal conflict. *Nature*, **246**, 15–18.
- Metcalf, N.B. & Thorpe, J.E. (1992) Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology Supplement B*, **41**, 93–99.
- Nisbet, R.M. (1997) Delay-differential equations for structured populations. *Structured-Population Models in Marine, Terrestrial, and Freshwater Systems* (eds S. Tuljapurkar & H. Caswell), pp. 89–118. Chapman & Hall, New York.
- Nordeng, H. (1983) Solution to the ‘Char Problem’ based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Science*, **40**, 1372–1387.
- Nordeng, H., Bratland, P. & Skurdal, J. (1989) Patterns of smolt transformation in the resident fraction of anadromous Arctic charr *Salvelinus alpinus*; genetic and environmental influence. *Biology of Charrs and Masu Salmon* (eds H. Kawanabe, F. Yamazaki & D.L.G. Noakes), pp. 483–488. Kyoto University, Japan.
- Parker, H.H. (1995) *Population ecology of landlocked Arctic charr, Salvelinus alpinus L., in the Canadian High Arctic*. PhD Thesis, Open University.
- Parker, H.H. (1997) Growth or reproduction: the life history gamble of landlocked Arctic charr. *Fish Ecology in Arctic North America* (ed. J. Reynolds), pp. 214–223. American Fisheries Society Symposium 19, Bethesda, Maryland.
- Parker, H.H. & Johnson, L. (1991) Population structure, ecological segregation and reproduction in non-anadromous Arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in the Canadian high Arctic. *Journal of Fish Biology*, **38**, 123–147.
- Rice, W.R. & Hostert, E.E. (1993) Laboratory experiments on speciation: what have we learned in 40 years? *Evolution*, **47**, 1637–1653.
- Rice, W.R. & Salt, G.W. (1990) The evolution of reproductive isolation as a correlated character under sympatric conditions: experimental evidence. *Evolution*, **44**, 1140–1152.
- Sargent, R.C., Taylor, P.D. & Gross, M.R. (1987) Parental care and the evolution of egg size in fishes. *American Naturalist*, **129**, 32–46.
- Skulason, S., Snorrason, S.S., Noakes, D.L.G. & Ferguson, M.M. (1996) Genetic basis of life history variations among sympatric morphs of the Arctic charr, *Salvelinus alpinus*. *Canadian Journal of Fisheries and Aquatic Science*, **53**, 1807–1813.
- Skulason, S., Snorrason, S.S., Ota, D. & Noakes, D.L.G. (1993) Genetically based differences in foraging behaviour among sympatric morphs of Arctic charr (Pisces: Salmonidae). *Animal Behaviour*, **45**, 1179–1192.
- Snorrason, S.S., Skulason, S., Sandlund, O.T., Malmquist, H.J., Jonsson, B. & Jonasson, P.M. (1989) Shape polymorphism in Arctic charr, *Salvelinus alpinus*, in Thingvallavatn, Iceland. *Biology of Charrs and Masu Salmon* (eds H. Kawanabe, F. Yamazaki & D.L.G. Noakes), pp. 393–404. Kyoto University, Japan.
- Stearns, S.C. & Crandall, R.E. (1984) Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. *Fish Reproduction: strategies and tactics* (eds G.W. Potts & R.J. Wootton), pp. 13–33. Academic Press, London.
- Svedang, H. (1991) Effects of food quality on maturation rate in Arctic charr, *Salvelinus alpinus* L. *Journal of Fish Biology*, **39**, 495–505.
- Svenning, M.-A., Smith-Nilsen, A. & Jobling, M. (1992) Sea water migration of Arctic charr (*Salvelinus alpinus* L.) – correlation between freshwater growth and seaward migration, based on back-calculation from otoliths. *Nordic Journal of Freshwater Research*, **67**, 18–26.
- Thorpe, J.E., Adams, C.E., Miles, M.S. & Keay, D.S. (1989) Some influences of photoperiod and temperature on opportunity for growth in juvenile Atlantic salmon, *Salmo salar* L. *Aquaculture*, **82**, 119–126.
- Wallace, J.C. & Aasjord, D. (1984) An investigation of the consequences of egg size for the culture of Arctic charr,

Salvelinus alpinus (L.). *Journal of Fish Biology*, **24**, 427–435.

Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, **15**, 393–425.

Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.

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Appendix I: default parameter values

The following rough values are taken from unpublished data for Lake C, Borup Fjord 81°N (Parker & Johnson 1991). Dwarfs typically spawn at age 8 years and weigh 40 g, whereas the respective values for normals are 16 years and 160 g. Recruitment from dwarf to normal occurs at 8 years. For both types, energy invested in reproduction is approximately proportional to weight.

Assuming that age and size at maturity are optimal, the time to maturity (8 years for both strategies) is related to the mortality rate experienced in the dwarf habitat. A very crude calculation of fitness optimization assumes a constant mortality regime (μ), linear growth rate (g), semelparity, and energy invested in reproduction related to body size by some constant c . From these assumptions,

$$\text{size} = gT$$

and

$$\text{energy invested in reproduction} = cgT$$

where T is the age at maturity.

If fitness is measured as the lifetime reproductive output, R_o , then, for a semelparous organism,

$$R_o = cgT \exp(-\mu T)$$

This will be maximized with respect to age at maturity when

$$\frac{dR_o}{dt} = 0,$$

i.e.

$$\mu = 1/T$$

Given the value of T is 8 years, $\mu = 1/8 = 0.125 \text{ years}^{-1}$.

The ratio of dwarf to normal fecundity is 1 : 4. For the delay-differential equation model, we used $r_d = 10$ and $r_n = 40$. For the simpler model, the fecundities were scaled relative to the delayed models to ensure that similar equilibrium values were achieved. Given μ_d as found above, D^* as an output from the DDE model, and K_d (Table 1), this gives a value of r_d which is approximately 1.5, and $r_n = 6$ preserves the ratio observed in the field. The biological interpretation of this scaling is that, during the time prior to maturity, each individual is subject to a mortality risk as an immature. Immatures are not modelled in the simpler model, and this scaling constitutes an approximation to the cumulative mortality experienced during the juvenile stage.