Evolutionary stable migration in salmon: a simulation study of homing and straying

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The evolutionary stable homing and straying of migratory salmon populations are studied in this paper. Homing behaviour is a well-known character in the life history of many migratory fish. After emerging as fry Pacific salmon spend one to three years in fresh water and then migrate out to sea. After spending several years migrating in the sea the adults return to spawn in their natal rivers. The few available estimates e.g. in sockeye salmon populations show that straying, i.e., spawning in non-natal rivers, also occurs. It has been proposed that the fraction of straying increases as the river-lake systems where the fish reproduce and where the young fish spend their first years become more uncertain. In this paper I develop a simulation model to study the evolutionary stable homing and straying strategies of migratory salmon populations. Special reference is made to the problem of how uncertainties in reproduction affect homing and straying in salmon. I also discuss the relationship between evolutionary risk spreading and evolutionary stable strategies.

1. Introduction

Homing is a well-known character of the life history of many migratory fish, in particular in salmon. Pacific and Atlantic salmon spend one to three years in fresh water and then migrate out to sea. After migrating and feeding for several years in the sea the mature salmon return to spawn in their natal rivers. The few available estimates of homing and straying e.g. in sockeye salmon populations show that straying, i.e., spawning in a non-natal river, also occurs.

Quinn (1984, 1985) proposed that homing and straying are alternative reproductive or life-his-tory strategies which are "in dynamic balance" defining the proportions of homing and straying salmon in the population. The balance, which is under direct or indirect genetic control, is related to habitat instability. In particular, the strategies depend on the temporal heterogeneity of the river-lake systems where the fish reproduce and where the young fish spend their first years. Hence, salmon populations spawning in large, temporally stable rivers should have higher homing rates than those spawning in smaller, temporally uncertain rivers.

There exist differences in the homing rates among the Pacific salmon species and popula-

tions, and in some salmon the straying rate is considerable (for reviews of the evidence of homing and straying in Pacific salmon, see Quinn (1984, 1985), McIsaac & Quinn (1988), and in Atlantic salmon, see e.g. Folke (1986), Hegberget et al. (1988). In a study in Babine Lake, British Columbia (McCart, 1970, reviewed by Quinn, 1984), mature sockeye salmon (*Oncorhynchus nerka*) were taken from spawning areas in a large stable river or in small unstable rivers and released off the mouths of the streams. All (100%) of the salmon from a large stable river were recaptured in that river and 87% of the salmon from unstable streams were recaptured on the spawning grounds of those streams.

The homing rates of chinook salmon (*O. tshawytscha*) and coho salmon (*O. kisutch*) also vary between populations. In a study in the Cowlitz River 98.6% of marked chinook salmon were recovered in that river (Quinn 1984). Snyder (1931) and Sholes & Hallock (1979) observed, however, higher straying rates for chinook salmon in California (13% and 10%, respectively). Similar differences are also found in coho salmon; Donaldson & Allen (1958) observed in a transplantation experiment that coho salmon returned almost exclusively to the release sites. Shapavalov & Taft (1954) reported lower homing rates (85% and 73%) in wild coho salmon (referred to as "silver salmon") in two adjacent, small, unstable, coastal streams in California.

In this paper I develop a simulation model to characterize evolutionary stable homing behaviour in salmon. My purpose is not to present an accurate model for any river system where salmon spawn. Nor do I intend to seek a single homing and straying strategy related to a particular environment. I show by using a fairly simple stochastic discrete time simulation model that straying can be a part of an evolutionary stable migration strategy in salmon. I also study the ways in which different uncertainty patterns affect the evolutionary stable homing rates.

The paper is organized as follows. In section 2 the model for studying evolutionary stable homing behaviour of salmon is developed. In section 3 evolutionary stable strategies of animals reproducing in uncertain environments are defined and discussed. In section 4 comparative numerical simulation studies are presented.

2. A model of homing

The model of migration and homing of salmon in a heterogeneous environment is based on studies of the life history of the coho salmon *O. kisutch* (Shapavalov & Taft 1954). The life history of the coho salmon *O. kisutch* is relatively simple, and thus, provides a suitable reference for the problem formulation. The life history of the coho salmon *O. kisutch* can be shortly characterized as follows (Shapavalov & Taft 1954):

1) all the adults die after spawning;
2) all the juveniles migrate to the sea during their second year and reach sexual maturity there;
3) all the adults return to spawn either in their second or third year.

For simplicity, I assume here that the age J at which the fish mature is fixed. This assumption is a strong one: it makes each age class genetically independent of the others, and hence, the stocks spawning in adjacent rivers can be more genetically correlated than the age classes in one river. I do not include, however, genetics in the model studied in this paper.

Next I present an approach characterizing the homing behaviour of salmon. Then I go on to show that under the assumptions given in this paper the problem of homing can be reformulated from the point of view of one natal river only.

Consider a two-river system. Assume that reproduction in one river is much more successful than in the other, that is, the same number of spawners produce on average more offspring in one river than in the other. Thus, we consider a case in which the two rivers are of different sizes — one is large and the other small. The general pattern of the migration behaviour of salmon is illustrated in Fig. 1.

For each individual one of the rivers constitutes his or her natal river. The following assumption is crucial for the results obtained in this paper: the mature salmon are identical such that the expected reproductive success of any individual in any river is independent of the natal river.

A natural way to characterize the homing behaviour of migrating salmon is to define homing as the probability of a mature salmon choosing his or her natal river for spawning. Straying then means that salmon spawn in a river other than the
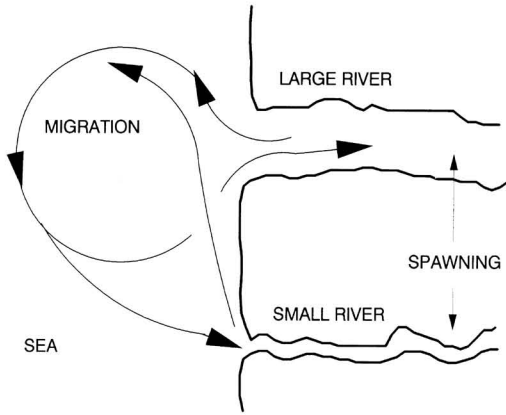
Fig. 1. An illustrative description of a migration-reproduction cycle in salmon. The salmon are born in either of the two rivers. They mature during migration in the sea and then return to the rivers for spawning.

natal river. In this approach the strategy is defined as the probability of an individual homing back to its natal river. Then, the strategy could be a function of the river, in which case the problem quickly becomes very complicated due to the increased number of strategies. In a two-river system there would be two strategies, say p_L and p_S, for the larger and the smaller river, respectively.

In this paper I choose, however, a slightly different approach for studying the homing behaviour of salmon. Since we assume that there are no differences between the mature individuals choosing a river for spawning, the "decision problem" is the same for each individual at this stage of the life cycle of returning back from the sea to the spawning habitats. Hence, I assume that individuals with different natal rivers behave in a similar way: the homing strategy p_L (for individuals born in the large river) corresponds to the homing strategy $1 - p_S$ (for individuals born in the small river). For example, if $p_L = 0.7$ is an evolutionary stable strategy for individuals born in the large river then $p_S = 0.3$ is the corresponding evolutionary stable strategy for individuals born in the small river.

Henceforth I refer to the large river as the "home river" and *consider the homing strategy*

from the point of view of the individuals born in that river. The *homing strategy* is defined here as the probability of any mature salmon born in the large "home river" choosing that river for spawning. Straying means that salmon born in the "home river" spawn in the small "stray river". Hence, the proportion $(1 - \gamma)$ of the individuals born in the "home river" strays, that is, these fish spawn in the "stray river". It should be kept in mind that I consider the problem of homing from the point of view of the individuals born in the large "home river" under the following assumption: if individuals born in the large "home river" use strategy γ then the individuals born in the small river use strategy $1 - \gamma$. Note also that strategy γ in the definition of homing is identical with strategy p_L discussed above.

I assume that populations using different strategies are non-interbreeding. This assumption has been so far, a standard in the literature dealing with evolutionary stable strategies (see, e.g. Hastings 1983, Brown & Vincent 1987). The different populations interact with each other through the density dependence of the reproductive dynamics (cf. equations (2.1) – (2.5)). Genetic interaction between the different strategies is, however, omitted.

When dealing with evolutionary stable strategies one needs to consider two different strategies, say γ_1 and γ_2 at a time, where the subscripts 1 and 2 are used to denote individuals using resident strategy and mutant strategy, respectively. Further, let k denote a time index and let j denote an age index. Let $N_1(k,j)$ and $N_2(k,j)$ denote the sizes of the age class j at time k of the salmon populations using resident and mutant strategies 1 and 2, respectively. The mortality parameter M_i, $i = 1,2$, is assumed to depend on age only. Since salmon spend time, at least partially, in different (river and sea) habitats at different ages, the age dependent mortality can be used to describe the mortalities in different environments. The model could be easily extended to include the cases where the mortality depends on the strategy or on the natal river. Density-independent survival of an age cohort is given by

$$N_i(k + 1, \ j + 1) = N_i(k, j) \ e^{-M_i} \ , \quad (2.1)$$

where $i = 1,2$, $k = 0, \dots$, and $j = 0, \dots, J$.

Salmon that mature during year k spawn during that year. Let subscript H denote the "home river" and subscript S the "stray river", that is, the river entered by straying salmon. Then the reproductive success in each river can be modelled as

$$N_{ir}(k,0) = S_{ir}(k)Y_r(S_r(k),\theta_{rk}),\quad (2.2)$$

where $i = 1,2, r = H, S$, and where $N_{ir}(k,0)$ denotes the offspring of type i produced in river r, $S_{ir}(k)$ denotes the parent stock of type i reproducing in river r, and $S_{r(k)}$ is the total parent stock in river r, $r = H,S$. The parent stocks are given for the home river as

$$S_H(k) = \gamma_1 N_1(k,J) + \gamma_2 N_2(k,J).\quad (2.3)$$

and for the stray river as

$$S_S(k) = (1-\gamma_1)N_1(k,J) + (1-\gamma_2)N_2(k,J).$$
$$(2.4)$$

Assuming a Ricker stock recruitment relationship (Ricker, 1954) the per capita stock recruitment relation is given by

$$Y_r(S_r(k),\theta_{r,k}) = \theta_{r,k}e^{\alpha_r - \beta_r S_r(k)},\quad (2.5)$$

where $r = H,S$, and α_i and β_i are constant parameters and $\theta_{r,k}$ is a stochastic parameter to be defined next.

Let the stochastic parameter $\theta_{r,k}$ describe the environmental fluctuations in year k in the river r, $r = H,S$. The environmental fluctuation $(\theta_{r,k})_{k=0}^{\infty}$ is assumed to be an independent and identically distributed (i.i.d.) random variable. I also assume that the parameters θ_H and θ_S are independent of the population densities $N_i(k,j)$ for any k and j.

In the simulation examples I will study the following basic patterns of uncertainty:

1) permanent rivers with no uncertainty,
2) the large river is permanent and the small river is uncertain,
3) the large river is uncertain and the small river is permanent, and
4) both rivers are uncertain such that the fluctuations in them are independent.

The common case of correlated uncertainties is beyond the scope of this paper. An analysis of a river system in which the uncertainties correlate may yield, however, new insight, at least if local adaptation is included in the model.

3. ESS homing strategies

An evolutionary stable strategy is a strategy that protects the population against invasion from any other rare population using a different strategy (ESS — see Maynard Smith, 1976). An ESS homing strategy has the property that when it is common no other mutant strategy can increase.

The approach to the problem of deriving conditions for an ESS strategy follows Ellner (1985a, b). Consider model (2.1) – (2.5) and assume first that only one strategy is present in the population. Two population growth patterns can be observed under fluctuating conditions. First, the population can become extinct. Second, the population fluctuates between an upper and a non-zero lower limit. The latter implies that the population does not become extinct.

In order to be able to develop a definition for an ESS one needs to gain insight into the dynamics of a strategy when the population is rare. Consider next the expected value of the per capita growth rate for the population using strategy γ. Define now the expected value of the logarithm of the per capita growth rate for the population using strategy γ as (Ellner's 1985 a,b, see also Karlin & Lieberman 1975)

$$v(\gamma) = \lim_{n \to \infty} \frac{1}{n} \sum_{l=1}^{n} \ln(\gamma Y_h(0,\theta_{Hl}) + (1-\gamma)Y_S(0,\theta_{Sl})),\quad (3.1)$$

where γ is the homing strategy applied by the population, and l is an index sampling stochastic environmental conditions during reproduction. It should be noted that (3.1) does not include dynamics between generations, that is, (2.1) – (2.5) are not utilized here. Equation (3.1) describes the expected reproductive success of the strategy when rare and no other strategies are present. Insight into the reproductive success can be obtained by

considering the sign of the quantity $v(\gamma)$: if $v(\gamma) < 0$ then the strategy γ will ultimately become extinct. If $v(\gamma) > 0$, then the population level can converge to a stationary distribution (a distribution which is independent of time and the initial conditions). In that case the strategy is said to be *viable*.

Next I return to consider the general model (2.1) – (2.5) and discuss the seeking of evolutionary stable homing strategies. The approach is based on the notion of a stochastic process converging to a unique stationary distribution (Ellner 1985 a,b).

Let γ_1 and γ_2 denote the resident and mutant strategies, and let $N_1(\cdot,J)$ and $N_2(\cdot,J)$ respectively denote the parent stock sizes of resident and invading populations.

Assume that the resident strategy is in its stationary distribution and consider the expected growth rate of the invading population, when it is rare. One first computes the stationary distribution for the resident population size of strategy γ_1. This can be done by simulating the population dynamics system (2.1) – (2.5) over a sufficiently long time period by assuming that the invading strategy is absent. Let $\tilde{N}_1(k,J)$ denote the stationary distribution of the parent stock size of the resident strategy.

Consider next the expected growth rate of the invading population. When the invading strategy is rare the contribution of this to the total density is neglected. However, the density of the resident parent stock size affects the growth rate of the mutant strategy. I model this assuming that only the resident parent stock size affects the density dependent stock-recruitment process. Then the model becomes

$$N_2(k + J, J) = \pi_{j=1}^{J} e^{-M_j} N_2(k,0) \quad (3.2)$$

$$N_2(k,0) = N_2(k,J)[\gamma_2 Y_{2H} (\gamma_1 \tilde{N}_1(k,J), \theta_{Hk})$$
$$+ (1-\gamma_2) Y_{2S} ((1-\gamma_1)\tilde{N}_1(k,J), \theta_{Sk})], \quad (3.3)$$

where Y_{2H} and Y_{2S} denote the per capita growth functions of the invading strategy in the two rivers H and S, and $\tilde{N}_1(k,J)$ denotes the resident strategy

in its stationary distribution. The mean logarithmic growth rate of the invading strategy is

$$\rho(\gamma_1\gamma_2) = \lim_{n \to \infty} \frac{1}{n} \sum_{l=1}^{n} \ln\{(\pi_{j=1}^{J} e^{-M_j})$$
$$\times [\gamma_2 Y_{2H} (\gamma_1 \tilde{N}_1(l,J), \theta_{Hl})$$
$$+ (1-\gamma_2) Y_{2S} ((1-\gamma_1)\tilde{N}_1(l,J), \theta_{Sl})]\}. \quad (3.4)$$

If the mean logarithmic growth rate of some invading strategy is positive, then the resident strategy is not able to resist the invasion of the mutant strategy in the long run, that is, the resident strategy is not an evolutionary stable strategy. On the other hand, if the resident strategy is evolutionary stable, the mean logarithmic growth rate of any invading strategy is negative.

In the search for an ESS I follow Kaitala et al. (1989). First, consider only viable strategies, i.e. strategies for which $v(\gamma) > 0$, are considered. Secondly, a candidate ESS strategy for the resident population is selected. Thirdly, simulations are carried out such that the stationary distribution for the resident strategy is generated. Fourthly, the mean logarithmic growth rate of all candidates for the invading strategy are calculated using (3.4). If the candidate ESS strategy cannot resist the invasion of one or more of the mutant strategies, then another candidate for the ESS strategy is selected. The only numerical method capable of locating all the ESS solutions is a search through all the different values of γ.

4. Comparative simulation studies

4.1. Parameter values

The following parameter values were used in simulation studies. The salmon mature at age $J = 2$. The zero mortality rate does not affect the qualitative results of the study, and thus I choose $M_1 = M_2 = 0.0$. The difference between the home river and the stray river can be seen in the recruitment functions. I assume that for each population density each individual is able to produce under constant environmental conditions considerably more offspring in the home river than it is able to

produce in the non-home river. Thus, I choose α_H = 1.0, α_S = 0.1, and $\beta_H = \beta_S = 0.03$. The expected values θ_H and θ_S are equal to one, and when θ_H and θ_S are uncertain, their values are uniformly distributed on [0,2].

4.2. Constant environment

In this subsection I shall consider the deterministic version of the model $(2.1) - (2.5)$, where all the fluctuations are replaced by their expected values $(\theta_H = 1, \theta_S = 1)$. In deterministic cases, the stationary distribution of a single strategy model usually reduces to an equilibrium state. Hence, when I study the problem in which a mutant strategy attempts to invade the population, I assume that the population size of the resident strategy is at a unique equilibrium level.

It appears that the strategy which maintains an equilibrium population level is an ESS in a constant environment. This strategy is solved as follows. Consider the case in which only the resident population is present. Let N denote the number of females maturing annually at the equilibrium. Then γN females spawn in the home river and the number $(1 - \gamma) N$ females spawn in the stray river. Now using $(2.1) - (2.5)$ we obtain the following conditions for the equilibrium

$$\gamma N = e^{-(M_1+M_2)} \gamma N e^{\alpha_H - \beta_H \gamma N} \qquad (4.1)$$

and

$$(1 - \gamma) N = e^{-(M_1+M_2)} (1 - \gamma) N e^{\alpha_S - \beta_S (1-\gamma)N} \qquad (4.2)$$

and

$$1 = e^{-(M_1+M_2) + \alpha_H - \beta_H \gamma N} \qquad (4.3)$$

and

$$1 = e^{-(M_1+M_2) + \alpha_S - \beta_S (1-\gamma)N} \qquad (4.4)$$

Thus, the equilibrium conditions can be expressed as

$$\beta_H \gamma N = -(M_1 + M_2) + \alpha_H \qquad (4.5)$$

and

$$\beta_S (1 - \gamma) N = -(M_1 + M_2) + \alpha_S . \qquad (4.6)$$

The evolutionary stable strategy can be solved from equations (4.5) and (4.6) and is given by

$$\gamma = \frac{\beta_S (\alpha_H - M_1 - M_2)}{\beta_S (\alpha_H - M_1 - M_2) + \beta_H (\alpha_S - M_1 - M_2)} \qquad (4.7)$$

The ESS strategy is characterized by the property that each reproducing individual is replaced by one offspring at the equilibrium in each of the environments (see eqs. (4.3) and (4.4)). In the special case of no mortality and with $\beta_H = \beta_S$ the evolutionary stable strategy is

$$\gamma = \frac{\alpha_H}{\alpha_H + \alpha_S} \qquad (4.8)$$

which in the example is $\gamma = 0.91$.

The equilibrium can be maintained in two different ways. The first alternative is that the offspring return to their natal river. This behaviour contradicts, however, with the original problem setting, and hence, it is assumed that the probability that an offspring returns to its home river is defined by the strategy γ.

The analysis of the deterministic model is a special case of a model studied by Alain Hastings (1983). Hastings studied a spatially variable environment consisting of a number of patches, but with no temporal variation. He showed that the zero net dispersal situation is the only evolutionary stable dispersal strategy. This corresponds to the assumption that at equilibrium the number of salmon reproducing in a particular river is equal to the number of salmon that the river is able to contribute to the total population. Both Hasting's result and my interpretation are equivalent to stating that the evolutionary stable strategy corresponds to migration between habitats being in balance, i.e., emigration equals immigration.

The evolutionary stable strategy ($\gamma = 0.91$) does not maximize the total population size in a deterministic habitat system (Hastings, 1983). The strategy that maximizes the total population sizes at the equilibrium is $\gamma = 0.58$. In general the ESS maximizes the average per capita reproduction rate in both habitats (Hastings, 1983).
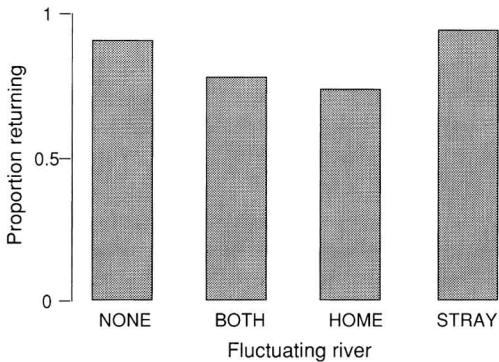
Fig. 2. The ESS homing strategy γ for salmon born in the larger river H under different uncertainty patterns. The ESS homing strategy for salmon born in the smaller river S is $1 - \gamma$ (see section 2). (NONE = no fluctuations; BOTH = both rivers fluctuate; HOME RIVER = "home river" fluctuates and "stray river" is constant; STRAY RIVER = "stray river" fluctuates and "home river" is constant).

The results dealing with reproduction in a stable (constant) river system do not characterize homing rates during the time when the population is not in equilibrium. In an uncertain environment no equilibrium level exists, as population parameters vary with changes in environmental conditions (e.g. the value of θ_H and θ_S fluctuate in (2.5)).

4.3. A fluctuating environment

Consider next the case in which the conditions for reproduction in the two rivers fluctuate independently. I assume that the uncertainty parameters θ_H and θ_S are either constant, or one or both rivers fluctuate such that they have a uniform distribution with mean value equal to 1.0. The computations of ESS strategies represent averages of three independent results iterated over 5000 generations.

When there is variation in both rivers, then the evolutionary stable homing fraction is smaller than in the constant environment (see Fig. 2). Further insight is obtained by letting only one of the rivers vary at a time. If the home river fluctuates, then the fraction of mature salmon entering it decreases compared to the constant environment. Conversely, if the stray river fluctuates,

then the fraction of mature salmon entering the home river increases. Hence, the offspring of a female undergoing the evolutionary stable spawning migration tend to avoid fluctuating rivers. These results are in good agreement with the results obtained by Kaitala et al. 1989.

The above result of avoiding fluctuating rivers does not mean, however, that the animals act so as to minimize the variance in the population size as predicted by the theory of risk spreading (see, e.g., Seger & Brockmann (1987)). This point is illustrated by the following example. Consider a population that originally spawns in a stable home river, but a fraction of the mature siblings has the opportunity to migrate into a less stable, unpredictably fluctuating river. Simulation studies show that any strategy in which a proportion of siblings migrate for spawning into the small uncertain river will take over rapidly in the population if the strategy competes with the strategy in which *all* the offspring return to the stable home river. One of these strategies including straying is the ESS homing strategy (Fig. 2). This is the case despite the fact that distributing the reproductive effort between two different habitats also increases the variance in the number of the offspring and in the population size. The theory of risk spreading predicts that animals should behave in a manner that minimizes the variance in the population level or in the number of offspring. This prediction is not supported by the above result characterizing the ESS spawning migration (for a more detailed discussion of risk spreading and ESS, see Kaitala et al. 1989).

5. Conclusions

In this paper I have studied in this paper evolutionary stable homing and straying strategies in migratory salmon stocks. The emphasis in the approach presented here lies on developing conceptual and mathematical tools for tackling problems of evolutionary stable strategies for animals utilizing patchy and unpredictably fluctuating habitats.

The ESS model developed in this paper shows that between-river straying should occur to some extent during the spawning migration whenever there exist chances for reproduction in the non-

natal rivers. The smaller the relative size of a river, the smaller the proportion of mature salmon which should home during the spawning migration. An increased uncertainty in reproduction also decreases the proportion of homing salmon.

The results of this paper have been derived from the model which does not take into account the possible role of genetic heterogeneity in the population (see e.g. Getz & Kaitala 1989 and the references therein). A theory capable of dealing with genetic dynamics in the context of evolutionary stable strategies is a challenge for future work.

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