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INVESTIGATING EVOLUTIONARY TRADE-OFFS IN WILD POPULATIONS OF ATLANTIC SALMON (*SALMO SALAR*): INCORPORATING DETECTION PROBABILITIES AND INDIVIDUAL HETEROGENEITY

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Evolutionary trade-offs among demographic parameters are important determinants of life-history evolution. Investigating such trade-offs under natural conditions has been limited by inappropriate analytical methods that fail to address the bias in demographic estimates that can result when issues of detection (uncertain detection of individual) are ignored. We propose a new statistical approach to quantify evolutionary trade-offs in wild populations. Our method is based on a state-space modeling framework that focuses on both the demographic process of interest as well as the observation process. As a case study, we used individual mark–recapture data for stream-dwelling Atlantic salmon juveniles in the Scorff River (Southern Brittany, France). In freshwater, juveniles face two life-history choices: migration to the ocean and sexual maturation (for males). Trade-offs may appear with these life-history choices and survival, because all are energy dependent. We found a cost of reproduction on survival for fish staying in freshwater and a survival advantage associated with the "decision" to migrate. Our modeling framework opens up promising prospects for the study of evolutionary trade-offs when some life-history traits are not, or only partially, observable.

KEY WORDS: **Bayesian inference, cost of reproduction, life-history theory, selective survival, state-space model.**

Life-history theory seeks to explain the complexity of life cycles and diversity of living organisms through the action of natural selection on evolutionary mechanisms (Stearns 1992). Life histories are marked by the expression of traits that are closely related to fitness such as age, fertility, or longevity. The evolution of life-history traits (e.g., demographic parameters such as survival probability or number of offsprings produced), and associated plasticity, can affect population dynamics (Roff 1992; Proaktor et al. 2008) as well as determine the ability of individuals to adapt to environmental change (Roff 1992; Stearns 1992; Clutton-Brock 1998; Roff et al. 2006).

If life-history traits were independent, individuals would simply tend to optimize each trait to maximize individual fitness. Because resources (time, space, energy) are limited, individuals must allocate resources among the various functions essential to survival and reproduction (Van Noordwijk and De Jong 1986). When life-history traits are positively dependent on the same resource, they are negatively related to each other. This interdependence is called an evolutionary trade-off (Van Noordwijk and De Jong 1986; Roff 1992; Stearns 1992). The trade-off can be optimized by natural selection as it ultimately influences fitness (Roff 1992; Stearns 1992; Roff et al. 2006).

Stearns (1992) defines 45 kinds of trade-offs between life-history traits, of which the costs of reproduction (trade-offs between reproduction and survival, current, and future reproduction or growth) are the most often studied (Stearns 1992; Roff and Fairbairn 2007). Trade-offs are considered one of the most critical factors in the evolution of life-history traits and therefore play a key role in the life-history theory (Stearns 1992; Clutton-Brock 1998). Interest in studying life-history trade-offs and their consequences under natural conditions is growing (Clark and Martin 2007; Harshman and Zera 2007; Townsend and Anderson 2007), with particular emphasis on accounting for individual quality (Bonenfant et al. 2003; Proaktor et al. 2008; Weladji et al. 2008; Hamel et al. 2009).

The study of evolutionary trade-offs has long been limited by inappropriate methods and affected by many confounding factors (Townsend and Anderson 2007). To highlight trade-offs, individual fitness components need to be assessed. This suggests tracking an individual for all, or part of, its life history. Manipulative approaches to studying trade-offs has revealed much useful information (Zera and Harshman 2001; Harshman and Zera 2007). However, the patterns highlighted through such studies are only "potential" trade-offs (Viallefont et al. 1995; Townsend and Anderson 2007) because studying evolutionary trade-offs in a controlled environment does not take environmental interactions into account (Stearns 1992).

The study of evolutionary processes under natural conditions raises methodological issues. First, the exhaustive monitoring of individuals over time is often impossible in the wild. The detection of an individual is often a random process, with a probability of detection less than 1. Consequently, two important components of fitness—survival and reproduction—are only partially observed: if an individual goes undetected, is it dead or alive? If alive, is it breeding or not? This issue of uncertain detection has long been ignored in evolutionary biology (Clobert 1995; Cam 2009; Conroy 2009), which might have led to flawed inference when addressing evolutionary questions (Gimenez et al. 2008; Hadfield 2008; Nakagawa and Freckleton 2008). Uncertainty in the observation process can also be inherent in the sampled individuals when some traits cannot be fully observed (e.g., reproductive state) or precisely measured (e.g., size; Catchpole et al. 2008; Hadfield 2008; King et al. 2008).

In addition, accounting for individual quality in trade-offs analyses has been problematic because of the inequality of individuals with regard to the acquisition of resources (Stearns 1992; Cam 2009). This variation in individual quality may interfere with identifying trade-offs (Nichols et al. 1994; Doughty and Shine 1997; Cam et al. 2002). For example, Blums et al. (2005) concludes that both reproductive and survival components of fitness are positively correlated with individual quality for females of three duck species and consequently impair the identification of a cost of reproduction. Weladji et al. (2008) in female reindeer (*Rangifer tarandus*) and Hamel et al. (2009) in ungulate populations demonstrate that the heterogeneity in individual quality overrides trade-offs between current reproduction and future performance. These recent studies concluded that individual heterogeneity should be accounted for when assessing trade-offs.

Field methods used to collect data for testing trade-off predictions rely upon mark–recapture (MR) methods that explicitly account for the detection process (Lebreton et al. 1992). The definition of groups of individuals corresponding to life cycle stages is now used in evolutionary biology investigations based on MR experiments (Brown and Thomson 2004; Cam 2009) and is widely used to investigate evolutionary trade-offs (Nichols et al. 1994; Tavecchia et al. 2001; Moyes et al. 2006; Townsend and Anderson 2007). We demonstrate extensions to go beyond this first step in accounting for individual variation by including other sources of individual heterogeneity both known and unknown (Gimenez et al. 2006; Metcalf and Koons 2007; Royle 2008). Individual heterogeneity may be of known origin, as in the studies mentioned in the previous paragraph, or of unknown origin. In the former, individual heterogeneity is incorporated into a model using covariates as fixed effects (e.g., Gimenez et al. 2009) such as size or states (e.g., breeder vs. nonbreeder), whereas in the latter, individual random effects have to be employed. Service (2000), Cam et al. (2002) and Wintrebert et al. (2005) show that considering individual heterogeneity through the use of random effects was essential to identify senescence in survival. However, these studies all assume perfect detectability, motivating the need for further developments to explicitly account for a detection probability less than 1.

Here, we develop a general framework to assess trade-offs among life-history traits in natural conditions, which addresses both the issues of detectability less than 1 and individual heterogeneity. We propose a novel approach that combines the three following components within a single framework: (1) Modeling the complete life cycle and the associated transitions between states (alive or dead, breeding or not breeding, migrating or resident); (2) Integrating individual heterogeneity of known (fixed effect) or unknown (random effect) origin potentially affecting life-history traits involved in the trade-offs of interest; and (3) Taking uncertainty in detection into account.

We adopt a state-space modeling approach to separate the demographic process of biological interest, which integrates the individual heterogeneity, from the observation process through the detection of marked individuals (Buckland et al. 2004; Rivot et al. 2004; Gimenez et al. 2007; Royle 2008).

Salmonids provide a relevant biological model to study evolutionary questions such as the evolution of life-history traits (e.g., age and size at first maturity), of philopatry, of semelparity vs. iteroparity (Crespi and Teo 2002; Hendry and Stearns 2004), of alternative breeding tactics (Gross 1996), and of life-history trade-offs (Hendry and Stearns 2004). As a case study, we analyze the MR dataset collected on the Atlantic salmon (*Salmo salar*) population of the Scorff river (Southern Brittany, France). Atlantic salmon display a complex life cycle and a variety of life histories. The choice among alternative life histories ultimately depends on their costs and benefits, that is, trade-offs.

Atlantic salmon is an anadromous species that has a life cycle in both freshwater and the ocean (Gueguen and Prouzet 1994). In Brittany (Fig. 1), the juvenile phase takes place in freshwater and lasts 1 or 2 years. Thereafter, the fish migrate to the ocean and return after 1 or 2 years to their native stream to breed. Among males, some individuals may breed before undertaking their seaward migration. We focused on young Atlantic salmon during the freshwater phase of the life cycle. During this phase, individuals may adopt different life-history tactics. First, they have to decide whether to migrate to the ocean after their first year of life or to reside in the freshwater an additional year. Migration to the ocean is accompanied by a smolting process that prepares individuals for sea water life. Second, they have to decide whether to mature or not before migrating to the ocean. The latter choice involves only males during their second year in freshwater.

Atlantic salmon can be described as a conditional strategist (sensu Gross 1996) with status-dependent choice among alternative life-history tactics (migrating to sea or not, delaying reproduction or not). These life-history tactics depend on, and modify, the way energy is acquired, stored, and used by individuals (Thorpe et al. 1998). During the first winter, future migrants (smolts) adopt a very different behavior from those intended to reside an additional year in the river (Metcalfe and Thorpe 1992; McCormick et al. 1998). Such fish try to maximize their growth and may therefore be exposed to a higher risk of predation (McCormick et al. 1998). The predation risk is increased during the downstream migration in early spring as well (Larsson 1985; Moore et al. 1995). The physiological process of smolting requires energy that may be lacking for ensuring survival (McCormick et al. 1998; Thorpe and Metcalfe 1998). Sexual maturation and reproduction of resident males in freshwater is also energetically demanding (Jonsson et al. 1991; Rowe et al. 1991; Fleming 1996; Arndt

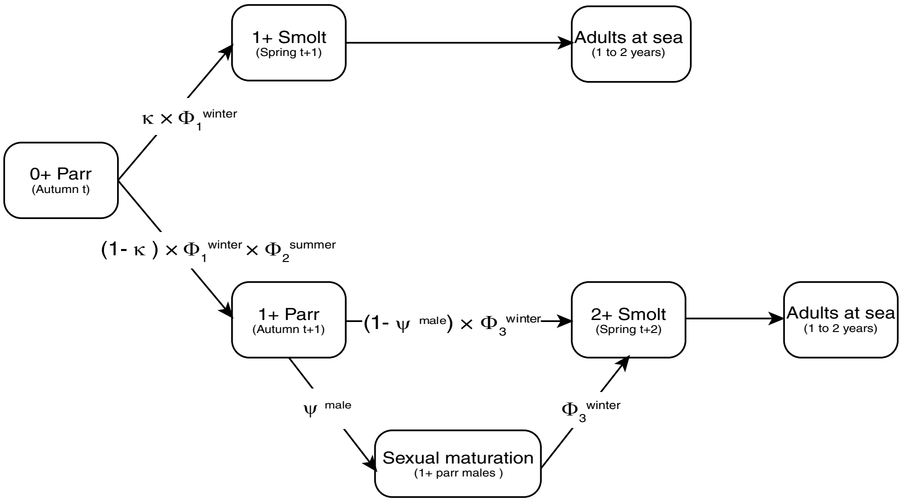

Figure 1. **Life cycle of the Atlantic salmon in the Scorff, Brittany (France). Reproduction occurs in freshwater in December and eggs are buried in the river bed gravel. Fry emerge from the spawning r in early spring. After a few months of life, juveniles, then called "0+ parr," choose between migrating to sea the following spring (1+ smolt stage) with a probability κ or staying another year in freshwater (1+ parr) with a probability $1 - \kappa$. The probability of winter survival of the 0+ parr between the first autumn and the following spring is Φ_1^{winter}. The probability of summer survival of the 1+ parr is Φ_2^{summer}. Some of the males remaining in freshwater become sexually mature at the 1+ parr stage with a probability of maturing Ψ. The probability of winter survival of the 1+ parr between the second autumn and the following spring is Φ_3^{winter}. Virtually all surviving juveniles (previously mature or not) will migrate to the sea in the following spring (2+ smolt). Migration to the sea is accompanied by physiological, morphological, and behavioral changes (i.e., smolting process), which prepares individuals for sea water life. After spending between one or two years in the North Atlantic Ocean, adults return to breed in their natal river. The post-spawning mortality is close to 100% for anadromous individuals (i.e., having undertaken the oceanic migration) while mortality is lower for males having matured as parr.**

2000). Combined with the exposure to the agonistic behavior of the large anadromous males on the spawning grounds (Hutchings and Myers 1987; Fleming 1996), it should lead to reduced survival (Jonsson et al. 1997; Hendry and Berg 1999; Fleming and Reynolds 2004). Consequently, both the decision to migrate to the ocean and the reproduction of males are expected to reduce survival. We propose to demonstrate the relevance of our novel state space modeling approach by quantifying two potential trade-offs in one cohort of juvenile Atlantic salmon in the wild: a survival cost of migration and a survival cost of reproduction.

Material and Methods

STUDY SITE AND MR DATA COLLECTION

The Scorff river is a small coastal river (75 km including 15 km of estuary) of Southern Brittany (France). Atlantic salmon colonization is essentially restricted to the main river over a 50 km stretch starting at the head of tide.

In the following, we use the term "0+" for individuals of less than one year of age in freshwater, "1+" for those of more than 1 year of age and "2+" for those of more than 2 years of age. Juvenile are named "parr" if residents in freshwater and "smolts" when they migrate to the sea.

In autumn 2005, 0+ parr were sampled by electrofishing at 39 stations along the main course of the Scorff. Every fish captured was measured (fork length, to the nearest millimeter) and individually marked with a PIT (passive integrative transponder) tag (11 mm long, 2.2 mm in diameter) inserted into the peritoneal cavity according to the protocol described in Acolas et al. (2007). This marking technique is known to have little effect on young salmon and a very low rate of tag loss (Gries and Letcher 2002; Letcher and Gries 2003).

In spring 2006, downstream migrating 1+ smolts were captured at two successive traps located at the lower end of the river system below all sites where 0+ parr were marked. At both facilities, all individuals previously PIT tagged were identified. In addition, untagged fish caught at the first upstream trap (i.e., the Leslé Mill) were in turn marked by removing a small piece of a pelvic fin. At the second trap (i.e., the Princes Mill), located at the head of tide 600 m downstream from the Leslé Mill, all individuals previously fin-clipped were identified. Fin-clipping data provided supplemental information for assessing the detection probabilities of the PIT tagged individuals (see section "Statistical inference in a Bayesian framework").

In autumn 2006, the 1+ parr were sampled by electrofishing according to same protocol used for the 0+ parr the previous year. Marked fish were identified and untagged fish were PIT tagged. Sexually maturing and already spermating males were detected by gently pressing their belly. In spring 2007, the 2+ smolts were trapped, checked for PIT tags, and fin-clipped if unmarked as for 1+ smolts.

Eventually, anadromous salmon could be recaptured in 2007 and 2008 when returning to the Scorff river. They were sampled at the Princes Mill facility in a trap designed to catch upstream migrating adults. PIT-tagged individuals were systematically detected.

Table 1 summarizes the data from individuals tagged at 0+ and 1+ parr stages and recaptured at each observation event, as well as from smolts captured and fin-clipped at each trap.

STATE-SPACE MODELING FRAMEWORK

The data resulted from the partial observation (detection or not) of events that were generated from a demographic process (the sequence of the life-cycle stages, Fig. 1). The need for a convenient and flexible framework to account explicitly for these two components has led to the development of state-space models (SSMs) (Clark 2003; Rivot 2003; Buckland et al. 2004). Recently, SSMs have been used for estimating animal survival (Gimenez et al. 2007) from MR data, while incorporating individual heterogeneity (Gimenez et al. 2006; Royle 2008; see also Gimenez and Choquet 2010). In SSMs, the relationship between the observation and the demographic process is governed by two sets of equations, namely the state and the observation equations (Harvey

Table 1. Summary of tag/recapture data for each observation event and each method of tagging (PIT-tag or Fin clip) for one cohort of Atlantic salmon.

	Capture–recapture at each stage of life				
Tag	0+ Parr	1+ Smolt	1+ Parr	2+ Smolt	Adults
Passive integrated transponder (PIT)					
Tagged at 0+ parr stage	1829	67	29	39	5
Tagged at 1+ parr stage			281	55	
Fin clip					
Captured and tagged at Leslé Mill		1291		1751	
Captured at Princes Mill and untagged at Leslé Mill		820		594	
Captured at Princes Mill and tagged at Leslé Mill		179		262	

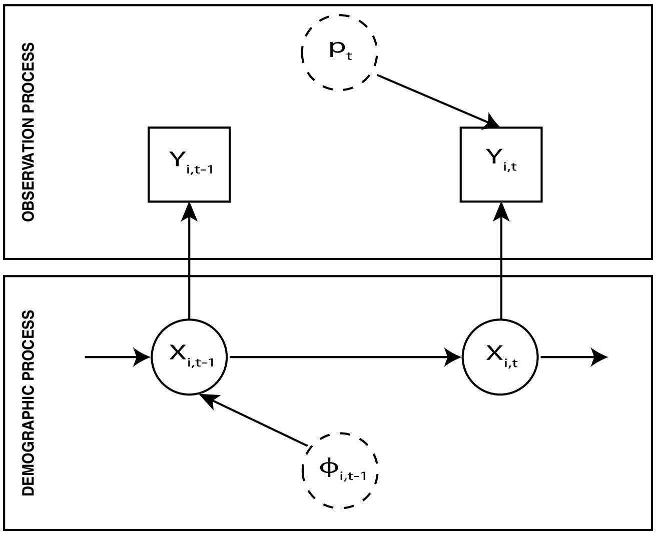

Figure 2. Graphical representation of a state-space model (SSM) for a juvenile individual *i* between two sampling occasions $t - 1$ and *t* (see eqs. 1 and 2). The first component of the SSM is a demographic process characterized by a succession of hidden states (solid circles), also called latent states. The demographic process depends on parameters corresponding to transitions probabilities between successive states (dashed circles). The unknown state of individual *i* at time *t* ($X_{i,t}$) is drawn from a Bernoulli distribution depending on its state at time $t - 1$ ($X_{i,t-1}$) and the probability of transition between these two states (e.g., the survival probability $\Phi_{i,t-1}$). The observational data (solid square) through the observation process are the visible part of the demographic process. Observations are also obtained conditionally on latent states and the parameters of the observation process associated (dashed ellipses). The observation or not of individual *i* at time *t* ($Y_{i,t}$) is drawn from a Bernoulli distribution that depends on the detection probability p_t at time *t* and conditional on individual *i* being alive at time *t* ($X_{i,t} = 1$). This formulation separates the nuisance parameters (detection probabilities) from the parameters of interest for example survival probability, the latter being involved exclusively in the state equation. The resulting SSM is a combination of a demographic process and an observation process.

et al. 2004; Clark 2007). For the sake of illustration, we first go through a straightforward example. Let us focus on the case of a juvenile *i* between two sampling occasions $t - 1$ and *t* (Fig. 2). Conditional on its state at time $t - 1$ (alive or dead), this individual may be alive or dead at the next sampling occasion with some probability. Formally, we denote $X_{i,t}$ a binary random variable corresponding to the state of the individual *i* at time *t*, which takes the value 1 if the individual is alive at *t*, and 0 otherwise. Then, $X_{i,t}$ given $X_{i,t-1}$ is distributed according to a Bernoulli distribution with probability depending on the survival probability $\phi_{i,t-1}$ (Gimenez et al. 2007; Royle 2008). This leads to the state equation:

$$X_{i,t} \mid X_{i,t-1} \sim \text{Bernoulli}(X_{i,t-1} \times \phi_{i,t-1}). \tag{1}$$

When individual *i* is alive at *t* ($X_{i,t} = 1$), it can be observed or not, whereas when dead ($X_{i,t} = 0$), it necessarily goes undetected (in our case the detection of dead fish holding a PIT tag was impractical). We denote $Y_{i,t}$ a binary random variable corresponding to the observation of the individual *i* at time *t*, which takes the value 1 if the individual is observed and 0 otherwise. Given the state $X_{i,t}$, $Y_{i,t}$ is distributed according to a Bernoulli distribution with probability depending on the detection probability p_t at time *t* (Gimenez et al. 2007; Royle 2008). This leads to the observation equation

$$Y_{i,t} \mid X_{i,t} \sim \text{Bernoulli}(X_{i,t} \times p_t). \tag{2}$$

Usually with MR methods, the focus is on estimating the transition probabilities that make the link between the demographic states. By using SSMs, we can feasibly access the states of each individual while acknowledging they may be only partially observed. In what follows, we extended this simple approach to the freshwater phase of Atlantic salmon life cycle.

DEMOGRAPHIC PROCESS

The complete life history of Atlantic salmon from the 0+ parr stage in autumn to the migration to sea can be summarized by the following sequence of events (Fig. 1): (1) Decision at the first autumn of smolting at one year of age (1+ smolt) or to stay an additional year in freshwater (1+ parr); (2) Winter survival of the 0+ parr between the first autumn and the following spring (at the time of recapture of the 1+ smolts); (3) Summer survival of the 1+ parr between spring and autumn; (4) Sexual maturation of males at 1+ parr stage; and (5) Winter survival of the 1+ parr between the second autumn and the following spring (at the time of recapture of the 2+ smolts).

We assumed that sexual maturation and second winter survival were governed by the same processes for 1+ parr captured in autumn 2006 but untagged at 0+ parr stage and for the individuals tagged at the 0+ parr stage.

Each of these events is binary and was modeled as a random state variable following a Bernoulli distribution as above (Table 2). We accounted for individual heterogeneity regarding these random events by assuming the associated probabilities may vary among individuals. The modeling of this variability is a key feature in our approach and is detailed in the following.

EVOLUTIONARY TRADE-OFFS OF ULTIMATE INTEREST AND INDIVIDUAL HETEROGENEITY

Both the decision of smolting at age 1+ and the reproduction of 1+ males are expected to reduce survival. We modeled these potential trades-offs at the individual level (index *i*) by linking the probabilities of winter survival to the state

Table 2. States (indicators), transition probabilities (life-history traits of interest) and equations of the demographic process modeling the sequence of events corresponding to the life history of Atlantic salmon from the 0+ parr stage in autumn to the migration to the ocean. Equations defining individual specific transition probabilities are given in the text.

State	Definition	Associated probability	Modeling
Smolt0	0+ Parr in autumn/futurs 1+ smolts	κ_i: Probability to smoltify at 1 year of age (eq. 5)	$\text{Smolt0}_i \sim \text{Bernoulli}(\kappa_i)$
Smolt1	Surviving 1+ smolts in spring	$\phi_{1,i}$: Probability of first winter survival in the (eq. 3)	$\text{Smolt1}_i \sim \text{Bernoulli}(\phi_{1,i} \times \text{Smolt0}_i)$
Parr1	Surviving 1+ parr in spring		$\text{Parr1}_i \sim \text{Bernoulli}(\phi_{1,i} \times 1 - \text{Smolt0}_i)$
Parr1.1	Surviving 1+ parr in autumn	$\phi_{2,i}$: Probability of summer survival (eq. 7)	$\text{Parr1.1}_i \sim \text{Bernoulli}(\phi_{2,i} \times \text{Parr1}_i)$
Parr1.mat	Mature males 1+ parr in autumn	ψ_i^{male}: Probability of maturing for males (eq. 6)	$\text{Parr1.mat}_i \sim \text{Bernoulli}(0.5 \times \psi_i^{\text{male}} \times \text{Parr1.1}_i)$
Smolt2	Surviving 2+ smolts in spring	$\phi_{3,i}$: Probability of winter survival in the second year of life (eq. 4)	$\text{Smolt2}_i \sim \text{Bernoulli}(\phi_{3,i} \times \text{Parr1}_i)$

indicator of the decision of smolting (Smolt0_i) or of maturation (Parr1.mat_i):

$$\text{logit}(\phi_{1,i}) = \alpha_1 + \alpha_2 \times \text{Smolt0}_i + \varepsilon_i \tag{3}$$

$$\text{logit}(\phi_{3,i}) = \delta_1 + \delta_2 \times \text{Parr.mat1}_i + \varepsilon_i \tag{4}$$

where $\phi_{1,i}$ stands for the probability of first winter survival (0+ parr) of an individual i and $\phi_{3,i}$ for the probability of second winter survival (1+ parr). We used a logit link function to ensure that probabilities lie on [0, 1]. Smolt0_i and Parr1.mat_i are the smolting and the maturation indicators that take the value 1 if the individual is smolting or maturing respectively and 0 otherwise. Parameters α_2 and δ_2 reflect the influence of the decision of smolting or of maturing on winter survival at 0+ and 1+ parr stage, respectively. If these parameters are different from 0, then evidence exists for a trade-off. For instance, if δ_2 is negative, then the winter survival $\phi_{3,i}$ of a maturing 1+ male parr ($\text{Parr1.mat}_i = 1$) is lower than that of a nonmaturing 1+ parr (male or female, $\text{Parr1.mat}_i = 0$), suggesting a survival cost of reproduction. Negative survival differentials α_2 and δ_2 implies individual probabilities of survival over first and second winter are positively correlated with the choice of staying in freshwater and remaining immature, respectively. ε_i is a normally distributed random effect accounting for individual heterogeneity in survival due to unknown causes. We assumed that this unobservable individual survival potential is the same for each survival event of an individual's life (Cam et al. 2002; Royle 2008). Thus we make the assumption of dependence between each of the survival events in the life history of a given individual: having a high survival probability during the first winter reveals a good survival ability of the individual that is transmitted to all survival events (i.e., better chance to stay alive during the following survival events). As survival is energy demanding, higher survival potential should be related to higher energy storage and a more efficient use of available energy for growth.

The survival probabilities $\phi_{1,i}$ and $\phi_{3,i}$ are defined for every fish marked and depend on the state variables Smolt0_i and Parr1.mat_i. This approach requires in turn that the process governing smolting and maturation be modeled such that these traits are defined for every individual, whether it has been observed (i.e., recaptured) or not.

CHOICE BETWEEN ALTERNATIVE LIFE-HISTORY TACTICS

Age at smolting depends positively on growth during the first months of life in freshwater (Nicieza et al. 1991; Baglinière et al. 1993; Thorpe and Metcalfe 1998). Using the conceptual framework of probabilistic reaction norms proposed by Heino et al. (2002), we represented this relationship by a logit-linear relationship between the individual probability of smolting at age 1+ (κ_i) and the size at the 0+ parr stage

$$\text{logit}(\kappa_i) = \beta_1 + \beta_2 \times Lf_i, \tag{5}$$

where Lf_i is the individual fork length (mm) centered on the sample mean. Parameter β_2 controls the influence of size at 0+ parr stage on smolting, and corresponds to the selection gradient of the probabilistic reaction norm for smolting. We expect the relationship to be positive, to reflect a positive size-dependent relationship of smolting at age 1+.

For most individuals, maturation state is unknown. Indeed, it is only observed for male 1+ parr captured in autumn, mature and detected as spermating. To define maturation state for every 1+ parr, whether marked in autumn 2005 as 0+ parr or in autumn 2006 as 1+ parr, we modeled sexual maturation of males at the 1+ parr stage as a Bernoulli random event. The associated probability (i.e., of maturing at 1+ parr stage) is the product of the probability of sexual maturation for a male and the probability to be a male. As we considered that the life-history process before the 1+ parr stage in autumn was not sex dependent, we assumed that the probability for a 1+ parr to be a male was 0.5 (balanced sex-ratio). The probability of sexual maturation for a male ψ_i^{male} was assumed to depend on unobserved individual quality reflected by the survival potential (individual random effect on survival ε_i)

$$\text{logit}\left(\psi_i^{\text{male}}\right) = \gamma_1 + \varepsilon_i. \tag{6}$$

As a male having a high survival potential ε_i should be an individual with a high level of energy storage and efficient in its use of available energy, it should in turn have a higher probability to mature at the 1+ parr stage. Indeed, sexual maturation of males at the 1+ parr stage depends on the accumulation of energy reserves and/or growth in the spring of the second year of life (Rowe and Thorpe 1990a; Prévost et al. 1992; Duston and Saunders 1997).

SUMMER SURVIVAL

To complete the life cycle, summer survival of the 1+ parr needs to be modeled. The survival of the resident 1+ parr between their initial marking in spring 2005 and their first recapture in autumn 2006 is made of two successive survival events: winter survival (from autumn 2005 to spring 2006) and summer survival (from spring 2006 to autumn 2006). The explicit distinction of these two survival events allows assessing the winter survival probability of 1+ parr, despite the absence of recapture observations for the 1+ parr in spring 2006.

Baglinière et al. (1994) showed that, in a tributary of the Scorff, summer survival of 1+ parr was higher than previous winter survival. We incorporated this information by specifying summer survival probability $\phi_{2,i}$ conditionally on winter survival $\phi_{1,i}$ as

$$\phi_{2,i} = \phi_{1,i} + (1 - \phi_{1,i}) \times \Delta_{\text{survival}}, \tag{7}$$

where Δ_{survival} is an unknown parameter between 0 and 1. Note that this formulation allows the random effect on survival ε_i to be transferred to $\phi_{2,i}$ via its dependence on $\phi_{1,i}$.

OBSERVATION PROCESS

Captures of tagged fish occurred at each stage of the life history of PIT-tagged individuals. At the individual level, capture was a binary random event modeled using a Bernoulli distribution. The associated probability was specific to each stage and capture device, but was assumed fixed across individuals. The first recapture event after tagging was the trapping of the 1+ smolts (spring 2006) both at the Leslé Mill with probability pL_1 and at the Princes Mill with probability pP_1. The 1+ parr remaining in freshwater (autumn 2006) were captured by electrofishing with probability pC_1. The 2+ smolts (spring 2007) were trapped at the Leslé Mill with probability pL_2 and the Princes Mill with probability pP_2. Finally, anadromous adults returning to freshwater (2007 and 2008) were recaptured at the Princes Mill with probability pA_1.

Among 1+ parr individuals, spermating males were systematically detected. Nonspermating fish can be females, nonmaturing males, or nonspermating maturing males. To reflect this uncertain detection of maturing males, we assumed that, for a male, the identification of its sexual maturation is random with probability pD (i.e., to be spermating).

STATISTICAL INFERENCE IN A BAYESIAN FRAMEWORK

To fit our SSM to MR data, we adopted a Bayesian approach using Markov chain Monte Carlo (MCMC) algorithms as recently suggested (Gimenez et al. 2007; Royle 2008). The Bayesian approach combines the likelihood (information available in the data) and prior distributions for parameters of interest (knowledge available before the experiment). From Bayes' theorem, statistical inference is conducted by combining prior information with the likelihood to obtain the posterior probability distribution of all the model unknowns, that is, individual states, transition probabilities between states and random effects, observation probabilities, and additional parameters (see Ellison 2004; Gelman 2004, and McCarthy 2007 for more details about the Bayesian statistical modeling approach).

Besides handling the complexity of our model, the Bayesian approach made the combination of multiple sources of information possible. This approach allowed us to take advantage of all sources of information available to improve the estimation of the parameters of the model. Apart from the observed data issuing from the PIT tagging program, other sources of information could be incorporated.

First, we took advantage of ancillary datasets to improve estimation of the smolt trapping probabilities. In parallel to the PIT tagging program, smolts were also marked every year by fin clipping at the Leslé Mill and recaptured downstream at the Princes Mill. We assumed that the probability of capture at both traps was the same for PIT-tagged, fin-clipped, and untagged smolts.

Second, we incorporated information through the prior probability distribution of the model parameters. Informative prior distribution can be used to improve the precision of parameter estimates and reduce the model complexity (McCarthy and Masters 2005). Prior information was available either from the literature or from additional data. For example, in agreement with what is known about the species biology, we considered the probability to survive in freshwater as being neither null nor equal to 1 between two consecutive stages. Consequently, we chose the prior distribution of parameters such that less importance was given to extreme values of survival probabilities (see Appendix S1 for more details). Note that when data were used to set informative priors, they were different from the observations corresponding to the observation process or the ancillary datasets described above. For all the other parameters we used the standard default approach of setting little informative priors.

The joint posterior distribution of all the model unknowns was derived by means of MCMC sampling. We used the OpenBUGS software for implementing MCMC sampling (Spiegelhalter et al. 2003). The OpenBUGS code of our model is available at http://www.cefe.cnrs.fr/biom/salmonOpenBUGS.txt. We ran three parallel MCMC chains and retained 50,000 iterations after an initial burn-in of 10,000 iterations. Convergence of MCMC sampling was assessed by means of the Brooks-Gelman-Rubin diagnostic (Brooks and Gelman 1998).

Results

The comparison of posterior to prior distributions suggested that the information contained in the data led to considerable updating of the prior distributions. In the following, medians and 95% credible intervals from the posterior distribution are reported (see also Table 3).

Table 3. **Summary of posterior distributions (medians and 95% posterior credible intervals) for demographic process parameters and the observation process parameters.**

Parameter	Definition	Posterior distribution	
		Median	95% credible interval
Demographic process			
β_2	Selection gradient of the size-dependent probabilistic reaction norm for smolting (eq. 5)	0.15	[0.111; 0.205]
α_1	First winter survival for futures 1+ parr (logit scale, eq. 3)	-1.47	[-2.64; -0.71]
α_2	Effect of the decision of smolting at 1 year of age on the first winter survival (logit scale, eq. 3)	1.66	[0.44; 3.53]
δ_1	Second winter survival for immature 1+ parr (males and females; logit scale, eq. 4)	-0.45	[-2.03; 0.48]
δ_2	Effect of the decision of maturing on the second winter survival (cost of reproduction for survival; logit scale, eq. 4)	-1.41	[-2.92; -0.20]
Δ_{survival}	Differential between first winter survival and following summer survival	0.401	[0.07; 0.86]
ψ^{male}	Mean probability of maturation for males at 1+ parr stage (eq. 6)	0.59	[0.22; 0.91]
σ_ε	Standard deviation of the random effect on survival and maturation	0.98	[0.42; 2.20]
Observation process			
pL^1	Detection probability at Leslé Mill at the 1+ smolt stage	0.19	[0.16; 0.21]
pP^1	Detection probability at Princes Mill at the 1+ smolt stage	0.14	[0.12; 0.16]
pL^2	Detection probability at Leslé Mill at the 2+ smolt stage	0.31	[0.29; 0.34]
pP_2	Detection probability at Princes Mill at the 2+ smolt stage	0.15	[0.14; 0.17]
pA_1	Detection probability of adults	0.03	[0.01; 0.05]
pC_1	Detection probability by electrofishing (in autumn) at the 1+ parr stage	0.14	[0.09; 0.23]
pD	Detection probability of males maturation	0.82	[0.62; 0.97]

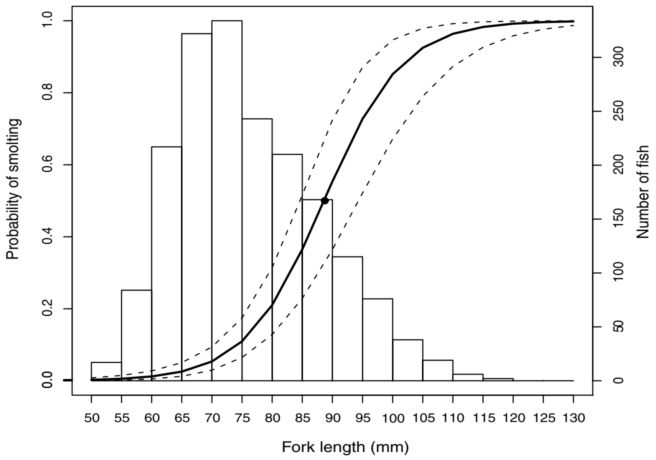

Figure 3. Probabilistic reaction norm for the age at smolting. The posterior median (solid line) and the 95% posterior probability (dashed lines) of the probability of smolting at 1 year of age are functions of fork length. A histogram of the size distribution of the 0+ parr sampled in autumn 2005 is also displayed. Posterior distributions are based on 50,000 MCMC samples.

OBSERVATION PROBABILITIES

Capture probabilities at traps varied from 0.12 to 0.34 in our study ("Observation process" in Table 3). Because of the use of ancillary data, detection probabilities were well estimated in comparison with noninformative prior distributions (see Appendix S1; Table 1), except for the probability of capture in autumn 2006 of the 1+ parr tagged in 2005 (0.14 [0.09; 0.23]). Smolt trap efficiencies varied from 2006 to 2007; they are known to be very sensitive to hydrological conditions (Rivot and Prévost 2002; E. Prévost, unpubl. data). The probability of detection of sexual maturation among the males at the 1+ parr stage was high (0.82 [0.62; 0.97]). The probability of detection of adults returning to freshwater was low (0.03 [0.01; 0.05]), but it reflected the combination of the survival at the ocean, and the probability of capture at Princes Mill.

AGE AT SMOLTING AND MATURATION

The gradient of the probabilistic reaction norm for the age at smolting was strictly positive (Pr [$\beta_2 > 0$] ≈ 100%). The decision of smolting at 1 year of age was strongly size dependent (Fig. 3). Fish smaller than 90 mm at the 0+ parr stage had an average probability of becoming a 1+ smolt below 0.5. This probability was very low for individuals smaller than 65 mm and close to 1 for individuals larger than 115 mm. Given the size distribution of the 0+ parr sampled and marked in 2005, the probability to become a 1+ smolt of an average individual was 0.14 [0.07; 0.23].

The probability of sexual maturation for a male at the 1+ parr stage (considering zero random effect) was high (0.59 [0.22; 0.91]).

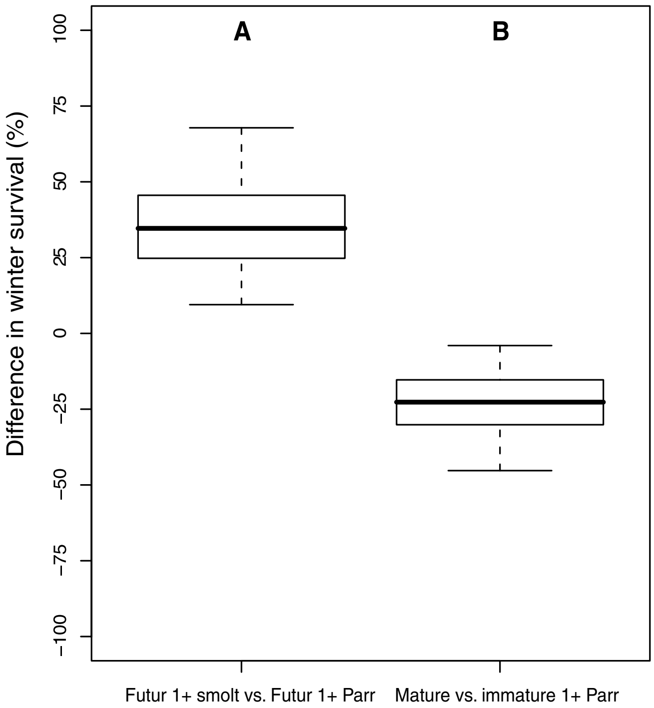

Figure 4. Posterior distributions of the difference in survival probability (considering zero random effect as null) for (A) future 1+ smolts versus future 1+ parr during the first winter and (B) mature 1+ parr versus immature 1+ males during the second winter (cost of reproduction for survival). Posterior distributions are based on 50,000 MCMC samples. The 2.5 (lower bound of the 95% credible interval), 25, 50 (median), 75, 97.5 (upper bound of the 95% credible interval) percentiles are displayed.

First winter survival and age at smolting

Parameter α_2 was estimated positive with probability >0.99 (1.44 [0.66; 3.53]; on the logit scale), revealing a selective survival in the first winter in favor of the 0+ parr that decided to smolt at 1 year of age the following spring. The difference of winter survival between future migrants and future residents was positive (0.35 [0.09; 0.68] considering zero random effect) (Fig. 4A). Winter survival of future migrants (1+ smolt) was 0.53 [0.32; 0.83] versus 0.19 [0.07; 0.33] for future 1+ parr staying in freshwater (considering zero random effect).

Cost of reproduction on second winter survival

Parameter δ_2 was estimated negative with probability >0.97 (−1.41 [−2.92; −0.20], logit scale) suggesting the existence of a selective survival depending on the sexual maturation status of the 1+ parr, that is, a cost of reproduction on the second winter survival. The difference in winter survival of mature and immature 1+ parr was negative (−0.23 [−0.04; −0.45] considering zero random effect) (Fig. 4B). Winter survival of a male previously mature at the 1+ parr stage was 0.14 [0.02; 0.35]) versus 0.39 [0.12; 0.62] for an immature (males and females together) 1+ parr (considering zero random effect).

Individual heterogeneity

Averages of the random effect for survival calculated over individuals surviving at each stage increased as the life cycle unfold. The average random effect was zero by definition at the 0+ parr stage, 0.53 [0.11; 2.36] for individuals surviving the first winter, 0.82 [0.16; 3.41] for those surviving till the 1+ parr stage in the fall, and 1.13 [0.23; 4.11] for surviving 2+ smolts. This increase suggests a selection over time of fish that were the most suited to survive in freshwater.

Discussion

Our Bayesian state space modeling approach allowed us to represent the whole life-history process of Atlantic salmon and to identify potential evolutionary trade-offs. This was achieved despite individual heterogeneity in life-history traits, and despite the fact that the life-history traits involved were only partially observed, due to detection probabilities less than one.

OBSERVATION PROCESS AND DETECTION PROBABILITIES

Studies of elements involved in potential selection processes under natural conditions, such as trade-offs and reaction norms, using MR experiments, have long ignored the issue of detectability less than one (Clobert 1995; Cam 2009). Gimenez et al. (2008) shows that directional selection on body mass of social weaver (*Philetairus socius*) is detected when detection probability is assumed to be one, while a stabilizing selection is found when this assumption is relaxed. Yoccoz et al. (2002) suggests that the variability in the detection process affects their ability to detect potential costs of reproduction in the Common Eider (*Somateria mollissima*). These results motivated the integration of detection probabilities in our approach for reliable inference about life-history traits. In our study, except for sexual maturation of males at 1+ parr stage, detection probabilities were much lower than 1, ranging from 0.12 to 0.34 depending on the observation process and the life-history stage considered (Table 3).

EVOLUTIONARY TRADE-OFFS AND INDIVIDUAL HETEROGENEITY

There is a growing interest in accounting for individual heterogeneity in demographic models for evolutionary studies (Cam et al. 2002; Conroy et al. 2002; Blums et al. 2005; Wintrebert et al. 2005; Royle 2008). Indeed, the assumption that individuals are equal in their ability to get resources or in the way they use them is not reasonable. Our modeling framework is flexible and offers several options for integrating individual heterogeneity in a single model. When the cause of the individual heterogeneity was identified and known, observed covariates were used, for example when incorporating the effect of the known size of the 0+ parr on the smolting decision by means of a probabilistic reaction norm. When the cause was identified but not or partially observable, unknown or partially known states were used as covariates, for example when modeling the potential evolutionary trade-offs by conditioning individual survival probabilities by partially observed traits. Last, when the cause was unknown, random effects were used to reflect variation in the individual ability to survive or to mature. Incidentally, we also note that the latter approach led to the classical conclusion that recurrent survival events tend to select over time the individuals with highest ability for survival (Cam et al. 2002; Wintrebert et al. 2005).

A cost of freshwater residency for survival?

Our analysis revealed a positive relationship between the first winter survival of the 0+ parr and their decision of smolting the following spring. This differential winter survival in favor of the 0+ parr having decided to smolt the following spring may be seen as a cost of staying an extra year in freshwater. This result is in contradiction with our initial prediction of a survival cost of migration. To our knowledge, this is the first time this result has been found in the wild, although this was shown under artificial rearing conditions (Pickering and Pottinger 1988). Baglinière et al. (1993) also showed a difference in winter survival under natural conditions between two size groups of 0+ parr, with the difference being in favor of the larger fish, and that larger fish are more likely to smolt at one year of age.

Our unexpected result should be taken with caution as it was derived from a single cohort analysis. Nevertheless, finding a positive correlation between life-history traits when negative correlation (i.e., trade-offs) is expected is not uncommon (Van Noordwijk and De Jong 1986; Glazier 1999; Brown 2003). Van Noordwijk and De Jong (1986) provide an explanation for some of these unanticipated results, which most likely applies to our study. They propose a model in which two traits (e.g., smolting and survival) compete for the same resource at the individual level, and where individuals differ both in their ability to acquire a resource (e.g., energy) and in the allocation of the latter to the traits at stake. Under this scheme, the amount of resource available for each trait depends positively on the total amount of resource acquired and negatively on the proportion allocated to the other trait. Evolutionary trade-offs result only from the sharing of a limited resource between two traits. When variation among individuals in resource acquisition is high relative to variation in allocation between traits, trade-offs operating at the individual level are likely to be obscured (Van Noordwijk and De Jong 1986; Brown 2003). Indeed, individuals with a higher ability for resource acquisition (Brown 2003; Cam 2009) can invest more into both traits. Consequently, a positive relationship between two traits is observed at the interindividual level, even when a negative relationship exists at the individual level (Cooch et al. 2002).

Future 1+ smolt and future 1+ parr differ greatly in their acquisition of resources during their first winter. Future smolts are aggressive and dominant, allowing them access to the most favorable foraging habitat (Harwood et al. 2003; Finstad et al. 2007). In turn, this aggressiveness gives them high metabolic and growth rates (Nicieza and Metcalfe 1999; Finstad et al. 2007). Individuals staying an extra year in freshwater reduce their activity level in winter and become anorexic (Metcalfe and Thorpe 1992; Thorpe et al. 1992; Metcalfe 1998). Following Van Noordwijk and De Jong (1986) reasoning, we think that the trade-off between smolting and the first winter survival is masked by the large variation in the acquisition of resources during the first winter between future 1+ smolts and future resident 1+ parr. The survival advantage resulting from the higher level of energy acquisition of the future smolts would be larger than the cost of smolting.

Cost of reproduction for survival

Our results suggested a cost of reproduction in survival. Mature male 1+ parr have a lower probability of winter survival (post-reproductive survival) than their immature counterparts. This supported our initial expectation based on previous studies (Baglinière et al. 1993; Whalen and Parrish 1999; Whalen et al. 2000; Jonsson and Jonsson 2005). Noteworthy, our study is the first to provide a quantitative estimate of such a cost of reproduction in wild Atlantic salmon. This quantification was made possible thanks to our state space modeling approach. Indeed, this gave us access to the maturation state of all 1+ parr tagged even though it was only observable for the spermating males captured at 1+ parr stage in autumn 2006.

There is room for improvement to our model. Regarding the demographic process, several simplifying assumptions can be relaxed. Given that by staying an additional year in freshwater, the males can have direct access to reproduction, sex-specific demographic strategies could be introduced even before the first reproductive event occurs. Sex-specific probabilistic reaction norms for the age at smolting could be incorporated. In spring of the second year of life, future maturing males at the 1+ parr stage have been shown to have higher energy reserves or growth rates than nonmaturing individuals (Rowe and Thorpe 1990a,b; Prévost et al. 1992; Duston and Saunders 1997). Instead of a probability of maturation being assumed constant across individuals, introducing a probabilistic reaction norm for the sexual maturation of the males (Morita and Fukuwaka 2006) would be interesting.

These potential improvements are examples picked for the sake of illustration. The important point is that our Bayesian state space modeling approach opens up prospects for these extensions. Overall, we contend the approach offers a generic framework for the study of evolutionary processes. Bayesian state space modeling is well suited for handling the conditioning structure of life-history strategies, which encompasses trade-offs, selective survival, and reaction norms, including when some of the life-history traits at stake are not (or partially) observable.

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Supporting Information

The following supporting information is available for this article:

Appendix S1. Choice of prior distributions
Figure S1. Plot of the Beta probability density function for 4 different sets of parameters. Beta(1, 1) is the uniform prior between 0 and 1. Beta(2, 2) is a slightly more informative probability distribution centered on 0.5 and giving a zero probability for values close to 0 and 1. Beta(1, 2) or Beta(2, 1) are triangular distributions giving a zero probability for values close to respectively 0 or 1.
Table S1. List of prior distributions assigned to unknown quantities of our model.

Supporting Information may be found in the online version of this article.