Investigating Atlantic salmon (Salmo salar) migration phenology using a long-term capture-recapture study : disentangling observation process from underlying ecological mechanisms using a Bayesian modelling approach

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University of Pau and pays de l'Adour
ED 211 - Sciences exactes et leurs applications

PhD thesis to obtain the title of **Doctor of Philosophy**

Speciality : Agronomy - Population biology and ecology

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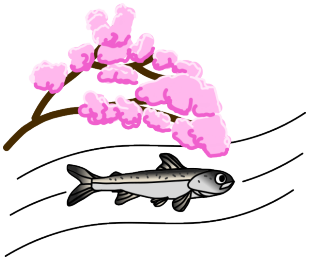

Under the supervision of Mathieu BUORO and Etienne PREVOST

Defended on November 6th, 2024
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Remerciements/Acknowledgments

First of all, I would like to thank my jury members, Emmanuelle Cam, Samu Mäntyniemi, Iain Malcolm and Eva Thorstad, who agreed to evaluate my work and for the very interesting discussions during my defense.

Ensuite, je voudrais remercier mes directeurs de thèse, Mathieu Buoro et Etienne Prévost. Merci pour tous ce que vous avez pu m'apprendre et pour le temps passé à répondre à mes questions. Merci aussi de m'avoir fait confiance, et de m'avoir permis de me lancer dans diverses aventures comme l'organisation de NoWPaS 2023.

Je tiens aussi à remercier l'équipe du Moulin des Princes, Nicolas Jeannot, Fabien Quendo et Yohann Guilloux pour tout ce qu'ils ont pu m'apprendre sur mon système d'étude, et sur les données dont je me suis servie. Merci Nicolas pour la visite détaillée du Scorff, et pour ton accueil toujours chaleureux. Et un grand merci à Nicolas et Fabien pour le temps passé à clarifier et vérifier les données, malgré nos demandes incessantes...

Un grand merci aux membres de mon comité de thèse, Colin Bouchard, Cyril Piou et Etienne Rivot. Merci pour toutes vos remarques et vos conseils qui ont fait avancer cette thèse. Je souhaite également exprimer ma gratitude envers Etienne Rivot en tant qu'enseignant. Merci pour le temps que tu m'as dédié, et pour tes conseils avisés lors de ma recherche de stage, puis de thèse. Je voudrais aussi remercier Colin en tant que collègue, merci aussi pour tous ces échanges, tes conseils, et... tes sarcasmes.

Ensuite, j'aimerais remercier tout le laboratoire ECOBIOP, parce que ma thèse n'aurait pas été la même sans vous. Merci à la direction, Jacques Labonne et Cédric Tentelier. Merci aussi à Cédric de m'avoir permis d'enseigner dans tes cours, et pour ton humour du même acabit que celui de Marius D. Et bien évidemment, MILESKER Pantxika pour toutes ces heures passées à organiser déplacements et autres... Merci aux autres membres de l'Aquapole que j'ai pu cotoyer, de l'UAR et de NUMEA.

Thank you to everyone who took part in NoWPaS 2022 and 2023, and in particular to the members of the NoWPaS 2023 committee. It was hard work, but we did it ! Une attention particulière à Coralie (depuis le début tu étais notre préférée) et Paolo, merci de rajouter un peu de piment dans cette aventure (Paolo, spero che la prossima volta che ci vedremo parlerai francese).

Un immense merci aux « jeunes » (doctorants, stagiaires, post-docs, ATER) de ECOBIOP et NUMEA qui ont pu passer par là au cours de ma thèse. La réussite d'une thèse passe aussi par l'environnement dans laquelle elle est menée, et quel meilleur environnement qu'avec vous ? Un grand merci à ceux qui nous ont accueillis avec le sourire, malgré la pandémie. Un merci particulier à Amaïa, pour tes conseils (et aussi pour ta thèse qui, à l'heure où j'écris m'est d'une grande aide...). Merci Marius D. pour ton humour du même acabit que celui de Cédric... On se rejoint in Hell(fest). Léa, t'es une championne, je n'aurais pu trouver meilleure voisine de bureau que toi. Mille merci aussi aux autres doctorantes d'ECOBIOP, arrivée après, Ambra (Grazie !), Eva (Milesker ! C'est bon tu as passé le test, tu es digne du meilleur bureau), Gaëlle (comment on dit merci en belge ?) (et Antoine, mais chuuuut). Merci aussi à Laura (et Loïc), Marius B., Hélène, Simon, Maud, Maxime D., Dorinda et les autres. Gros merci à Camille pour ton soutient en cette dernière année.

Enfin je ne remercierai jamais assez mes trois compagnons de routes, le Osasuna gang :

Mélanie (meilleur bureau), merci pour ton sourire, ton énergie, et d'être ce catalyseur d'aventures. Il n'y a bien qu'avec toi que je suivrais un inconnu dans une cave dans un pays étrangers. RDV aux prochains concerts (avec tes deux chevilles stp).

Soizig, merci d'avoir été mon alliée et ma concurrente du « nord » pendant ces 3 ans, même si tu jettes le beurre doux dehors (scandaleux). Comme on dit, jamais deux sans trois, j'ai donc hâte que l'on se retrouve de nouveau dans des laboratoires face à face, séparées par un couloir de la mort.

Stellia, on a pu avoir nos désaccords, et pourtant, c'est bien ensemble que l'on termine cette aventure (jusqu'au bout !). Cet été de redaction aurait été (encore plus) long sans toi, alors merci pour tout ! viens en Normandie, il y a du livarot. (Et je ne suis toujours pas bretonne, stop it)

Amélie H., tu te rajoutes à distance à cette bande infernale... Merci d'avoir été là pour parler code, modélo, genou pourri et écologie, merci pour ton énergie, et en attendant avec hâte nos futures randos.

Je remercie chaleureusement Jean-Claude et Josefa pour leur générosité et leur hospitalité, sans vous l'arrivée dans le pays basque n'aurait pas été la même (et merci d'avoir gardé la petite bête).

Mille merci à ma presque sœur, ma garde malade et podcasteuse préférée, Louise. Merci aussi à tous mes proches, plus ou moins lointain géographiquement, qui m'ont soutenu pendant ces 3 années. Tout d'abord, merci à mes

parents, pour votre aide pendant toutes ces années d'études, ces déménagements, et de supporter mes voyages un peu partout (je crois que ce n'est pas fini, désolée). Merci aussi maman pour tes relectures, même si tu n'y comprends pas grand-chose. Merci à Lise d'être si chia... euh, d'être une super sœur qui m'emmène aux JO, et d'avoir relu ma thèse (non) (ah si). Merci à mes grands-parents (coucou !), à David et Yumi (Arigatō), et à mes amis, Amélie N., Mikaëla, Sarah, Mélanie C., Marine, Junyi, Diane, Jeanne, Théo, Pierre, Louis, Victoire, Angeline, Mathys, Laurent, Sophie, Charlène, Clara, les « plans foireux », Smaug et Ashitaka et les autres. Merci aussi à Pascal, Claudine et Charlotte. Merci à M. Cappe et Clydie d'avoir cru en moi, et de m'avoir laissée être qui je suis.

Et parce qu'une thèse, c'est une épreuve d'endurance, je remercie tous ceux qui m'ont aidé à tenir, Camille G., Florence, Ninon, et tout le club atlantique taekwondo.

Enfin, Alan, comment te remercier ? Merci d'être là malgré tout, merci pour ton aide, merci pour tes « bêtises », merci pour tes intrusions (imposteur !) et merci simplement d'exister.

Pour finir, mon genou ne remercie pas le comptoir de Gantxiki.

"Just keep swimming"

Finding Nemo

Résumé

Les activités humaines sont à l'origine d'une crise de la biodiversité sans précédent. Les espèces migratrices sont particulièrement menacées, parce que la migration est risquée, et rend en outre ces espèces dépendantes de multiples environnements et de leur connectivité. La phénologie, c'est-à-dire le rythme auquel une espèce réalise un événement de son cycle de vie, influe fortement le coût global de ce dernier. Dans cette thèse, je me concentre sur la phénologie de la première migration vers la mer du saumon atlantique (*Salmo salar*), un événement crucial dans son cycle de vie. Le changement climatique perturbe de plus en plus la phénologie de nombreuses espèces, y compris les espèces migratrices. Il modifie notamment les traits d'histoire de vie et les facteurs environnementaux qui déclenchent la migration. Il peut en résulter une asynchronie entre les conditions requises par l'espèce pendant, ou à la suite de la migration considérée. La compréhension des mécanismes sous-jacents aux changements phénologiques est essentielle pour prédire l'impact que ces perturbations pourraient avoir sur les espèces. Cependant, ces mécanismes restent mal compris en raison de données incomplètes et/ou d'approches inadéquates pour leur analyse statistique. Pour étudier la première migration vers la mer du saumon atlantique, j'ai utilisé un suivi à long terme (25 ans) par marquage-recapture dans le Scorff (Bretagne, France). Les données collectées en milieu naturel sont sujettes à des variations dans le processus d'observation qui peuvent masquer ou biaiser notre appréhension des processus biologiques sous-jacents. Ceci est particulièrement important lorsqu'un facteur environnemental (tel que le débit) influence à la fois l'observation (par exemple l'efficacité d'un piège) et le processus biologique (déclenchement de la migration). Pour éviter des interprétations erronées, je propose une approche de modélisation bayésienne hiérarchique et mécaniste qui sépare explicitement le processus d'observation (capture par piégeage) et le processus dynamique d'intérêt (phénologie de la migration), les deux étant influencés par différents effets des facteurs environnementaux. Un premier modèle fournit une estimation des probabilités de capture et de leurs variations au cours du temps, ensuite utilisées dans un second modèle pour identifier les mécanismes de la phénologie de migration. Ce second modèle met en évidence l'importance de la température, du débit et de la variation du débit dans la décision de migration. Ces facteurs peuvent être perturbés par le changement climatique, je termine donc en explorant les conséquences possibles de ce dernier sur la phénologie et la taille des jeunes saumons lors de la migration vers la mer, les deux étant cruciales pour sa fitness. Ma thèse souligne l'importance de la modélisation mécaniste dans la compréhension des changements de la phénologie, et offre une perspective supplémentaire pour comprendre le déclin en cours des populations de saumon Atlantique.

Mots clés : Saumon atlantique, phénologie, migration, capture-marquage-recapture, modèle mecaniste, processus d'observation

Abstract

Human activities are at the root of an unprecedented biodiversity crisis. Migratory species are particularly at risk, because migration is risky and makes these species dependent on multiple environments and their connectivity. Phenology, i.e. the timing at which a species completes an event of its life cycle, has a strong influence on the overall cost of that event. In this thesis, I focus on the phenology of the first seaward migration of Atlantic salmon (*Salmo salar*, A. salmon), a crucial event in its life cycle. Climate change is increasingly disrupting the phenology of many species, including migratory species. In particular, it is altering the life-history traits and environmental cues that trigger migration. This can result in asynchrony between the conditions required by the species during, or following, the migration in question. Understanding the mechanisms underlying phenological changes is essential for predicting the impact that these disturbances could have on species. However, these mechanisms remain poorly understood due to incomplete data and/or inadequate approaches to their statistical analysis. To study the first seaward migration of A. salmon, I used long-term (25 years) mark-recapture monitoring in the Scorff river (Brittany, France). Data collected in the natural environment are subject to variations in the observation process that can mask or bias our understanding of the underlying biological processes. This is particularly important when an environmental factor (such as flow rate) influences both the observation (for example, the effectiveness of a trap) and the biological process (triggering of migration). To avoid misinterpretations, I propose a hierarchical, mechanistic Bayesian modelling approach that explicitly separates the observation process (capture efficiency) and the dynamic process of interest (migration phenology), both of which are influenced by different effects of environmental factors. A first model provides an estimate of capture probabilities and their variations over time, which are then used in a second model to identify the mechanisms of migration phenology. This second model highlights the importance of temperature, discharge and discharge variation in the migration decision. These factors may be disrupted by climate change, so I conclude by exploring the possible consequences of climate change on the phenology and size of young salmon during their migration to the sea, both of which are crucial to their fitness. My thesis highlights the importance of mechanistic modelling in understanding changes in phenology, and offers an additional perspective for understanding the ongoing decline in Atlantic salmon populations.

Keywords : Atlantic salmon, phenology, migration, capture-mark-recapture, mechanistic model, observation process

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A. salmon	Atlantic salmon
AIS	Alien Invasive Species
CDF	Cumulative distribution function
CF	Cumulative capture frequency
CMR	Capture Mark Recapture
DOY	Day of year
Eq.	Equation
Fig.	Figure
ppi	Posterior probability intervals

Chapter 1

Introduction

Current global changes caused by human activities are having a significant impact on biodiversity. Species have the capacity to modify their ecological niches in response to these changes along different axes, notably physiological, geographical and temporal, i.e. phenological (Bellard et al., 2012). Phenological changes, such as changes in flowering, reproduction or migration timing, are one of the main responses of biodiversity observed during the 20th century (Bellard et al., 2012). These changes can have profound consequences for the fitness of individuals, influencing their survival and/or reproductive success. Over time, these changes can influence population demographics, contributing to the sixth mass extinction of biodiversity.

In some contexts, migratory species are more at risk of extinction than resident species (Hardesty-Moore et al., 2018). This seems to be partly linked to the loss of connectivity and the dangers they face during their migration. Migration phenology, by synchronising migration with the beneficial travel and/or arrival conditions, helps to reduce the overall cost of migration (Bauer et al., 2015; Charmantier et al., 2014; Visser et al., 2012; Koelzsch et al., 2014). Consequently, disruption in migration phenology may increase the risk to these species.

In this introductory chapter, I address the following question: **What are the mechanisms by which climate change modifies phenology, and what are the consequences for species?** I then apply these questions more specifically to a crucial stage in the life-cycle of certain species, including Atlantic salmon (*Salmo salar*): **migration**.

1.1 Phenology, an adaptive process disrupted by climate change: what consequences for the migration?

1.1.1 Importance and functioning of phenology

Phenology : definition and scale

The phenology is the science of the occurrence of a biological event (Lieth, 1974), and by extension, also refers to the timing of the biological event itself (Macphie et al., 2024). Phenology seeks to understand the periodicity of a biological event and its synchronisation with cues (Lieth, 1974; Macphie et al., 2024). One of the most famous example is the blooming of the cherry blosoom, the sakura (*Prunus jamasakura*) in Japan. The flowering date of sakura (Fig. 1.1.c.) has been recorded for centuries, back to 812 AD (Visser, 2022) , because of its cultural importance. These tree flowers mostly during April, but the exact date is variable from year to year. The temperature and the photoperiod are assumed to be the cues that trigger the flowering (Visser, 2022).

The time frame considered here is not the individual's own timeline, i.e. the age of the individual or the age from which they decide to cover a particular stage in their life-cycle (life history trait), even though this is a factor that can influence an individual's phenology (Bonamour et al., 2020). The time frame considered here is an external frame of reference, often a calendar. Still, phenology can be studied across different time scales.

In temperate regions, the environment changes annually due to seasonal variations, making the phenology strongly linked with seasons. Hence, many phenological studies are conducted on an annual basis. However, in certain extreme regions, the occurrence of certain biological events is synchronised over a period shorter or longer than the year. For example, the spectacular flowering in the Acatama desert follows a periodicity of several years. In fact, in this desert, droughts last from 2 to 5 years. The flowers only bloom after a certain amount of rain at a specific time-window in winter, so they do not bloom on an annual basis but depending on the drought duration (Vidiella et al., 1999).
More generally, in tropical regions, the season are more tenuous and can have less effect on the community. The wet and dry seasons may be a cue for certain species, but other parameters such as el Niño, which is cyclical over a period of 2 to 7 years, impose a completely different periodicity. Therefore the phenology strategies of the tropical species are diverse and must be looked at different time scale, often longer than a year (Sakai, 2001).

Figure 1.1 – **Biological event illustration**: a. Sperm whales (*Physeter macrocephalus*) in Guadeloupe, France: solitary and migratory, male sperm whales come to warmer waters at the same period each year to breed. b. Greater flamingos (*Phoenicopterus roseus*) in Camargue, France: bird reproduction is a highly studied phenological event. c. Sakura (*Prunus spp.*), in Japan: The cherry blossom is an iconic phenological event. d. Flax flowering (*Linum usitatissimum*) in Normandy, France: the phenology of crops is also closely monitored, with here the ephemeral flowering of flax forming pretty blue fields.

Phenology can also be studied at different geographical scales. As environmental conditions change depending on the geographical area, the phenology of an event may vary across the range of a species. Even on a local scale, phenology can vary according to microclimate, genetic variation and local adaptation the population. For example, the great tit (*Parus major*) breeding phenology is correlated with the phenology of the vegetation within a few hundred metres of their nest (Hinks et al., 2015). Thus, the geographical scale must be carefully defined.

Finally, phenology can be studied at different levels of biological organisation, from the individual to the ecosystem. It is common to study the phenology of an entire community, as the needs of species that compose it can be very similar. For example, the blooming of phytoplankton or the leaf budding on trees in the same forest. Interactions between species, in particular between prey and predators, constitutes a large part of phenology studies, thanks in particular to within the match-mismatch hypothesis (see section 1.1.2).

An adaptive process depending on cues

In the life history theory, evolution occurs as a response to natural selection to optimize the survival and the reproduction of the individuals, i.e. the two components of fitness (Fabian et al., 2012). Life history strategies have different consequences on the fitness of an individual, that is why some strategies are selected more than other in a population. Phenology often influences fitness (e.g. the timing of reproduction) and is considered a key component of life history strategy (Macphie et al., 2024). Indeed, an individual who synchronises the different stages of its life-cycle with the optimal external conditions can enhance fitness. For example, the winter moth (*Operophtera brumata*) that synchronizes the hatching of its eggs with the bud burst of the pedunculate oak (*Quercus robur*) maximizes its fitness. If they hatch too early before the bud burst, they would not find enough food, which decrease their survival. If they hatch too late, they would feed on older leaves, which decrease the growth of the caterpillars and thus of their fecundity. Hence, if the winter moths synchronize their reproduction with the bud burst, the caterpillars can feed on young leaves, promoting the growth (e.g. the fecundity) and the survival of the caterpillar, thus for their fitness and their parents' fitness (Van Asch et al., 2007).

Because timing of events is often based on external signals such as environmental or social factors, phenological plasticity (phenotypic plasticity in the timing of life-history transitions) plays an important role in the response to environmental changes. This plasticity allows the species to accommodate to

the variation of the external conditions such as the variability of the weather each year (Hendry, 2017; Macphie et al., 2024). To pursue the example of the winter moth, the hatching date varies from year to year depending on the temperature (Van Asch et al., 2007). For the plasticity to be adaptive, it should be influenced by reliable cues (Hendry, 2017). For the phenology, the cues used by species were selected through evolution as a reliable predictor of the favorable environmental conditions.

For a life-cycle event to occur, individuals must be ready to ensure it. For example, an individual must be sexually mature to reproduce. Then they can become sensitive to the cues that trigger the event itself. Cues influencing the phenology can be separated in internal factor, time related factors and external factors (Duriez et al., 2009). The internal cues enable the individual to be ready. These internal cues, such as the endogenous circadian rhythms (Wells et al., 2022; Chuine et al., 2017), are determined by the genetics. Indeed, evolution can influence phenology because it is partly determined by genetics. Thanks to the new tools that make it possible to study population genomics, studies are being carried out to find the genetic basis of phenology. For example, Barry et al. (2024b) identified the region associated with the pink salmon (*Oncorhynchus gorbuscha*) migration timing. Studies of this kind can also highlight local adaptations, as in the case of the European beech (*Fagus sylvatica*), whose bud burst phenology, genetically determined, changes according to the climate (Meger et al., 2021). The physiological state of the individual is also an internal cue involved in the phenology determination. The individual must attain a certain physiological state to ensure some specific life-cycle events. For example, the starry flounder (*Platichthys stellatus*) must attain a critical size before enduring metamorphosis. This may be because they necessitate a certain amount of energy after metamorphosis, and the critical size ensure they have the energy needed (Policansky, 1983).

When an individual is ready, it can be sensitive to other cues during a specific window of sensitivity (Gienapp et al., 2014). The other cues are external, and can be divided into abiotic and biotic types. Abiotic cues, such as the photoperiod, are reliable as they remain constant from year to year. The photoperiod is often used by species as an indicator of the annual cycle (Macphie et al., 2024). But other environmental factors are variable from year to year, and some of them are used as cues for the phenology depending on the ecosystems. Indeed, in polar regions, snowmelt and warmer temperature, coupled with photoperiod, are often cues used by species (Macphie et al., 2024; Visser, 2022). On the contrary, the tropical regions present less seasonal variation, and species used more diverse and variable cues like the rainfall or the drought (Macphie et al., 2024; Sakai et al., 2019; Visser, 2022). In temperate regions, the temperature is more reliable than the snowmelt in polar regions, making temperature, sometimes combined with the photoperiod, the main cues in temperate regions (Macphie et al., 2024). For instance, the phenology of the winter moth hatching is sensitive to the temperature

(Van Asch et al., 2007). To conclude, even if the cues they are sensitive to is species-specific, species within an ecosystem frequently share some abiotic cues, as they are a reliable predictor of the environmental conditions.

The final category is biotic cues which involve the influence of other species, such as the presence of a predator or prey. They can also be population-specific parameters, such as sex-ratio, or density. For example, for the species *Trogoderma glabrum*, female pupation is triggered by the density and the presence of males (Beck, 1971). Biotic factors also comprise social interactions, learning... The case of collective migration in sockeye salmon *(Oncoryhnchus nerka)* is an example of social interaction. They migrate towards their spawning site in "discrete pulses", which seems to be a social behaviour: the salmon sweep each other along (Berdahl et al., 2017).

Limits and constraints of the phenology: is phenology always optimized?

There are, however, certain restrictions on how closely the ideal conditions and a species' timing may coincide with each other. Constraints and trade-off among the life history traits can limit the possibility to adapt the strategy (Stearns, 1992; Stearns, 2000; Fabian et al., 2012). There are many reasons why the phenology of a life-cycle event is not optimized, as reviewed by Singer et al. (2010). I will explain some of them below, though the list is not exhaustive.

First of all, genetic constraints may limit phenological adaptation (Hendry, 2017; Singer et al., 2010). Constraints can occur at the molecular level when two life history traits, one related to phenology, are genetically linked but subject to different selection pressures. This genetic linkage can hinder the independent adaptation of each trait. Ultimately, phenological responses are limited by factors such as genetic variations, genetic and physiological correlations, and the intensity and speed of environmental changes, which can be faster than the genetic adaptation (Bauer et al., 2011).

Another constraint to the phenological response is the life-cycle itself: the timing of an event can depend on the timing of the preceding events. For example, an individual cannot reproduce if it has not matured yet. Therefore, the phenology of the reproduction is constraint on the left of the time scale by the phenology of the maturation. This can be more or less constraining depending on the life-cycle.

An individual must maximize its fitness on the whole life-cycle (i.e. Life Time Reproductive success, Ehrlén, 2015). Sometimes, there are trade-off between the phenology of an event and another life-history trait. Therefore, the phenology of the event is "sacrified" because the cost of the asynchrony is less important than the other trait. For example, the bay checkerspot butterfly (*Euphydryas editha bayensis*), lays its eggs on a plant so that the larvae can feed before to enter in diapause. But the bay checkerspot lay late in the season, and some of the larvae hatch on a dried or a senescing host. Therefore, the hatching of the larvae is asynchronous with the more favorable condition, meaning a sufficiently vigorous host to assure the growth of the larvae before the diapause. If this asynchrony is not fully understood, a trade-off between the fecundity of the parents and the survival of the larvae is suspected. The longer the parents delay reproduction, the more they grow and enhance their fecundity, but it comes at the detriment of larvae survival (Singer et al., 2010).

Even if the mean phenology of the population is synchronous with the optimal conditions for a given event, it can be advantageous for some individuals to advance or delay their event. For example, arriving too early on the breeding ground can be detrimental if exposed to harsh environmental conditions. However, if the territorial competition is strong, arriving before the optimal timing can be advantageous as the early bird will secure the best territories to breed (Johansson et al., 2012).

Another reason why phenology can be suboptimal is when the correlation between the cue and the environment factor needed by the species is weak. This can result in phenology being more or less synchronised with the environmental factor. This is of particular importance in the context of climate change, which can disrupt the relationship between the cues and the environment, making the cue a less reliable predictor of optimal conditions (see section 1.1.2).

1.1.2 When phenology is shaken up by climate change

The evidence of a change

Some phenological events have been observed to occur earlier or latter over some decades. As seen in the section 1.1.1, the japan cherry blossom is recorded for centuries. Since the 1830's, however, the date of this events has advanced (fig.1.2), a change that correlates with the rising temperatures. Therefore, the advancing date of the sakura seems to be a marker of the influence of the climate change on its phenology (Visser, 2022).

Another famous example is the effect of climate change on the crop, such as vine maturation. The vine phenology is closely related to the temperature, and because of the increasing temperature, its phenology has advanced.

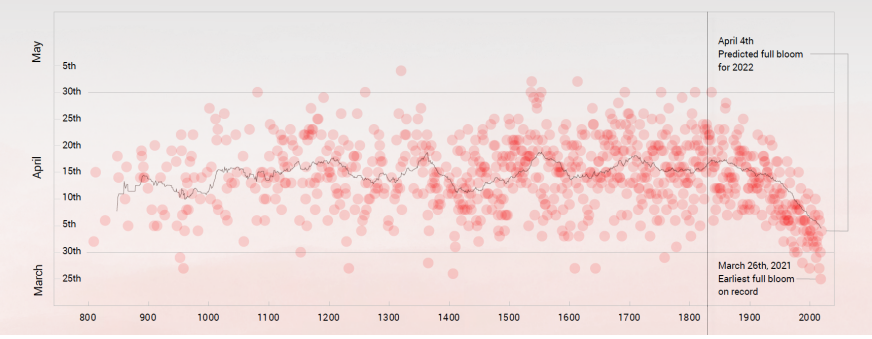

Figure 1.2 – **Blooming of the cherry blossom over 1200 years, in Japan, from Visser (2022).**: the vertical line indicate the 1830's

This is particularly visible from the harvest dates. For example in some French vineyards, the harvest date has advanced by 2 weeks since the 1980's, and is predicted to continue to advance. This can affect the wine quality, and therefore economical and sociological consequences (Leeuwen et al., 2016).

These two examples are impacting by their cultural and sociological importance, but there are only the tip of the iceberg. Many studies now focus on the impact of the climate change across different taxa, and the conclusion is univocal, the climate does has impact on the phenology of multiple species (Piao et al., 2019; Visser, 2022; Macphie et al., 2024; Charmantier et al., 2014; Wells et al., 2022). For instance, birds are showing advancements in their timing of migration and breeding (Charmantier et al., 2014; Visser, 2022), plants are flowering earlier (Visser, 2022), and some mammals are emerging earlier from their hibernation (Wells et al., 2022).

Next, I reviewed the main impacts of climate change on phenology, and what are the consequences at the individual levels, and at the population level, focusing on wild species.

How can climate change impacts phenology?

Species present diverse reactions and sensitivity to climate change (Piao et al., 2019; Sakai et al., 2019; Macphie et al., 2024; Visser, 2022; Iler et al., 2021; Thackeray et al., 2016). **What are the mechanism of the phenological shift? How can we explain the variability in phenological response?**

Climate change can affect the phenology of species for different reasons. First, it can impact directly the physiology of individuals and therefore life history traits, including their phenology. For example, temperature influences growth; higher temperature, up to a species-specific optimum (Gray et al.,

2016), can reduce developmental time (Gillooly et al., 2002). Therefore, an individual can be ready for the event earlier. Another example comes from the increased concentration of CO_2 in the atmosphere which can prolong certain events such as the growing season for some plants species, or delay others, like senescence. However, the underlying molecular mechanisms of these changes are not well understood (Gray et al., 2016).

Secondly, climate change can modify the cues that the species use to determine their phenology. However, the responses driven by these modifications vary among species and individuals due to differences in the underlying biological mechanisms involved (Chmura et al., 2019). To what extent an organism or species can modify its phenology to cope with the environmental change depends on factors such as its plasticity (Hendry, 2017; Chmura et al., 2019), sensitivity to the modification, perception of the modification, and speed of response. Behaviour adaptations can also foster the response to these modifications (Chmura et al., 2019). The response would also depends on some constraints, as explained in the section above 1.1.1; the phenology can be constrained by the life-cycle or physiological state of the individual. Therefore, different species, populations or even individuals would have different responses to the same modification (Inouye et al., 2019). For example, at a micro geographic scale in 4 Mediterranean populations of blue tit (*Cyanistes caeruleus*), warmer temperatures are associated with early laying dates. The 4 populations present different plastic responses to warmer temperatures, with one population showing limited plasticity. In two of the populations, the inter-individual variation of plasticity was significant, meaning that some females present more a important modification of their laying date with the temperature than others. Therefore, even among geographically close populations of the same species, the phenological shift can differ because of differences in plasticity (Porlier et al., 2012). Different responses for laying date have been also observed within the British and the Dutch populations of blue tits (see section 1.1.2).

Many key-factors have been suggested in order to find some generality in the variability of the phenological shift, with some group showing more phenological shift than other. Among these factors, we can cite the latitude, the altitude, the habitats (marine, freshwater, terrestrial...), the length of the migration, the specialist or generalist diet at the early season vs late season behaviour (Chmura et al., 2019). For example, Thackeray et al. (2016) suggest that the sensitivity can change with the trophic level, with the primary consumers more likely to show a shift in their timing than primary producers and secondary consumer. The limits of theses studies is that there is often a confusion or incertitude between the role of the environment and the role of the organismal response. Do the species differ in the way they respond to the environmental change, or do they differ in the environmental shift they are exposed to ? (Chmura et al., 2019) (see section 1.3).

Also, species can rely on several cues that can lead to opposing responses.

In conclusion, phenological shifts exist and are projected to increase in the future, but predicting them remains challenging due to our lack of understanding of the mechanisms underlying responses to environmental changes. Still, these shifts are expected to have consequences for individual fitness, and consequently, for the population demography. The following sections aim to examine these predictions.

Consequences: asynchrony with optimal environmental conditions?

Climate change can disrupt the synchrony between the conditions that an individual require and the optimal environmental conditions, due to an insufficient response to a changing cue (see section 1.1.2). Sometimes the cue itself corresponds to the optimal environmental factor that the species needs, while in other cases, it merely serves as an indirect indicator. Then, a change in the relationship between the cue and the optimal environmental condition can make the cue unreliable. For example, the flower are fragile structure that are sensitive to frost (Chuine et al., 2017). Warm spring temperature are a cue to flowering in many plants (Visser, 2022; Leeuwen et al., 2016; Wheeler et al., 2015), and warm temperature serves as an indicator of low frost risk. But in the context of climate change, the correlation between the cue and the optimal condition can be reduced (Charmantier et al., 2014). In the example above, warmer spring temperature and early snowmelt can lead to earlier flowering (Leeuwen et al., 2016; Visser, 2022). Nevertheless, earlier warm spring temperatures do not guarantee the absence of frost, therefore earlier flowering can increase the risk of exposure to frost damage (Wheeler et al., 2015).

The figure (fig.1.3) illustrates different causes of asynchrony. Let us take a simple example with one variable cue that determines the phenology of an organism, allowing it to synchronize its phenology with an environmental factors. In the panel a, this is the initial situation, the organism responds immediately (which is not always the case) to the cue and is synchronized with the environmental factor important for its fitness. In panels b to e, the cue is advanced, with different reactions of the organism. In b, the organism follows the cue, and the cue is correlated with the environmental factor. Therefore, the organism is still synchronized with the environmental factor. In d, the organism follows the cue but the cue is no longer a reliable predictor of the environmental factor (the correlation has decreased), leading to an asynchrony between the organism phenology and the environmental factor.

In c, the cue is still well synchronized with the environmental factor, but the organism does not succeed in following well the cue. In panel e, the organism is also unable to follow the cue, plus the cue is no longer a reliable predictor of the environmental factor. In the present case, the imperfect response of the organism to the cue modification buffers the asynchrony. Note that the e situation can also lead to asynchrony, for example if the environmental factor is delayed. Consequently, different situation can lead to asynchrony, whether because of organism's reason or heterogeneous changes in environment (IPCC, 2014) leading to weaker correlation between the cue and the environmental factor of interest. But this case may be too simplistic. In reality, organisms need often more than one environmental factor (f), and can rely on different cues, leading to even more possible situations and asynchrony.

A disturbance of the phenology of an organism can modify the environment it has to endure, which can have negative consequences for the fitness of the individual. Facing new environmental conditions, the survival or the fecundity can be reduced. For example, earlier breeding in white stork *Ciconia ciconia* expose the juveniles to more extreme weather conditions, leading to reduce survival (Visser, 2022). Similarly, early flowering exposes to a risk of frost damage, which can reduce the plant fecundity.

Nevertheless, the consequence is not always negative. For example, because of earlier snowmelt and latter snow fall, the active season for mammalian hibernators can be longer. In some case, it can be detrimental such as for the Alpine marmots (Wells et al., 2022), maybe due to longer period exposed to predation. But in other case, it can be advantageous by reducing the cost of the hibernation and allowing the animal to grow more (especially the juveniles), such as for the yellow-bellied marmots (Wells et al., 2022). Therefore, generalization must be made with caution and predictions can be difficult to make.

In this section, the asynchrony is treated with abiotic parameters, but there can be also asynchrony with biotic parameters. Asynchrony with biotic parameter, the so-called "match-mismatch theory" (Cushing, 1969), is treated in the next section.

The match-mismatch theory

To optimize its fitness, a predator should synchronize its life-cycle with the peak abundance of its resource. This is the basis of the match-mismatch theory, attributed to Cushing (1969). Cushing based his theory on the fact that certain fish reproduce at roughly the same time each year, with successful recruitment depending on the synchronisation between the hatching

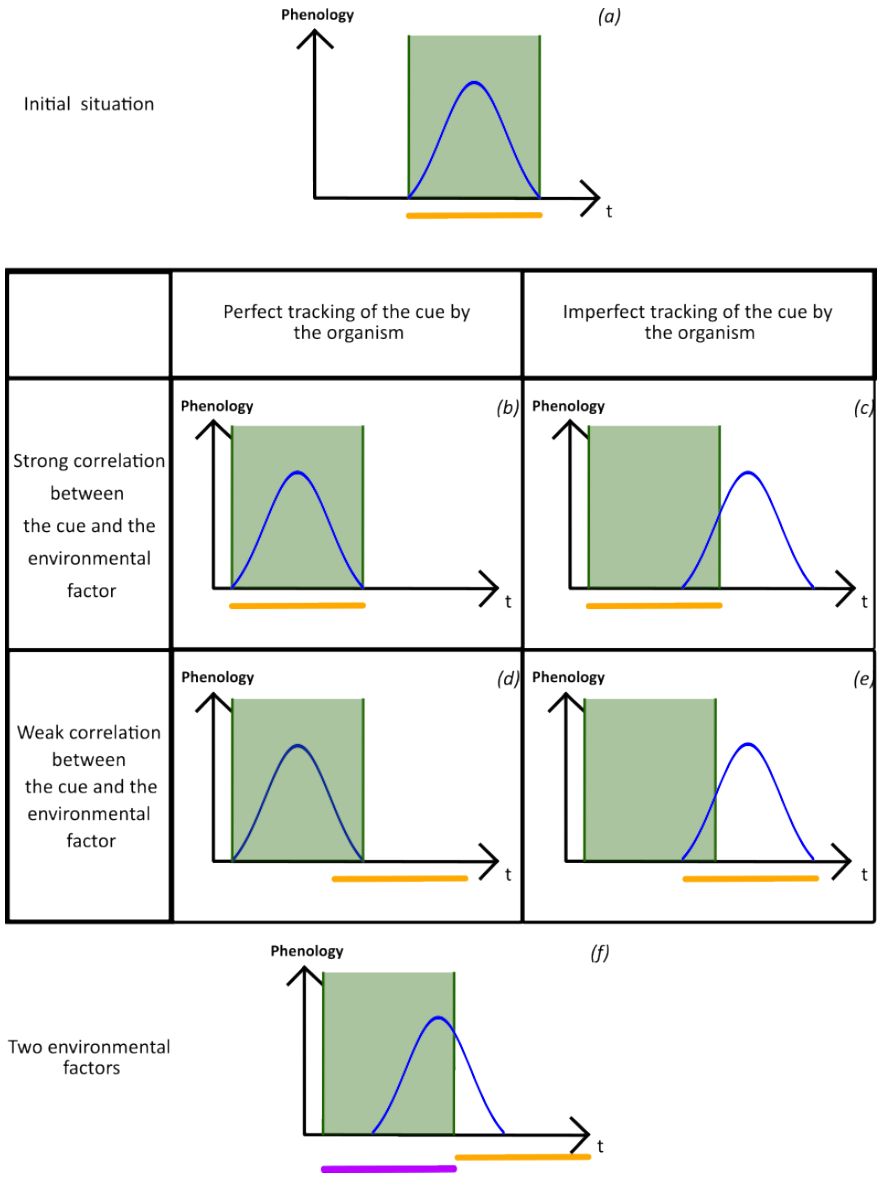

Figure 1.3 – **Possible phenological response of an organism in a changing environment.** The blue curve represents the organism phenology, the green rectangle represents the cue and the colored lines represent an optimal environmental factor. Modified from Iler et al. (2021).

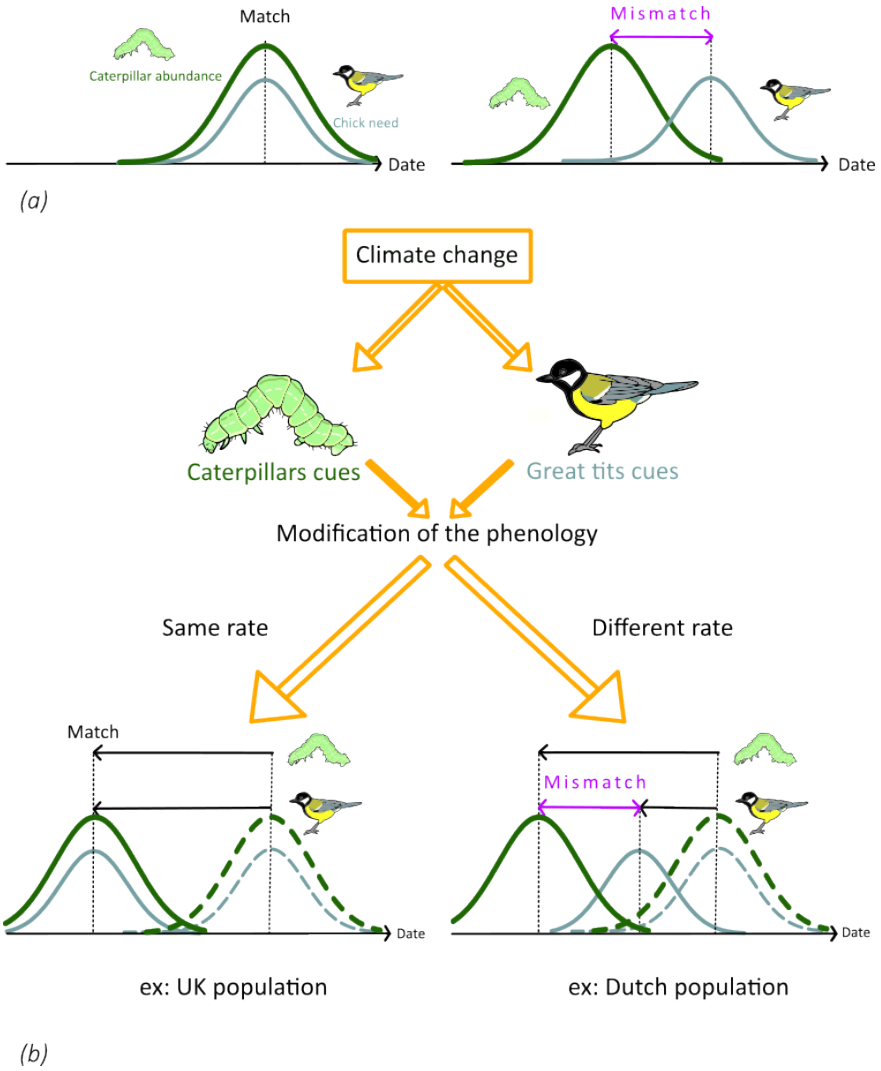

Figure 1.4 – **Illustration of the match-mismatch hypothesis with the study case of the great tit and the caterpillars** a. Match between peak caterpillar abundance and the needs of the great tit (left) and mismatch (right). b. Solid line: phenology with climate change, dotted line: phenology before climate change. Climate change effect on the phenology of the two species in two populations. In the UK, the two species change their phenology at the same rate, which maintains the match, whereas in the Dutch population, the change of phenology of the two species differ, leading to a mismatch.

of the larvae and the peak in plankton abundance. The hypothesis is that when the larvae arrive during the peak of plankton, their food, they have an optimal growth and survival: this is considered a match. However, if they arrive too late or too early, this is a mismatch, and this is detrimental to the recruitment. In this original sense, match-mismatch theory focuses on a predator relying strongly on a seasonal resource. Therefore, in case of a mismatch, the individual fitness of the predator decreases.

Nevertheless, species can interact with an other species, via other relationships such as competition, predation, mutualism... Therefore, the match-mismatch theory has been extended to treat the effect of a mismatch in other type of relationship. Certain authors prefer to use the concept of synchrony and asynchrony, that can be more nuanced that match-mismatch (Johansson et al., 2015). Even in the case of other relationships than prey-predator, the focus is on the species that benefit from the synchrony (Johansson et al., 2015). However, the case of prey/predator remains the most studied (Iler et al., 2021; Visser et al., 2019).

Two species (or group of species such as the plankton in the preceding example) in interaction can have different cues that determine their timing. They can also have different responses to climate change (see section 1.1.2), different rates of change. This can lead to different changes in their respective phenology, causing mismatch. This is the same principle as seen in Fig.1.3, replacing the environmental factor by the phenology of another species. This is why it is suggested that climate change will increase the mismatch occurrence (Visser et al., 2019).

A famous and well-known case is the example of the caterpillar, principally the winter moth, and the great tit. Great tit chicks feed on caterpillars, and their peak nutritional needs occurring approximately 8-10 days after hatching. Caterpillars hatch with the leaf emergence, and reach a peak abundance during the spring. Therefore, when the parents great tit adjust their breeding at a precise date, synchronising the chick peak nutritional needs with the abundance peak of the caterpillar, the chick's survival is optimized. This is a match. If parents do not succeed in synchronizing this peak, this is detrimental for the chick survival and therefore for their individual fitness (Reed et al., 2013; Simmonds et al., 2020). This is a mismatch (Fig. 1.4. a.).

However, the mismatch is not the same for all tit populations. In the United Kingdom (UK), both caterpillars and great tits have advanced their phenology of around 14 days in 50 years. Therefore they are still in "match"

(Charmantier et al., 2008). In contrast, in Netherlands, the caterpillar phenology is advancing more rapidly than the phenology of great tits, leading to a mismatch (Reed et al., 2013; Simmonds et al., 2020).

It has to be noted that the match-mismatch theory present limits, as a mismatch has fitness consequences only when some restrictive hypothesis are met. For instance, the predator must rely strongly on one species or a group of species (such as caterpillars), at a precise moment of its life-cycle, and the resource must be seasonal with a narrow window of occurrence (Kharouba et al., 2023; Iler et al., 2021; Johansson et al., 2015). Furthermore, other components such as density-dependence can buffer the mismatch effect (see review by Johansson et al., 2015).

Hereafter, I will use the term "mismatch" to refer to asynchrony in biotic relationship (predation, prey...) and "asynchrony" mostly for discrepancies with abiotic factors (temperature, weather...).

Demographic consequences

Mismatch and asynchrony can decrease the fitness of an individual. *But what about the population? Will this lead to a population collapse?* Maximizing the fitness of individuals do not always enhance the population growth. Therefore, a change in the phenology could have a variety of consequences on the population (Lindén, 2018).

Let us take the example of great tits again. In the case of the Dutch population, the individual fitness of the asynchronous parents decreases compared to early breeder. Nevertheless, no demographic consequences were found (Reed et al., 2013). This can be due to density dependence as the competition among the chick was relaxed (Iler et al., 2021; Visser et al., 2019). This can also be due to other factors that are more determinant on the chick survival at the population scale (Reed et al., 2013). Even if asynchrony reduces the fitness during an event, individuals have to maximize their fitness over all the life-cycle, and then this reduction can be counter-balanced (Ehrlén, 2015). Their last hypothesis was that the signal could be very noisy and prevent the detection of a demographic impact.

This example points out that other factors can buffer the phenological effect on demography. This can explain why in their review, Iler et al. (2021) found that the negative impacts of mismatch on demography are found only in restrictive cases. In some cases, it can even have positive impacts (Iler et al., 2021). For instance, a prey can benefit from the mismatch with its predators such as in the case of mismatch maintained by "arms race" (Singer et al., 2010).

Other factors of importance that can modulate both the fitness and demographic impact of the phenological shift are the eco-evolutionnary process. Actually, species can buffer the effect of climate change by limiting the mismatch through micro-evolution.

Back to the great tit example. There is no or few demographic consequences for now for the Dutch population, but the climate change is projected to intensify (IPCC, 2014). Simulation studies have been carried out to identify whether different scenarios of climate change can lead to demographic consequences on great tits. During some decades, the great tit plasticity can buffer the climate change effect, by keeping the mismatch of the population sufficiently short to not produce demographic consequences. But the prey phenology changes at a faster rate (Gienapp et al., 2013; Reed et al., 2013; Simmonds et al., 2020). As the climate change progress, neither the plasticity nor the micro-evolution are enough to keep this mismatch under a certain threshold. When this threshold is attained, the simulated abundance of great tit decreases, with a risk of extinction (Simmonds et al., 2020; Visser et al., 2019).

The case of the great tit illustrates that the phenological shift do not lead to a population collapse immediately, and that micro-evolution can buffer the climate change effects. To fully understand the impact of phenological shift on population demography, the eco-evolutionary processes must also be taken into account. Since species and populations differ in their plasticity and genetic variance, they can also differ in their adaptive potential. In addition, plasticity and genetic variance interact, making the prediction of phenological response even more complex. For example, Anderson et al. (2013) simulate the impact of phenological shift on marine migrating species, with different levels of plasticity and genetic variance. After a few decades of increased climate change, their scenarios show a risk of extinction of the population due to asynchrony. With fixed plasticity, an average genetic variance was optimal compare to stronger or weaker values. High plasticity is an advantage in the short term, but in the long term it prevents adaptation, leading to the risk of extinction of the population. Even if no effect is observed for the moment, this could be a tickin time-bomb hidden by the plasticity (Simmonds et al., 2020; Anderson et al., 2013).

In conclusion, mismatch and asynchrony have been shown in some case to have negative impact on population demography (Iler et al., 2021; Visser et al., 2019). However, for the moment, it is difficult to disentangle and quantify the processes involved in order to make accurate projections (Chmura et al., 2019; Iler et al., 2021; Visser et al., 2019; Johansson et al., 2015).

1.1.3 Migration phenology

The steps and the cues of migration phenology

Migration is "a periodic movement of animals between habitats" (Visser, 2022), which includes round-trip movements (Newton, 2024a). Migration allows species to benefit from the resources of the different habitats they move to, at the most favourable time (Newton, 2024a). For instance, migrating birds migrate to breeding grounds when the food is the most abundant, which is an optimal conditions for their offspring and for themselves (Newton, 2024a). Then, migration is an important part of the life-cycle of some species, but it can be a costly and hazardous stage. Indeed, migration is energy consuming, and can expose to high risk of predation, bad weather conditions etc. (Newton, 2024b). Adaptation of the behaviour, of the physiology, of the phenotypic plasticity and of the phenology can help to reduce the overall cost of the migration (Alerstam, 2011).

The phenology of migration is the timing at which the individual onsets its migration from an habitat to another (Bauer et al., 2015). Precisely, the migration process can be divided in four steps: the preparation of migration, the departure, the journey and the arrival (Johansson et al., 2015). Therefore, studying the phenology of migration consists in studying the time and duration of these different steps (Bauer et al., 2015). What causes the preparation and departure of an individual? Is there any change in the behaviour and duration of the migration? How does the time of departure or arrival affect fitness? How does the time of departure or arrival affect population dynamic?

As for other phenological process, many cues are used by species, indicating them the timing of each step of migration that optimize their fitness. These cues are similar to those triggering other phenological processes (see section 1.1.1), and can initiate the preparation to migrate and departure. It is important to note that internal cues are essential for migratory species as 1) migration is highly energy consuming and 2) the external cues in the departure environment can be poor predictors of the conditions in the arrival environment.

The energetic state of the individual can play a role in departure decision. An individual migrates only when “a threshold state is reached” Bauer et al., 2011, meaning it has accumulated enough energy reserves to engage physiological or morphological changes required and undertake the energy-demanding journey. For instance, some birds stop off at stopover sites during their migration, allowing them to rest and restore their energy reserves. This can explain why some of them pursue their migration only after a certain amount

of time (Roques et al., 2021). Some birds which migrate through an ecological barrier, leave the stopover site only when they have reached a certain energy deposition, sufficient to pass through the barrier. For other species, without ecological barrier, the departure depends on the energetic deposition rate (Schaub et al., 2008).

Secondly, migration behaviour is partially controlled by genetics (Bearhop et al., 2005; Bauer et al., 2011) as some species present an endogenous circannual rhythm, predisposing them to migrate at certain time. For instance, endogenous circannual rhythm of birds is involved in the preparation, departure or behaviour during migration (Gwinner, 2003; Newton, 2024a). Laboratory experiments have shown that the endogenous circannual rhythm works independently of the environmental cues (Newton, 2024b).

The importance of migration phenology and climate change threat

The timing of migration is important because it has consequences on the biotic and abiotic conditions during the journey and upon arrival.

Biotic conditions include the prey availability and presence of predator. For example, the migration phenology of the barnacle goose allow them to arrive at the onset of spring at each stopover, when the food availability increases, allowing them to replete enough energy before continuing their migration (Koelzsch et al., 2014). Parasites and diseases are important too, as migrants seem to be adapted to the parasites and diseases they encounter on their way during migration. Therefore, change in the timing of migration can have consequences on the host-parasite relationship (Møller et al., 2010; Altizer et al., 2011).

Survival depends also on the abiotic conditions. An asynchrony between migration timing and abiotic conditions required by the organism can reduce survival and thus their fitness (Bauer et al., 2015). For example, the white storks (*Ciconia ciconia*) present a high variability in the migration timing, but the birds are exposed to different weather conditions. Indeed, early birds benefit from better weather conditions such as more supportive winds, and then spend less energy for their migration than the latter birds (Acácio et al., 2022). This shows that migration timing is crucial to encounter optimal migratory conditions.

It should be noted that, as seen in the section 1.1.1, migration phenology can be suboptimal. For example, birds preferentially synchronise their reproduction with the optimal conditions, but to the detriment of migration conditions. This could explain why immature birds (non-breeders) sometimes have a

different migration timing compared to breeders. As they are not constrained by reproduction, they adjust to the optimal travel conditions (Newton, 2024b).

As with other events in the life-cycle, climate change can disrupt phenology and threaten species (see section 1.1.2). Long-travelling species are particularly at risk, as climate change can disturb differently the departure and arrival environments. Therefore, if for any reasons, the cues of departure are not synchronous anymore with the optimal travel or arrival conditions, it can be a risk for the individual survival (Charmantier et al., 2014; Visser et al., 2012; Koelzsch et al., 2014 and see fig. 1.3). This can lead to asynchrony or mismatch during migration and on arrival. In some scenarios, climate change can even lead to the cessation or shortening of some species' migrations (Newton, 2024a).

1.2 Study case of an anadromous species: the Atlantic salmon

To explore and illustrate in more details the phenological process and its consequences on a species, my dissertation focuses on the Atlantic salmon, an emblematic species for its long-distance migration between river and ocean. The phenology of migration to the ocean plays an important role in juvenile survival, with potential eco-evolutionary consequences for populations.

1.2.1 Life-cycle

Atlantic salmon is a teleost fish with a complex cycle of life, which includes migrations between the river and the sea (Fig. 1.5). This first paragraph briefly introduces the life-cycle of this species (Fig. 1.5). A. salmon populations are distributed in the North hemisphere between North America, Greenland and Europe, until the Barents sea (Fig. 1.7) (Thorstad et al., 2010). This range of distribution and diversity of environments leads to high variations in life-history traits between different populations (Thorstad et al., 2010). Briefly, salmon juveniles are born in freshwater streams, where predation is relatively low but food resources are scarce, before migrating to richer but more dangerous, marine environments where they continue to grow and mature (Rikardsen et al., 2010). Below, I provide a more detailed description of the A. salmon life-cycle (Fig. 1.5).

Salmons lay their eggs in the gravel in freshwater from September to February. They hatch during the spring and first remain in the gravel beforeemerging (Thorstad et al., 2010). The juveniles, named parrs, could remain from 1 to 8 years in the river before undertaking a migration to the

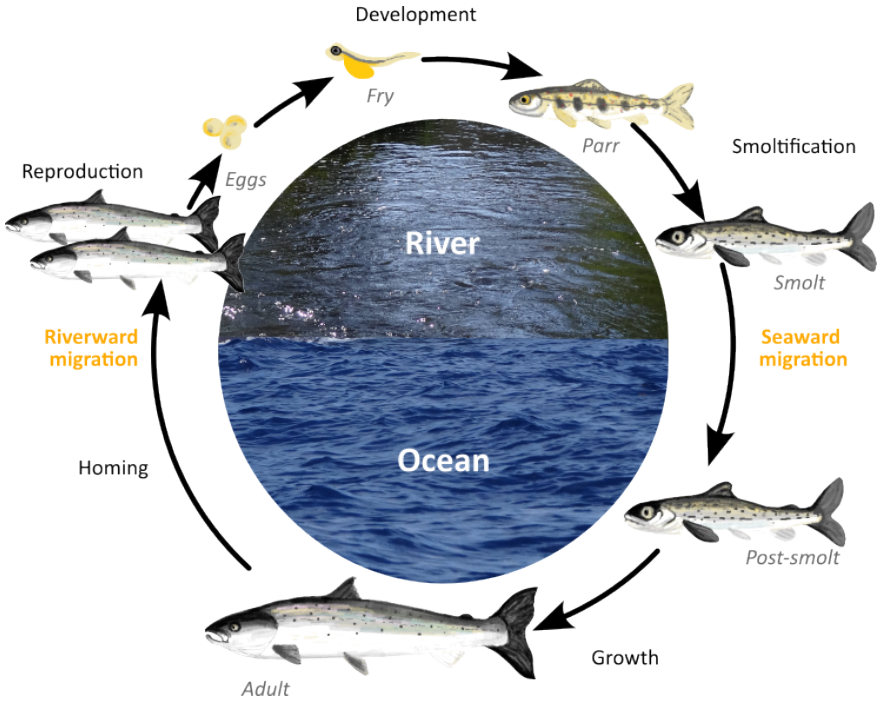

Figure 1.5 – **life-cycle of the Atlantic salmon.**

sea during the spring (Thorpe et al., 1998; Thorstad et al., 2010; Vladic et al., 2015). This migration comes with morphological, physiological and behavioural changes, allowing the salmon to cope with sea water (McCormick et al., 1998; Thorstad et al., 2010; Vladic et al., 2015). For example, morphological changes include modification of the skin colours: the body becomes more silvery and the fin darker (see Fig. 1.6). Many physiological changes are linked with the osmoregulation such as the increase in gill Na+, K+-ATPase activity. All these transformations constitute the smoltification (Fig. 1.6). Additionally, during their migration, they adopt a schooling behaviour to optimize their survival (McCormick et al., 1998).

When they arrive at sea, smolts become post-smolts and endure a first phase of adaptation to saltwater. It is a particularly hazardous phase as they are confronted with a high predation level (McCormick et al., 1998; Thorstad et al., 2010). They then migrate to marine growth areas, where they grow for a certain amount of time, before returning to their home river to reproduce. This phase of life is difficult to monitor and remains poorly understood (Thorstad et al., 2010; Hedger et al., 2013). For instance, we have few knowledge on their migration routes in the sea (Dadswell et al., 2010; Olmos et al., 2020; Gilbey et al., 2021; Thorstad et al., 2010). Dadswell et al. (2010) suggest the "merry go round" hypothesis, meaning that post-smolt reach the north Atlantic subpolar gyre current and then navigate to feeding grounds (Fig. 1.7). This hypothesis seems supported by recent genetic analysis (Gilbey et al., 2021). Once they reach the current, they seem to follow areas

which correspond to their condition requirements, in term of salinity, water depths, and especially temperature, i.e. water temperature around 5-8 °C (Dadswell et al., 2010; Guðjónsson et al., 2015; Gilbey et al., 2021).

(a) Parr

(b) Smolts

Figure 1.6 –
Parr and smolts of A. salmon during monitoring. Parr, with its characteristic coat, and smolts with different degrees of smoltification, from the least smoltified at the top to the most smoltified at the bottom.

The time spend at sea varies by latitude and accross populations, and also differ between the sexes. For example, females usually spend 2 to 3 years in the sea before returning to the river (Thorstad et al., 2010; Vladic et al., 2015), while males mostly spend from 1 to 3 years at sea. Grilses are the fast-growing males which spend only a year at sea (Vladic et al., 2015). A. salmon is a philopatric species meaning that salmons return to their natal river (also called homing). How they do to find their way is not fully understood, but it is likely that salmon uses several cues, depending the distance they are from their breeding sites, such as olfactory cues and the magnetic field (Moore et al., 1990; Vladic et al., 2015). Nevertheless, some salmon disperse into other rivers, i.e. into other populations, forming a metapopulation. This dispersal leads to a genetic flow that can benefit the metapopulation (Lamarins et al., 2022).

During their riverward migration, adult salmons sexually mature. After spawning, some salmons die directly in the river (Vladic et al., 2015). The other, called kelt, spend a certain among of time in the river before going back to the sea (Thorstad et al., 2010), such as in the Miramichi River, where they spend 6 to 10 months in the river before migrating to the sea (Reid et al., 2012). Contrary to a lot of salmonid species, a non-negligible part of Atlantic salmon are iteroparous, i.e. they go back to the river to spawn several times (Thorstad et al., 2010; Reid et al., 2012; Vladic et al., 2015). The number of times salmon can spawn is not known, but it appears that some can

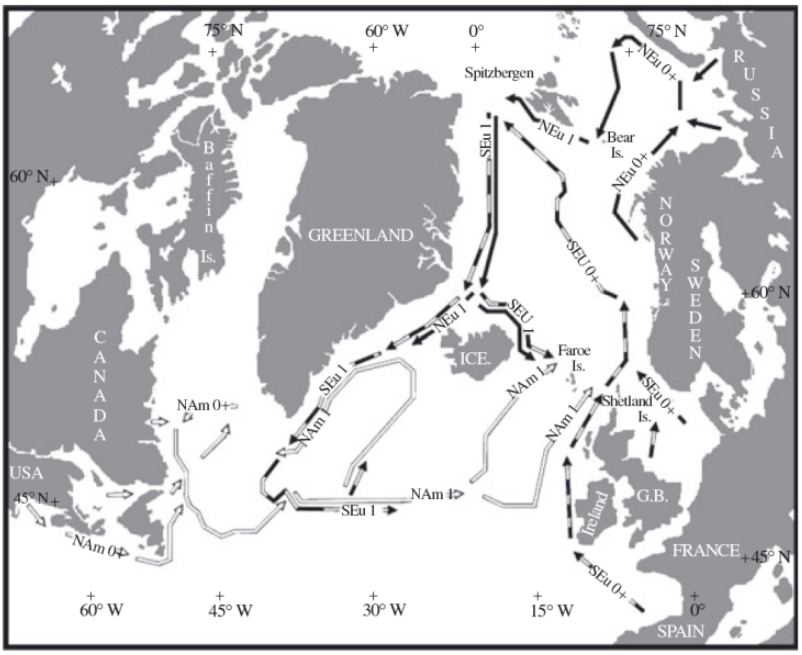

Figure 1.7 – **Atlantic salmon's journey according to its age and geographical origin.** From Dadswell et al. (2010). 0+ : first year at sea, 1: one seawinter, NAm: from north America, NEu: from northern Europe, SEu: from southern Europe

reproduce more than 6 times (Thorstad et al., 2010; Reid et al., 2012). These repeating-spawners can reproduce annually, they are consecutive spawner, or biennially, they are alternate spawners (Jonsson, 1991; Thorstad et al., 2010; Reid et al., 2012). Some male salmons can mature at the parr stage without migrating to the ocean. They are called precocious parrs. During the reproduction, they are in competition with bigger anadromous males. A better sperm quality and the use a the "sneaking" strategy allow them to fertilize a part of the eggs. They can become smolts after this first maturation (Thorstad et al., 2010; Vladic et al., 2015).

1.2.2 Smoltification and seaward migration

From now on, I will focus on the seaward migration of the Atlantic salmon, along with the smoltification process (Fig. 1.5). As seen above, the salmon migration process is divided into four stages: 1) preparation for migration, 2) departure, 3) journey and 4) arrival.

The preparation

Salmons smoltify at various ages (Thorpe et al., 1998; Thorstad et al., 2010; Vladic et al., 2015), reflecting a wide variety of life strategies. The decision for a parr to endure a migration seems to be taken during a period in the summer, long before the smoltification the following spring (Thorpe et al., 1998). This life history decision seems to be linked with body size at the end of summer, but also to genetic factors (Debes et al., 2020). Indeed, the probability to migrate within a age group increases with bodysize, especially at young ages (1, 2 year) (Jonsson et al., 2016).

At the end of the growth season (autumn), parrs show a bimodal length distribution, with some parrs slow growing and other fast growing. The longer parrs of the age cohort seem to smoltify the following year, whereas the smaller remain in the river one more year (McCormick et al., 1998; Buoro et al., 2010; Vladic et al., 2015; Jonsson et al., 2016). However, if we compare between cohorts, the older parrs produce larger smolts, as they have had more time to grow up in the river (Jonsson et al., 2016). Thus, the parrs that smolts the youngest show accelerated growth before migrating, as if to catch up with the size of the oldest smolts (Jonsson et al., 2016). Therefore, size is important in the smoltification decision, and a size threshold has been suggested (Thorstad et al., 2010). Other authors found that this is the growth rate that matters more than the size does (ØKland et al., 1993). Another study suggested that genetic potential for growth rate also influences the decision to migrate (Debes et al., 2020). In any case, growth seems to be an important factor determining the decision to smoltify the next spring, or to stay another year, but with variety of life strategies. This diversity of life strategies is consistent with the great variability of smolt sizes (Antonsson et al., 2002; Todd et al.,

2012).

What could explain the importance of parr growth in the smoltification decision is that the smolt size is crucial for the migration, due to size dependent sea survival (Gregory et al., 2019, see section 1.2.3). Smolts size seems to be genetically determined (McCormick et al., 1998; Rogell et al., 2013; Debes et al., 2020) and specific to a population, even within the same river, suggesting that it is a local adaptation (Heggberget et al., 1986; Antonsson et al., 2002). Therefore, this smoltification decision and the life strategy can also depend on the population.

Another strategy for the male is to mature as parr. The precocious maturation allows the parr to avoid the mortality linked with the migration. The decision of mature early seems to be linked with the growth rate and the energetic status (Thorpe et al., 1998; Vladic et al., 2015). Thorpe et al. (1998) suggested that if the lipid composition of the body is good enough, the male parr will mature rather than smoltify. In fact, the metabolic rate and how the parr allocate its energy seems to determine what strategy, smoltify or mature, has the greatest cost for the parr. Therefore, the decision of precocious maturation is linked with the physiology and the environment of the individual. Genetics must be of importance in the physiological process (Birnie-Gauvin et al., 2021).

Therefore, the decision mechanism is not fully understood yet but seems to be taken long time before the smoltification and to depend on both genetic aspect and energetical status (internal factors). The decision appears to influence the winter behaviour, parrs that will remain in the freshwater feed less during the winter (Thorpe et al., 1998; Vladic et al., 2015).

During the migration window the following spring, parrs that "decided" to migrate undergo the preparation process to migrate, the smoltification. As for many other species, the phenology of the salmon migration seems sensitive to the photoperiod. Actually, an increase in the photoperiod seems to enhance the production or the responsiveness of some hormones, particularly the growth hormone and the cortisol (McCormick et al., 1998). These hormones are involved in physiological changes allowing salinity tolerance. Broadly, the increase of the photoperiod stimulates the smoltification (McCormick et al., 2011). Also, it has been suggested that A. salmons present an endogenous cycle of endocrine activity: hormones involved in the smoltification increase at a certain period. Therefore, there is a critical time window during which salmons are most likely to smoltify, an essential step before initiating departure

(McCormick et al., 1995; McCormick et al., 1998).

The departure

Many factors are involved in the departure decision of the salmon, especially internal and environmental factors, but also time related factors such as photoperiod.

The departure is controlled by internal factors, especially if the salmon is ready to migrate. First of all, the gill Na+, K+-ATPase activity, which is involved in the sea tolerance and sea survival (Stich et al., 2015b), can be used as a marker of physiological readiness (Zydlewski et al., 2005; Stich et al., 2015b). It has been shown that high or low gill Na+, K+-ATPase activity can delay the migration (Stich et al., 2015b). Furthermore, this gill Na+, K+-ATPase activity increases during a window and then decreases (Zydlewski et al., 2005). Thus, this physiological aspect can limit the time of migration as the endocrine activity (McCormick et al., 1998; Zydlewski et al., 2005). It has been suggested that this window is also behavioural (Zydlewski et al., 2005). Lastly, timing of smoltification and migration is expected to be under genetic influence, because the response to the external conditions differ across populations or subpopulations (Heggberget et al., 1986; McCormick et al., 1998; Antonsson et al., 2002; Stewart et al., 2006; Bjerck et al., 2021). The age may also be a factor influencing the date of departure of the smolt, as older (and longer) smolts are found to migrate earlier than younger ones (Jonsson et al., 1990; Jutila et al., 2008).

As seen before, increasing photoperiod stimulates smoltification, which triggers migration (Spence et al., 2014; Simmons et al., 2021a). Increasing photoperiod can also stimulates the movement rate (Stich et al., 2015a; Stich et al., 2015b). Therefore, the timing of smolt migration is strongly linked with the latitude (Russell et al., 2012; Otero et al., 2013). Russell et al. (2012) showed that julian day at which 50% of smolts were captured (i.e. were migrating) increase by 3.3d/°Latitude for the Western Atlantic populations, and 2.9d/°Latitude for Eastern Atlantic populations. Consequently, smolts migrate mostly during April at their southern distribution area, whereas they migrate during June at their Northern distribution area. The difference observed between the Western and Eastern populations can also have some genetic components (Russell et al., 2012; Otero et al., 2013).

Among external cues, environmental factors such as water temperature has been shown to impact the departure in some rivers (Jonsson, 1991; Zydlewski et al., 2005; Kennedy et al., 2010; Spence et al., 2014; Simmons

et al., 2021a; Vollset et al., 2021; Bjerck et al., 2021; Arevalo et al., 2021) or the movement rate (Stich et al., 2015a). Rather than a specific temperature threshold, it often appears that a rise in temperature triggers the onset of migration (Jonsson, 1991; Zydlewski et al., 2005). Low temperature can also reduce the influence of the photoperiod on the smoltification, therefore, at low temperature, the smoltification is delayed (McCormick et al., 2000). Furthermore, warm temperature during the winter and the early spring seems to stimulate early migration, maybe by favoring increasing growth (Simmons et al., 2021a). The Frome river for example, presents winter temperature warm enough to allow parrs to grow during winter, therefore warm winter can enhance this growth. Thus, parrs are more susceptible to be ready to smoltify earlier (Simmons et al., 2021a). Low temperature can also favour the nocturnal migration (Ibbotson et al., 2006). However, the effect of temperature can differ between rivers and populations (Jonsson, 1991; Spence et al., 2014; Aldvén et al., 2015; Debes et al., 2020; Simmons et al., 2021a). Also, the importance of water temperature can vary between river in comparison to other factors such as water discharge (Aldvén et al., 2015). For example, in river with increasing water discharge because of snow melt in spring, temperature and water discharge are negatively correlated. In this context, water discharge is more influent on the migration phenology than temperature (Hvidsten et al., 1995; Spence et al., 2014). In other rivers, increasing temperatures and high water discharge stimulate the migration, but temperature has a larger effect (Antonsson et al., 2002).

Thus, water discharge is another important cue that influences the smoltification, but as for the water temperature, the effect of water discharge depends on the river (Jonsson, 1991; Hvidsten et al., 1995; Spence et al., 2014; Aldvén et al., 2015). In many river, the peaks in discharge are associated with migration pulse (Bjerck et al., 2021; Kennedy et al., 2010; Stich et al., 2015a) or faster migration (Persson et al., 2018). The day to day change of the discharge is also important, with higher migration probability with positive day to day discharge change, even if the discharge is low (Bjerck et al., 2021; Simmons et al., 2021a). However, some studies have found no discharge effect (Vollset et al., 2021), while Stich et al. (2015b) found that salmons arrive later at the estuary when they experience high flow in the Penobscot river.

Because of the effects of temperature and discharge, drought can influence the migration period. Kastl et al. (2022) observed that drought (higher temperature and low flow) shortened the migration period of coho salmon (*Oncorhynchus kisutch*). Altogether, these observations suggest that temperature and water discharge seem to work in combination during an optimal phase given by the photoperiod and the internal factor.

To a little extent, moon phases seem to influence the timing of migration: salmon migrate more during the new moon (Jonsson, 1991; Hvidsten et al., 1995; Spence et al., 2014; Simmons et al., 2021a), even if some authors have found an important number of smolts near the full moon (Hvidsten et al., 1995). The impact of the moon cycle is likely due to the light, as migrating at darker night can help to reduce the predation pressure (Jonsson, 1991; Hvidsten et al., 1995; Simmons et al., 2021a).

To finish with external parameters, the distance from the ocean is likely to impact the departure timing of the salmon, as it seems that fish from upper sites in the river migrate earlier than fish near the ocean (Stewart et al., 2006; Stich et al., 2015a), with an increased movement rate (Stich et al., 2015a).

It has to be pointed out that the impact of these factor changes during the migration and during the migration window (Ibbotson et al., 2006; Simmons et al., 2021a). For example, the nocturnal behaviour change during the migration, with more smolts migrating during the day when they are near the sea (Ibbotson et al., 2006).

To finish, other external and biotic factors could impact the departure decision such as social interaction (Hvidsten et al., 1995; Berdahl et al., 2017), predator pressure, and food availability (Björnsson et al., 2011).

Therefore, many cues are involved in the smoltification and the departure, but they have not the same impact and importance depending on the population. This can be a local adaption (Antonsson et al., 2002; Heggberget et al., 1986; Spence et al., 2014), as the timing of the entry in the ocean have multiple consequences.

The journey

Salmon appears to adopt schooling behaviour during their migration (McCormick et al., 1998; Riley et al., 2007; Riley et al., 2014; Hvidsten et al., 1995). The smolt migration mostly occurs during the night (Hvidsten et al., 1995; Riley et al., 2007; Barry et al., 2024a), even if this behaviour change during the period with increasing diurnal migration at the end of the period (Ibbotson et al., 2006). This change in diurnal activity can be triggered by temperature (Fraser et al., 1993). Both the schooling and nocturnal behaviour can be a strategy to cope with predation risk. Indeed, they are exposed to predation from many animals during their migration, mammals, birds, and fish such as pike (Barry et al., 2024a; Thorstad et al., 2012; Klaminder et al.,

2019). Schooling is also a way to save energy (Zhang et al., 2024). Finally, migration speed appears to be highly variable, with the current helping to achieve high speeds. It can reach up to several tens of km per day (Thorstad et al., 2012).

The arrival

Here, we will consider the arrival at sea and their first few months at sea (see Fig. 1.7). As soon as smolts reach the salted water, they are categorized as "post-smolts". This name often remains valid until the 31st of December for reasons of practicality in stock assessment models (ICES, 2023).

In some studies, when smolts reach salted water, some appear to slow or to make some back and forth movement between the river and the estuary (Holm et al., 1982; Lacroix et al., 1996; Renkawitz et al., 2012; Lilly et al., 2022; Artero et al., 2020; Halfyard et al., 2013). If the smolt seems to be able to switch directly to salted water (Lacroix et al., 2005), some hypothesised that this period can be an accommodation period to the oceanic conditions (Renkawitz et al., 2012) or depend on the smoltification stage (Lacroix et al., 1996). It is possible that if some salmons initiate their migration before having completely smoltified, they wait near the estuary before entering in the bay (Strand et al., 2011).

One of the most important factors explaining the movement of the post-smolts in the estuary is the tide. Post-smolts generally leave the estuary at ebb tide, i.e. the transition between high tide towards low tide, (Davidsen et al., 2009; Lacroix et al., 1996; Lilly et al., 2022), but this is not always the case (Renkawitz et al., 2012). This can depend on local context as the tide is not as important in every system. Leaving at ebb tide and using the current allows the fish to save energy, utilizing the speed of the tide. However, to only follow the current is unproductive and can lead to more time spent in the estuary (Moriarty et al., 2016). Therefore, the movement of fish out of the estuary is not only passive but also active and directed, even if it is not known what cue they use to orientate (Renkawitz et al., 2012; Thorstad et al., 2012; Lacroix et al., 1996). Diving behaviours are also observed, it can be to avoid air predator, to forage or to wait/find (Renkawitz et al., 2012) better current conditions (Holm et al., 1982).

The moment they reach the marine water is an important stage of the life-cycle, as it is a bottleneck stage. Indeed, the mortality rate is high, but quite different depending on the studies. In their review, Thorstad et al. (2012) found mortality rates varying between 0.6 and 36%. This variability

in mortality rates can be due to experimental bias. Mortality rates are often calculated thanks to marking experiment, which can affect the survival of the fish, or increased artificially the mortality rate because of detection problem (Thorstad et al., 2012; Lilly et al., 2022). The differences can also come from the origin of the fish, wild or hatchery-reared salmon (for example Renkawitz et al., 2012; Lacroix et al., 1996). But ecological factors can also explain this variability.

First of all, the predation seems to be one of the most important cause of mortality at the arrival at sea (Thorstad et al., 2012; Jepsen et al., 2006; Hedger et al., 2011). The predators are diverse: seabirds as seagulls (*Larus sp.*) and great cormorants *Phalacrocorax carbosinensis*, fish as cod *Gadus morhua*, seabass *Dicentrarchus labrax* or saithe *Pollachius virens*, marine mammals as seals, etc. (Artero et al., 2023; Jepsen et al., 2006; Hedger et al., 2011; Mäntyniemi et al., 2012; Riley et al., 2011; Simmons et al., 2021b; Middlemas et al., 2003). For example, cod has been observed to aggregate at the estuary mouth during the smolt migration (Hedger et al., 2011). Therefore, difference in the presence of predators can be one of the factors explaining the variability in the mortality rate of the post-smolts. Geographical specifics can increase the risk of predation, particularly when smolts have to use restricted passages where predators can wait (Thorstad et al., 2012). The length of the estuary may also increase the risk, although this is not significant in Artero et al. (2023).

In addition to these risks of predation, human pressures can increase the risk of mortality in the estuary (Thorstad et al., 2012). However, the impact of the antropogenisation of the estuary is poorly known. For example, Artero et al. (2023) compared survival between 4 estuaries and found only a weak site effect, with the port estuary showing no significantly higher mortality than the other 3 sites. Rather, their results suggest that the complexity of the estuary (anthropogenic or geomorphological) may decrease the survival rate (Artero et al., 2023; Chaput et al., 2019), as they spend more time in the estuary (Davidsen et al., 2009).

The individual variability among smolts could also impact their survival. The timing of arrival in the estuary appears to be critical. The less time smolts spend in the estuary, the better their survival (Artero et al., 2023). However, it is not known whether the high mortality rate of the slowest post-smolts is a consequence of the time spent in the estuary, or whether the longer time spent in the estuary and the higher mortality are both a consequence of the poor quality of the post-smolts (Thorstad et al., 2012). Body length is suggested to also play an important role in the mortality rate. The advantage of being bigger can be explained by the exclusion of some predators: a bigger prey requires a bigger predator (Cohen et al., 1993). The advantage can also

be explained by the migration speed, as bigger post-smolts can swim faster (Remen et al., 2016; Thorstad et al., 2007), and therefore spend less time in the estuary, and maybe escape the predators easily. Another advantage is that bigger smolts can be better-quality smolts (Simmons et al., 2021a), and have better osmotic regulation (Halfyard et al., 2013). However, many studies did not found any evidence of a bodysize effect (Artero et al., 2023; Moccetti et al., 2023; Renkawitz et al., 2012; Lilly et al., 2022). But these studies are based on marked fish, sometimes hatchery-reared fish, i.e. fish chosen to reach a certain size limit so that they can be marked. For this reason, a size effect can be masked by the experimental bias. On the contrary, some studies did found relationship between the bodysize and the survival (Halfyard et al., 2013; Davidsen et al., 2009; Chaput et al., 2019; Thorstad et al., 2007). In Halfyard et al. (2013), they found a positive relationship between bodysize and survival rates in some rivers, and a negative relationship in others. They suggest it can depend on predators present in the estuary. Davidsen et al. (2009) did found a positive effect of bodysize in the river, but observed the contrary in the estuary. This appears contradictory, but they suggest that only the better-quality smolt of the smaller size class survive to the river, explaining their better survival in the estuary. In Chaput et al. (2019), they found positive effect of the length in 3 out of 4 rivers but hypothesized that the high mortality was due to the tagging process. In conclusion, even if the advantage of greater size in the estuary is found in certain cases, this effect remains to be clarified and qualified. Finally, Moccetti et al. (2023) found that the migration success might depend on the genes related to osmoregulation, and immune and stress response.

1.2.3 The importance of salmon phenology

In the preceding sections, we have seen that 1) the response to the cues that trigger the migration varies among populations and appears to be locally adapted 2) the arrival at sea is particularly hazardous and 3) many factors can explain the variability in the survival rates across populations and individuals, comprising the body length.

The first point shows that phenology of salmon migration, by being locally adapted, allows salmon to arrive with optimal marine conditions (Antonsson et al., 2002 and see the different migration dates according to geographical area in fig.1.9.a.).

The second point is important because the decline of many Atlantic salmon populations observed in recent decades (Chaput, 2012; Crozier et al., 2018; Middlemas et al., 2003), is likely due to a decline in marine survival since 1971 (Olmos et al., 2020). This is why the post-smolt stage, i.e. the first few months in the estuary and the journey to feeding sites, can be decisive in

maintaining the population (Thorstad et al., 2012). Therefore, salmons must arrive at the optimal timing to maximize their survival.

Then, smolt size has been found to be one of the main component increasing the return rate of salmons in their river (Bond et al., 2024; Jonsson et al., 2014; Gregory et al., 2019; Simmons et al., 2021b; Wilson et al., 2021). This can be explained by the same reason as the survival rate in the estuary (see section 1.2.2), fast swimming, fewer predators, and maybe better-quality smolt (Simmons et al., 2021a).

However, to reach the optimal length, smolts must have enough time to grow. This is why phenology is important here because if smolts migrate too early, with insufficient bodysize, the risk of mortality increases (Arevalo et al., 2021; Bond et al., 2024; Kennedy et al., 2010; Munsch et al., 2019; Simmons et al., 2021a). On the other hand, if smolts migrate too late, even with sufficient bodysize, they may arrive too late for the optimal marine conditions. In particular, they can miss the prey abundance peak, leading to a mismatch (Arevalo et al., 2021; Bond et al., 2024; Kennedy et al., 2010; Olmos et al., 2020; Thorstad et al., 2012; Rikardsen et al., 2010; Wilson et al., 2021).

Post-smolts feed on fish larvae such as sandeel (*Ammodytes spp.*), blue whiting (*Micromesistius poutassou*) and herring (*Clupea harengus*), and on zooplankton such as krill and amphipods (Haugland et al., 2006; Utne et al., 2022). The proportion of fish and zooplankton depends on the region and on the year, as well as the species. Post-smolts survival appears to be correlated with herring recruitment, although the causal relationship is not fully understood. This correlation suggests that herring may be an important resource for post-smolt survival (Mäntyniemi et al., 2012). The hatching of fish larvae is itself more or less synchronised with food abundance, i.e. the primary production (Cushing, 1969; Rikardsen et al., 2010). This is why marine primary producer blooms or zooplancton blooms have been used as a proxy for post-smolts feeding. It has been found to be linked, to a certain way, to post-smolts survival for the steelhead trout *Oncorhynchus mykiss* (Wilson et al., 2021), and for Atlantic salmon (Olmos et al., 2020).

Therefore the hypothesis is that there is an optimal timing for the salmon migration (Kennedy et al., 2010; McCormick et al., 1998; Scheuerell et al., 2009; Stich et al., 2015b; Thorstad et al., 2012; Wilson et al., 2021). To optimize its survival probability, the smolt must wait to attain a certain length or condition, allowing it to escape from some of its predators. However, smolts must migrate early enough to ensure that the food supply is sufficiently abundant to enable them to survive and grow during those dangerous first months at sea (Fig.1.8).

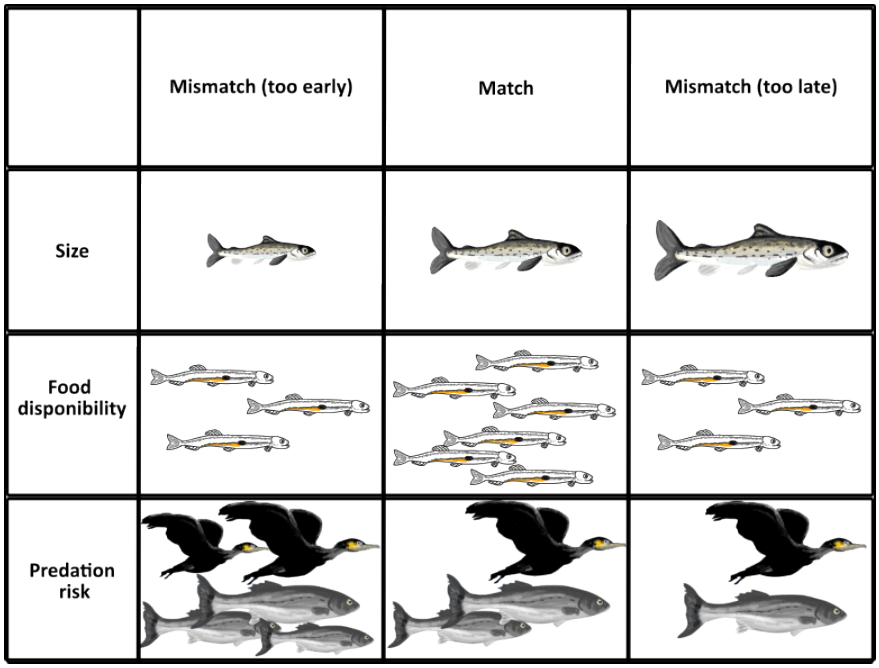

Figure 1.8 – **Illustration of the match-mismatch hypothesis for the salmon.** Migrating too early at small size increases the risk of predation, and can lead to a mismatch in food. Migrating too late at a greater size reduces the predation risk, but also reduces the food opportunity.

The problem is that climate change seems to impact Atlantic salmon phenology (Arevalo et al., 2021; Kovach et al., 2013; Russell et al., 2012; Otero et al., 2013). Indeed, salmon migration is getting earlier, as shown in the meta-analysis of Otero et al. (2013) (Fig. 1.9.d). This precocity is correlated with both river and sea surface temperatures (Fig. 1.9. b & c) and depends on the latitude (Fig. 1.9. a), as the migration date is locally adapted and depends on latitude as seen in section 1.2.2. In the same time, smolts have been observed to migrate at smaller length and body conditions for the past few decades (Arevalo et al., 2021; Kennedy et al., 2010; Russell et al., 2012).

In conclusion, the migration timing appears to be a compromise between length at migration and arrival during optimal oceanic conditions. However, climate change, by modifying environmental cues such as water temperature and discharge, may increase the risk of mismatch and mortality at sea.

1.3 Phenology and assessing its impact on individuals and populations: a current challenge

With the growing importance of understanding phenological shifts with the global change, it is vital to address the questions above, but also the

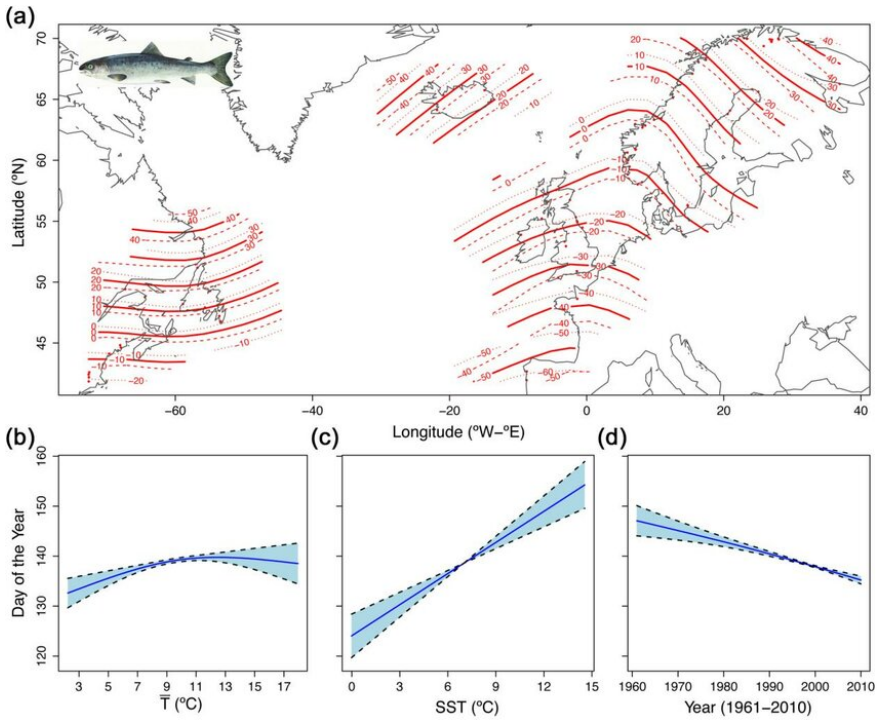

Figure 1.9 – **Meta-analysis results on the phenology of A. salmon, from Otero et al. (2013).** a. Difference in migration timing depending on the geography. The isopleth 0 shows the average migration date, the other isopleths the mean difference with this average. b. Effect of the mean river temperature on the onset of seaward migration. c. Effect of the Sea surface temperature on the onset of seaward migration. d. Trend of the migration date during the last five decades. Smolt drawing credits in panel (a): © Atlantic Salmon Federation (www.asf.ca)/J.O. Pennanen.

challenge of how to answer these questions. An important knowledge gap and challenge is the effect of phenological shift at the demographic level (Miller-Rushing et al., 2010; Iler et al., 2021 and see section 1.1.2). Also, in order to make realistic projections, eco-evolutionary processes and their underlying mechanisms need to be taken into account and they are still poorly understood (Ehrlén, 2015; Inouye et al., 2019).

Below, we explain some of the concerns we encountered in the literature review in the previous sections, which may be at the root of our knowledge gaps.

Practical challenges : from the monitoring to the analysis

Phenology studies face similar technical challenges to those encountered more broadly in ecology. These issues are grouped together under the acronym "LIES" by Chadwick et al. (2023): Latency, Identifiability, Effort, Scale.

To understand the phenology, data are collected, and metrics are used to resume the information contained in the data (Fig. 1.10). The choice of the metrics should be done with precaution. Often, the phenology distribution of a population is represented only by one or some metrics (Inouye et al., 2019) such as the date of peak abundance (e.g. Visser et al., 2012). However, some biological states can be hard to characterize by an easy-going metrics (Chuine et al., 2017). The choice of the metrics that does not represent well the phenology can lead to biased estimations and false perceptions of the phenology and its shift. For instance, the first appearance of migrating individuals is often used, especially for bird migration, but it can present strong biased compared to other metrics such as quantiles and mean. This may lead to poor estimations that scramble the signal from a phenology shift (Moussus et al., 2010).

Additionally, the definition of a biological event often differs from one author to another, and even more between different disciplines (Piao et al., 2019; Gray et al., 2016). This can lead to different choices of indicators for the same question. For instance, in the case of the mismatch between great tits and caterpillar peak, authors do not have the same definition for defining the reproduction timing. Some authors preferred to use the hatching date (Simmonds et al., 2020), whereas others use the laying date (Visser et al., 2021), each arguing that their choice was a better indicator of the great tit breeding phenology.

Therefore the choice of a metric is not only crucial for the quality of the estimation but also for the ability to generalize the conclusions, or to compare the results between studies, populations, species... For example, if you want to understand the species response to a change at global scale, you need to be able to compare the results on different populations (Chuine et al., 2017). The case

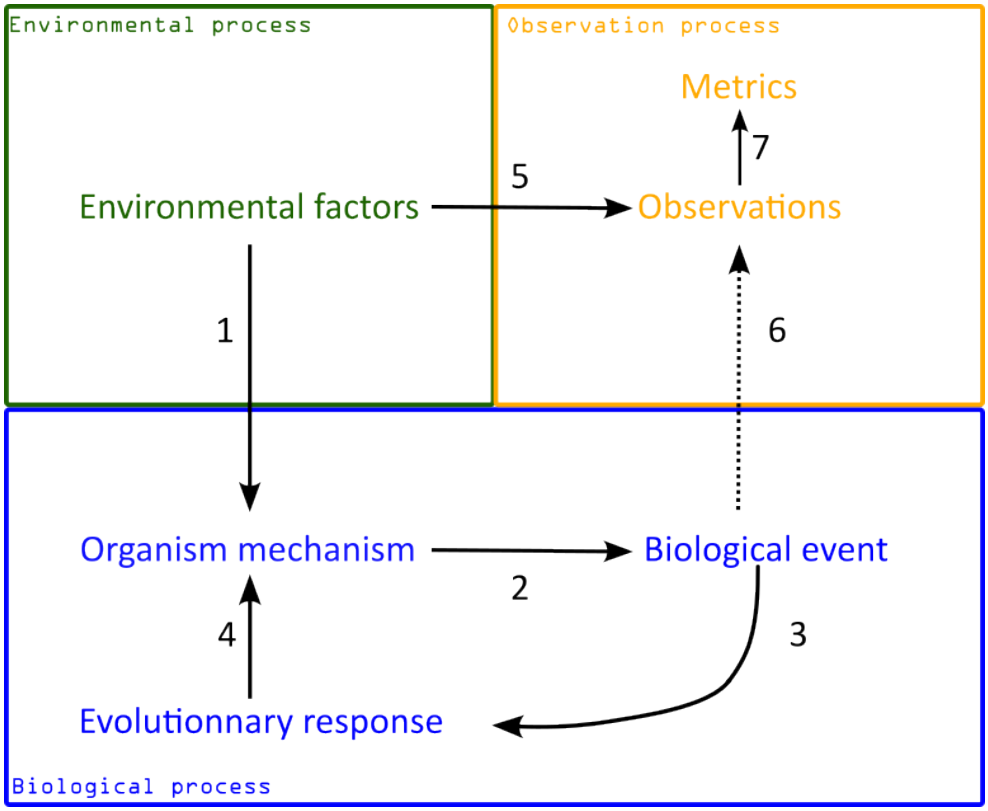

Figure 1.10 – **The diverse processes involved in an observation phenological experiment.** The arrows represent the different processes. The environment has an impact on organisms (1), which, depending on their internal factors, respond by adjusting their phenology (2). The phenology of the event may have effects on the fitness of the individual, so there may be eco-evolutionary feedbacks (3) that will modify the response of the organism (4). The environment also modifies the observation process (5), which is often a partial observation of the biological event (6). We then use metrics to summarise the information contained in the data (7). Inspired and modified from Chmura et al. (2019)

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of the bay checkerspot illustrates well this point (see section 1.1.1). The cause of the adaptive mismatch is not fully understood, and the effect of the climate change remains very speculative even if this species is very-well studied. Many studies already stress the need for standardized data and metrics, and more interdisciplinary work (Singer et al., 2010; Sakai et al., 2019; Chuine et al., 2017; Gray et al., 2016; Piao et al., 2019).

Concern 1: Choosing a metrics can be tricky, as it can be a source of bias and misrepresentation of the underlying process.

Another issue with the metrics chosen is the latency (Chadwick et al., 2023). The latency characterizes the fact that the process of interest is an hidden process (also called "latent"), that cannot be observed directly. Then, we have to choose a way to measure it through a proxy. However, the results may depend on the method used to measure it and on the metrics chosen. For example, the vegetation phenology across seasons, from spring to autumn, is a well-studied subject (Piao et al., 2019). But the metrics used to determine this stage are often visual metrics, based on direct observations or indirect via camera and satellites (Yang et al., 2014). Yang et al. (2014) tested the coherence between the phenology profile given by the satellites, the camera and the biochemical analysis (colorants concentration). While the satellites and the camera give coherent information, they found discrepancies with the biochemical analysis: the seasonal peak is 20 day earlier with the satellites-camera analysis than with the concentration analysis. Therefore, the picture of the latent tree phenology is not the same depending on what measurement technique (satellites-camera or chemical analysis) and what metrics we use (color peak or colorants concentration peak). Then, it is hard to compare results based on different metrics or methods, which argues once again for data standardisation.

Furthermore, the data recorded can depend on environmental factors (Fig.1.10). For example, satellites data, used to evaluate the vegetation phenology, must be corrected for cloud cover and view-angle. Sometimes, when every satellites views are contaminated by clouds, the correction is not possible, leading to missing data. These missing data can increase the uncertainty of the metrics such as the vegetation transition date (Zhang et al., 2009). A bigger issue is when the relationship between the latent process, here the biological event of interest, and the data, is variable. If it is not taken into account, this can lead to a biased estimate. For instance, pollen traps of different kind are used to study the vegetation phenology (e.g. Lü et al., 2020). But these traps, depending on their type, are sensitive to environmental conditions, with some that are more sensitive to the wind speed, and other to the humidity and precipitation (Latorre et al., 2008). Then, as the trap efficiency can vary with the environmental conditions, the data obtained do not reflect only the biological process (here, the pollen release), but also the interaction between

the trap efficiency and the environment. This is even more important when the environmental conditions impacting the trap efficiency can also impact the biological process itself, such as the humidity that can influence both the pollen variation and the efficiency of the trap (Lü et al., 2020; Latorre et al., 2008). It may create confusion preventing to understand the latent biological process of primary interest.

This latest example illustrates not only the latency issue but also the identifiability issue. An identifiability issue creates confusion in the relationship between variables. For instance, we cannot discern if there is a cause/consequences relationship, or a simple correlation relationship. This issue can arise for a lack of information in the data ("practical identifiability" in Chadwick et al. (2023)), but also from a lack of relevant data that does not allow the relationships between the variables to be distinguished ("mathematical identifiability" in Chadwick et al. (2023)). In the latest example, a change in the humidity can cause both variation of the pollen release and of the trap efficiency. If we do not have information on the latent observation process, i.e. the trap efficiency, we cannot disentangle this effect from the biological process. This identifiability issue is recurrent in phenological studies, as they are often based on correlation between variables, particularly with cues. Let us take the case where we have not managed to identify the real cue and use another variable that is correlated with the real cue. If the relationship between the two variables is of the order of 1, the projections we make can be close to reality. However, if the relationship between the two cues changes, the projections will fail to describe reality (Charmantier et al., 2014).

A solution is to record enough data, comprising the potential influential variables, and to model precisely the observation process.

Another issue with phenological data is the issue of the heterogenous effort, meaning the under representation and over representation of record of "some, for example, seasons, years, regions, individuals or population classes" (Chadwick et al., 2023). The result is a partial view of the problem, which can lead to errors of perception. This is a particular issue in phenological studies, as they have been widely conducted in temperate areas with marked seasons. This leads to a poor understanding of tropical area, for example the tropical forest (Sakai et al., 2019), or mammals such as bats (Wells et al., 2022), or also temperature insectivorous birds in contrast to others (Charmantier et al., 2014) . Also, some seasons have been studied more than others, for example spring vegetation phenology is better understood than autumn phenology (Piao et al., 2019). At the population scale, there can also be some effort issues for many reasons such as spaces being more sampled because they are easier to access. Especially, the temporal scale is important as phenological studies aim to understand the timing of the species. Citizen science is a good way to collect more data, however it comes with certain bias. For example, a well-known bias

in phenological studies is the first arrival date of migratory bird species. Citizens' reporting of the date of first arrival was more important during weekends than weekdays, and significantly higher than it should have been with equal effort on weekdays and weekends. This can easily be explained by the way of life of citizens that got more time to observe bird during weekends. This bias seems to be diminishing nowadays, but is still important to consider, especially when comparing old data with actual data when investigating climate change effects (Courter et al., 2013).

Finally, the scale issue refers to the discrepancy between the biological process and the scale at which we consider it (Chadwick et al., 2023). As seen in section 1.1.1, the time scale is particularly important in phenology. In temperate zones, the phenology is often annual, which is not always the case in tropical zones, which may have a longer or shorter cycles (Sakai et al., 2019; Visser, 2022). This is why working only on a yearly basis can be detrimental in these areas. Another problem is that we use one simple metrics for the whole population, often the first event date, or the mean date, which can mask major inter-individual variability. For example, if we compare the average date of a biological event for two years with very different environmental conditions, and they appear very similar, we can conclude that the population is not sensitive to these conditions. But with this one-off approximation, we have no idea of the duration of the event for the population as a whole. If, in reality, the duration of the event for the population as a whole was much longer in the second year, because of early or late individuals, or both, our conclusions would be flawed. This is why different measurements can give very different views of phenology shifts. Data on a more precise time scale can provide greater precision for understanding phenology (Inouye et al., 2019).

In response to these problems, the authors point out the need for long-term data, and also fine-time scale and individual data (Singer et al., 2010; Sakai et al., 2019; Chuine et al., 2017; Gray et al., 2016; Piao et al., 2019; Wells et al., 2022; Inouye et al., 2019).

Concern 2: The observation process, the measurement methods and the sampling (effort and scale), emerge from latent dynamic processes. If not carefully taken into account, this can lead to confusion that can be difficult to disentangle, or lead us to miss important information.

Through all these illustrations, we can see the challenges posed by the need for high-quality data and appropriate analyses to answer pressing climate change questions. But these challenges are not just technical. What is slowing down our ability to respond to these challenges is also more fundamental. How can we predict something correctly when we only have a vague idea of the processes involved?

Going beyond correlation: towards a mechanistic approach

In addition to the methodological problems inherent in collecting data in ecology, there is a more fundamental problem of scientific approach. This problem is that phenological mechanisms underlying a biological process are assumed, without being questioned, checked or understood precisely. Actually, many studies are based on correlation, which, as said in the previous section, can mask diverse types of relationship (Chmura et al., 2019; Piao et al., 2019). So our results are only a partial vision of the reality, even strong uncertainties that can lead to completely wrong projections. This is often the case in match-mismatch theory: many studies are based on this theory without collecting and testing its assumptions (Kharouba et al., 2020; Ehrlén, 2015). This can lead to unclear conclusions or even errors in attributing the type of relationship between the variable tested, preventing forecast projections. This is particularly striking in the case of the bay checkerspot, because even though it is much studied, and the mismatch established, the reasons for this mismatch are not fully understood, making it impossible to make projections (Singer et al., 2010).

Therefore, there can be confusion between biological and environmental processes (Chmura et al., 2019, fig.1.10), whereas both processes can act in synergy or in opposition. Thus, it is important to disentangle each effect to better understand the mechanism and have better prediction (Chmura et al., 2019).

First of all, scientists need to ensure we collect the necessary data to test the assumptions (Kharouba et al., 2020; Miller-Rushing et al., 2010).

Then, to understand the underlying mechanism, the focus must shift to tackling the molecular and physiological responses to climate change, allowing ecologists to better understand the process (Macphie et al., 2024; Chuine et al., 2017; Piao et al., 2019; Miller-Rushing et al., 2010; Gray et al., 2016).

Furthermore, the biological event of interest is linked with the other life-cycle events (see 1.1.1). This is why the authors call for better integration of the entire life-cycle into the analysis (Ehrlén, 2015).

Then, the eco-evolutionary processes are not always considered, whereas the evolutionary responses impact organism's response (Fig. 1.10, Chmura et al., 2019; Johansson et al., 2015; Charmantier et al., 2014). For example, even if bird phenology is often studied, to what extent their timing modification are due to plastic or evolutionary responses are poorly documented (Charmantier et al., 2014).

Concern 3: The mechanisms underlying phenological process are poorly understood. Focusing on mechanisms at different scales would provide a better understanding of phenological changes.

To be able to tackle these problematics, authors advocate for better modeling practices. Particularly, authors advocate for more mechanistic models (Chmura et al., 2019; Chuine et al., 2017). This involve the precise identification of latent processes, both observation and biological process.

In order to gain a better understanding of the consequences of phenology at population level, another recommendation is to develop models based on the entire life-cycle and demographic models (Ehrlén, 2015; Miller-Rushing et al., 2010).

Finally, the last recommendation is to work not only on a point measurement such as first arrival or average date, but also and above all on the distribution of phenology within the population (Inouye et al., 2019). Indeed, a one point measurement can hide many variation. For example, in Wilson et al. (2021), they found a constant mean migration date for steelhead trout over the years, but this may hide large variations in the total distribution. Notably, Bjerck et al. (2021) have shown that the distribution of the salmon migration is multimodal, so that the same average date can be derived from very different distribution profiles.

Concern 3: The use of more mechanistic models, which aims to disentangle all confounding effects, and broaden the scope of studies, would provide a better understanding of phenology.

1.4 Aims of the thesis

In this first chapter, we have seen that:

— Phenology is an important part of life-history trait strategies. Nevertheless, climate change disturbs phenology species in a heterogeneous way, which can put species at risk of asynchrony/mismatch with the optimal conditions for carrying out certain parts of the life-cycle.

— Migration is both a stage in the life-cycle that allows individuals to benefit from the advantages of different environments, and a stage fraught with dangers. Migration phenology helps to minimise the cost of this step by synchronising the timing of migration with the optimal conditions.

— Atlantic salmon, a migratory species, is a good example of these challenges, since its first few months at sea are particularly risky. Climate change is altering its phenology, which is thought to be one of the causes of its decline.

— Although changes in the phenology of species are often considered to be one of the main threats to biodiversity, they are still poorly understood. This may be due to a failure to take account of the underlying processes, i.e. biological mechanisms, but also observation and methodological processes.

Thus, the ultimate goal of my thesis is to gain a better understanding of the phenology of migration in Atlantic salmon, by identifying how the migratory departure process works and what determines it. The main challenge is to disentangle the observation process from the biological process which is of primary interest.

This will be done through:

1. A complete representation of the observation process and the underlying processes that generate the observed data at the daily scale. **(Chapter 2)**.

2. Then, on the basis of this analysis, I propose a mechanistic model to investigate the migration process, which explicitly represents the steps involved in salmon migration (preparation, departure) and how they change over time. **(Chapter 3)**.

3. In the final chapter, I discuss these approaches, results and implications, particularly as they relate to climate change. **(Chapter 4)**.

Chapter 2

Estimation of time-varying capture probability and abundance of migratory fishes by means of mark-recapture modelling

The data we use to study phenology come from a long-term capture-recapture experiment conducted using two traps. The aim of this second chapter is to understand the capture process that gave rise to the data, and how the environment can influence it. This section corresponds to an article submitted in *Canadian Journal of Fisheries and Aquatic Sciences*.

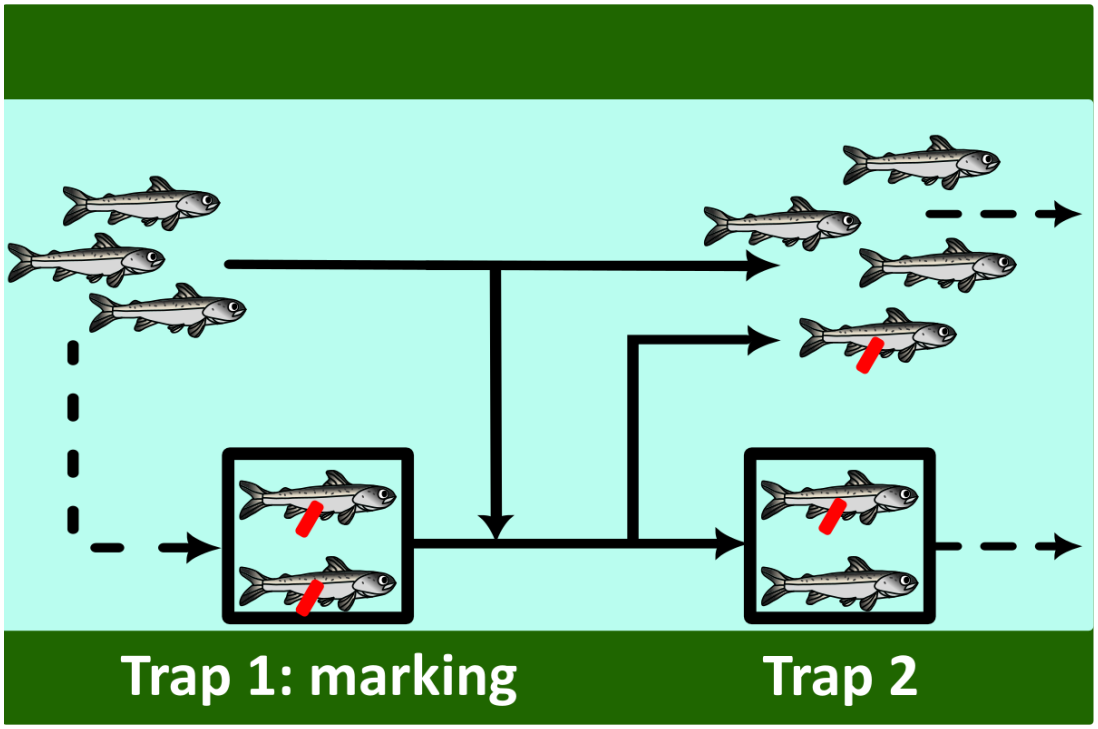

Figure 2.1 – **Experimental protocol for CMR data**

A re-examination of the estimation of time-varying capture probability and abundance of migratory fishes by means of mark-recapture modelling and sequential inference.

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Abstract

Estimating the abundance and migration patterns of fish from capture-recapture data remains challenging, particularly when capture probabilities and migration timing vary over time. This study introduces a Bayesian model designed to estimate the passage probabilities of marked individuals at recapture traps, considering the effects of time since marking, marking day, and recapture day. The model also accounts for individual aggregation behavior and environmental influences on capture probabilities. We applied this approach to a 25-year dataset of Atlantic salmon migration in the Scorff River, France. Our method employs a hierarchical framework to jointly analyze data across multiple years, improving accuracy. We propose a sequential Bayesian procedure for the estimation of capture probabilities and migration numbers, i.e. estimates capture probabilities in the first step and uses these estimates to determine migration numbers in the second step. We demonstrate that this approach provides more accurate estimates by conditioning the probabilities only on relevant data from marked individuals. This approach provides a more precise estimation of migration dynamics, with potential applications for various species undergoing unidirectional migration in consistent monitoring scenarios.

Keywords: Capture-recapture, Migration dynamics, Atlantic salmon, Bayesian modeling, Hierarchical modeling

2.1 Introduction

In the current dual context of biodiversity crisis and climate change, monitoring wild populations is particularly needed. Diadromous fish are particularly at risk (Brown et al., 2013; Waldman et al., 2022; Lassalle et al., 2009; Limburg et al., 2009). Under the impact of human activities, they suffer from both increased mortality (Kennedy et al., 2010; Martins et al., 2011; Cunningham et al., 2018) and changes in their phenology (Otero et al., 2013; Anderson et al., 2013), leading to a reduction in their abundance (Dadswell et al., 2021; Olmos et al., 2019).

For diadromous species, the transitions between freshwater and marine environments represent both critical phases in their life cycle, requiring ecological and physiological adaptations, and unique monitoring opportunities. During these transitions, an entire migrating cohort of a population uses a narrow river corridor in a unidirectional movement. Fixed capture devices have been developed to sample populations during these downstream or upstream migrations. These devices allow to observe migration phenology and to quantify abundance, often in conjunction with capture-mark-recapture (CMR) protocols.

In migratory salmonids, the downstream migration of juveniles (i.e. smolts) can be monitored by double trapping (e.g. Schwarz et al., 1994): a first trap allows the capture and marking of individuals, some of which are then recaptured at a second facility further downstream, which also collects unmarked individuals that escaped the first trap. A variant of this protocol can be implemented with a single trap, when marked individuals are returned upstream to be possibly recaptured a second time at the same facility (e.g. Mäntyniemi et al., 2002; Rivot et al., 2002). However, it has the double disadvantage of being less in tune with the natural migration dynamics of individuals, and of favoring a tendency for marked individuals to avoid or be attracted to the catching device they have already experienced. Combinations of more than two traps may also be used (e.g. Dauphin et al., 2023; Payton et al., 2021). These CMR protocols are often applied over several years on the same river as part of recurrent monitoring programs.

When for each year, CMR events are repeated regularly over time during the smolt outmigration period, for example on a daily time step, they provide information on migration phenology and migrant numbers. However, the numbers caught, whether marked or unmarked, are only partial and noisy observations of daily migrant numbers, the sum of which gives the total abundance of the annual migrating cohort.

Various statistical models have been proposed to analyze these CMR data and to infer the underlying quantities that are inaccessible to direct observation but of ultimate interest, primarily trapping efficiencies and numbers of migrants per time step (Bonner et al., 2011; Mäntyniemi et al., 2002; Schwarz et al.,

1999). They all consider that the number of individuals captured is a realization of a random process in which the fate of each individual is governed by a Bernoulli distribution with an associated probability of capture that remains unchanged depending on whether the individual was previously marked or not. They differ essentially in the way they take into account (i) temporal variations in the probability of capture, possibly under the influence of environmental variables (e.g. discharge, temperature), and (ii) the dependence of individuals in the capture process, due to the aggregation behavior of smolts during their migration (Davidsen et al., 2005).

Accounting for temporal fluctuations in capture probabilities can have a major impact on both the position and precision of estimates of total migrant numbers (Mäntyniemi et al., 2002). But it is also crucial for tracking the phenology of migration, i.e. the distribution of migrant numbers over time, as the same number caught can result in very different migrant numbers depending on the associated probability of capture. The aggregation of smolts during migration and/or capture increases the variability of numbers observed at traps, compared with a reference situation where individuals behave independently of one another. This over-dispersion of captures reduces the precision of estimates of migrant numbers and capture probabilities.

CMR protocols using double trapping of migrating individuals enable the assessment of temporal fluctuations in capture probabilities. However, they present a specific difficulty resulting from the fact that for each recapture event, the number of marked fish available for recapture is unknown, and depends on how the individuals resume their migration after marking. To solve this problem, it is necessary to explicitly model the temporal distribution of marked fishes passing at the recapture device. The modeling methods used condition the subsequent statistical inferences made to estimate daily recapture probabilities and daily migrant numbers. Inspiring from the model of Schwarz et al. (1993), Mäntyniemi et al. (2002) propose a random process where each fish marked on day i has a probability $\pi[i,j]$ of passing at the recapture trap on day $j \geq i$. The $\pi[i,j]$ are calculated according to a deterministic function corresponding to a lognormal distribution of transit times between the two traps. This distribution varies in position (i.e. mean transit time) and range (i.e. variability) according to the day of marking and its associated environmental conditions (e.g. discharge, temperature). Bonner et al. (2011) present a non-parametric alternative in which the $\pi[i,j]$ vary randomly around a mean that depends only on the time elapsed since marking. Neither of these approaches explicitly recognizes that smolt migration activity also varies over time according to the environmental conditions on each potential recapture day (McCormick et al., 1998; Thorstad et al., 2012). These variations in migration activity systematically vary the probability of passage at the recapture trap, whatever the initial marking day or the time elapsed since marking.

Modeling of the timing of passage at the recapture device allows for statistical inference of (re)capture probabilities from the number of marks released per day and the numbers subsequently recaptured per day of recapture. To estimate the daily numbers of migrants, additional modeling hypotheses can be made about their distribution over time, i.e. the phenology of migration. Mäntyniemi et al. (2002) propose a Dirichlet-multinomial approach. It requires specifying each of the daily parameters of the Dirichlet distribution which represents the available knowledge about the proportion of the total number of migrants that passes at the recapture device each day. This is not straightforward and the authors provide little guidance on implementation. Bonner et al. (2011) present an alternative Bayesian P-spline model. It requires making a set of rather arbitrary choices for tuning, the plausibility of which is difficult to assess relative to the ecology or behavior of the fish during the migration process of interest. Although not working in the context of a CMR protocol, Pulkkinen et al. (2020) remedy this shortcoming by proposing an explicit and sophisticated model for the temporal dynamics of the number of migrants under the influence of environmental conditions. However, this is achieved at the cost of introducing a rather large number of additional unknown quantities that need to be estimated. Whatever the merits of these different approaches, it would be useful to have a simpler and robust alternative to facilitate the estimation of the daily numbers of migrants and their total over a migration period, without the need to model migration phenology.

In this study, we propose a model in which the probability of passage of marked individuals at the recapture trap results from the combination of (i) an effect of the time elapsed since marking, (ii) an effect of the marking day and (iii) an effect of the recapture day. The aggregation behavior of individuals and the effect of environmental variables on fluctuations in capture probabilities are also taken into account, in line with (Mäntyniemi et al., 2002). Daily and annual numbers of migrants are estimated using a simple model of negative-binomial structure, based on mild assumptions about the distribution of daily numbers. These estimates are compared with those obtained by means of a more classical and simple approach of Petersen type (Schwarz et al., 1999), which ignores variations in the probability of capture over time. We also extend the annual models of Mäntyniemi et al. (2002) or Bonner et al. (2011) with a hierarchical approach that allows the joint treatment of a series of years for which the same CMR protocol was used. This enables an exchange of information between years during the statistical inference phase, which is carried out in a Bayesian framework.

From a Bayesian perspective, it would seem natural to use all available data to infer all quantities of interest at once, i.e. the daily capture probabilities, the daily and annual numbers of migrants. However, the capture data of unmarked individuals alone are essentially uninformative about the capture probabilities. They may even be misleading if large, resp. small, numbers of unmarked animals are captured for reasons independent of any increase, resp. decrease,

of the capture probability. We therefore propose a sequential procedure in which we estimate the capture probabilities in a first step, and then transfer the resulting estimates into the estimation the daily and annual numbers of migrants in a second step. Our procedure ensures that the capture probabilities are *a posteriori* conditioned only by the most relevant data issuing from the marked individuals.

We present and demonstrate our approach with a case study of the downstream migration of Atlantic salmon (*Salmo salar*) smolts in the Scorff River (Brittany, France) over a 25-year period (1998-2023).

2.2 Methods

2.2.1 Generic model description

We first present our generic CMR model which can be applied to any organism during a unidirectional migration with two consecutive traps and a series of years repeating the same CMR protocol. Individuals are captured at the first trap (trap1), individually marked, immediately released, and eventually recaptured later at the second trap (trap 2). In such a setting, trap 2 is of primary interest and trap1 is merely a marking facility. For any given year y, we successively describe three processes: (1) the migration of marked individuals and the timing of their passage at trap 2 depending on their release date, (2) the recapture of marked individuals at trap 2 and (3) the capture of the unmarked individuals at trap 2. The way in which these processes vary between years is then presented.

Time is discretized and we use daily steps in the sequel without loss of generality. The total duration of the migration period is D days. We rely on the classical assumptions of no mortality or emigration or tag loss between the two traps and no error of identification of marked individuals at trap 2. We also assume that the time elapsed since marking does not affect the probability of a marked individual to be recaptured (Mäntyniemi et al., 2002).

The model represents the process that generates the CMR data. Every year, they consist of the numbers of individuals marked at trap1 by marking day i, the numbers of marked individuals recaptured by marking day i and capture day at trap 2 j, and the numbers of unmarked individuals captured at trap 2. Only part of the individuals marked at trap1 are recaptured at trap 2, so their timing of passage at trap 2 is partially observed, and the migration process (1) is hidden or latent.

Migration process and timing of passage of marked individuals at trap 2

Whatever the precautions taken, capture and tagging are stressful for wild animals. Marked individuals may need some time to recover before resuming their migration. The distance between the two traps may also affect the timing of passage of marked individuals at trap 2. We modeled the passage at trap 2 as a time-to-event process, an approach classically used for survival or reliability analyses (Congdon, 2014). For any individual, the time elapsed between its release and its passage at trap 2 is a random variable that follows a probability distribution. This distribution is characterized by its hazard function which represents the instantaneous rate at which the passage events occur (see Congdon, 2014 p. 459). We chose to use a piecewise constant hazard function with daily time steps. Such an approach, also called piecewise exponential model, offers more flexibility than standard parametric models (e.g. log-normal as in Schwarz et al. (1994)), while remaining simple. We further assume that all the individuals marked on the same day i have the same hazard function, as in Schwarz et al. (1994) or in Mäntyniemi et al. (2002), and that all individuals have migrated by the end of the migration period. Under this model, the probability $\pi[i,j,y]$ for an individual marked on day i to pass at trap 2 on day j in year y is given by:

$$\begin{aligned}
&j = 1,...,i-1: && \pi[i,j,y] = 0 \\
&j = i: && \pi[i,i,y] = 1 - e^{(-\lambda[i,i,y])} \\
&j = i+1,...,D-1: && \pi[i,j,y] = \left(1 - \sum_{k=1}^{j-1} \pi[i,k,y]\right) \times \left(1 - e^{(-\lambda[i,j,y])}\right) \\
&j = D: && \pi[i,D,y] = 1 - \sum_{k=1}^{D-1} \pi[i,k,y]
\end{aligned} \tag{2.1}$$

where $\lambda[i,j,y]$ is the constant hazard on day j for individuals marked on day i in year y.

With the additional assumption that marked individuals are independent in their timing of passage at trap 2, the vector $\nu[i,1:D,y]$ of numbers of individuals marked on day i and passing at trap 2 from day 1 to D is distributed according to a multinomial distribution:

$$\nu[i,i:D,y] \sim Multinomial(\pi[i,1:D,y], n_{mark}[i,y]) \tag{2.2}$$

where $n_{mark}[i,y]$ is the number of individuals marked on day i in year y.

The hazard $\lambda[i,j,y]$ represents the intensity of passage of marked individuals at trap 2. It can be influenced by the day of marking i due to environmental and operational (e.g. personnel, duration of stay in the trap, state of the individuals marked...) conditions (Schwarz et al., 1994; Mäntyniemi et al.,

2002). But it may also be influenced by environmental conditions on the day of recapture j that regulate the migration of individuals irrespective of their day of marking (e.g. river discharge and temperature for fish). The setting of the marking facility at trap1, the average environmental conditions or the route between the two traps may also change from year to year and affect the timing of passage of marked individuals at trap 2. We therefore modeled $\lambda[i,j,y]$ according a year effect $\alpha_{base}[y]$, a day of marking effect $\alpha_{mark}[i,y]$ and a day of passage effect $\alpha_{migr}[j,y]$. Since $\lambda[i,j,y]$ is strictly positive, we used an exponential formulation:

$$j = i, ..., D: \qquad \lambda[i,j,y] = e^{(\alpha_{base}[y]+\alpha_{mark}[i,y]+\alpha_{migr}[j,y])} \tag{2.3}$$

with $\alpha_{mark}[i,y]$ and $\alpha_{migr}[j,y]$ being identically and independently distributed (iid) according to a normal distribution with 0 mean and standard deviation σ_{mark} and σ_{migr} respectively.

Although we acknowledge that environmental conditions may cause the $\alpha_{mark}[i,y]$ and $\alpha_{migr}[j,y]$ to vary, we do not follow Mäntyniemi et al. (2002) in explicitly modeling this causal relationship using observed covariates. The main reason is that the migration behavior of the marked individuals is not of ultimate interest here. Rather, it is a "nuisance" process, that we must account for though, in order for our model to be flexible enough to properly infer the daily variations of the capture probabilities presented in the next section.

Recapture process

Following Mäntyniemi et al. (2002), we model the recapture of marked individuals with a beta-binomial distribution. This allows to account for the overdispersion (relative to a binomial distribution) in the number of marked individuals recaptured due to an aggregation behavior:

$$n_{rec}[i,j,y] \sim BetaBinomial(p_{tr2}[j,y] \times \eta_{tr2}[y], (1-p_{tr2}[j,y]) \times \eta_{tr2}[y], \nu[i,j,y]) \tag{2.4}$$

with $n_{rec}[i,j,y]$ the number of fish marked on day i and recaptured on day j in year y, $p_{tr2}[j,y]$ the capture probability on day j in year y, and $\eta_{tr2}[y]$ the over-dispersion parameter in year y.

Trap efficiency is often influenced by environmental conditions, some of which can be measured and used as covariates to explain daily variations of the capture probability (e.g. river discharge for fish; Mäntyniemi et al., 2002). We model $p_{tr2}[i,y]$ in logit scale according to a linear relationship:

$$logit(p_{tr2}[j,y]) = \beta[1,y] + \beta[2,y] \times X[j,y] + \epsilon_{tr2}[j,y] \tag{2.5}$$

with $X[j,y]$ a standardized environmental covariate, $\beta[1,y]$ the mean capture probability in year y (logit scale), $\beta[2,y]$ the effect of the environmental co-

variate $X[j,y]$, and $\epsilon_{tr2}[j,y]$ a residual *iid* term, with mean 0 and standard deviation $\sigma_{tr2}[y]$ accounting for daily variations in the probability of capture due to unknown causes.

We explicitly model the influence of the environment on the capture probabilities because they are crucial quantities for estimating the daily number of unmarked individuals that are partially observed at trap 2. The formulation of equation 2.5 can easily be extended to more than one covariate.

Capture process of unmarked individuals

Relying on the standard hypothesis of CMR experiments that unmarked individuals behave in the same way as they marked counterparts in their capture process, the beta-binomial distribution is once again assumed for the number of unmarked individuals captured at trap 2 denoted $n_{um}[j,y]$:

$$n_{um}[j,y] \sim BetaBinomial(p_{tr2}[j,y] \times \eta_{tr2}[y], (1-p_{tr2}[j,y]) \times \eta_{tr2}[y], N_{um}[j,y]) \tag{2.6}$$

with $N_{um}[j,y]$ the total number of unmarked individuals passing at trap 2 on day j in year y.

Inspiring from Lindén et al. (2011), we model the daily variations of $N_{um}[j,y]$ with a negative binomial distribution, which is an over-dispersed version of the Poisson distribution, i.e. equivalent to a Poisson distribution whose mean parameter varies according to a gamma distribution with mean $m_N[y]$ and shape parameter κ_N:

$$N_{um}[j,y] \sim NegativeBinomial(m_N[y], \kappa_N) \tag{2.7}$$

This distribution is flexible enough to accommodate a variety of shapes for the distribution of $N_{um}[j,y]$, with probabilities monotonically decreasing from 0 if $\kappa_N < 1$ or a single mode otherwise. Note that, unlike Mäntyniemi et al. (2002) or Bonner et al. (2011), we do not make assumption about the evolution over time of $N_{um}[j,y]$. By default, we simply assume that $N_{um}[j,y]$ can vary widely and independently from day to day.

By summing the $N_{um}[j,y]$ and the numbers of marked individuals $n_{mark}[i,y]$, we obtain the total number of migrants per year $N_{tot}[y]$:

$$N_{tot}[y] = \sum_{j=1}^{D} N_{um}[j,y] + \sum_{j=1}^{D} n_{mark}[i,y] \tag{2.8}$$

Annual variations of the processes

We hierarchically model the year to year variation in the migration and (re)capture processes using random effects. We use normal, beta, or gamma distributions, depending on the quantities at stake, but not necessarily with their classical parametrization in order to facilitate the later assignment of priors (see section 2.2.3).

The average intensity of passage at trap 2 in year y (see eq. 2.3) can be expressed as:

$$\alpha_{base}[y] = -log(\mu[y]) \tag{2.9}$$

where $\mu[y]$ is the average migration time between traps in year y.

$\mu[y]$ is strictly positive but very large values are not plausible in practice. Therefore, we assumed that it varies between years within bounds according to a rescaled beta distribution:

$$\mu[y]/s \sim Beta(M_\mu/s, \rho_\mu) \tag{2.10}$$

where M_μ the mean of the $\mu[y]$, s is a scaling factor, i.e. the upper bound of the distribution, and ρ_μ is a quantity varying between 0 and 1 that controls the dispersion of the beta distribution. ρ_μ is the inverse of [the sample size + 1], the sample size of a beta distribution being the sum of its two classical shape parameters. The dispersion is 0 when $\rho_\mu = 0$ and is maximized when $\rho_\mu = 1$.

No other quantity controlling the annual timing of passage at trap 2 is explicitly modeled as varying from year to year. In particular, we use a single σ_{mark} and σ_{migr} irrespective of the year for the variation in the intensity of passage at trap 2 (eq.2.3). We choose this parsimonious option because these dispersion parameters are not of ultimate interest while they are difficult to infer from the available CMR data due to the latent nature of the migration process. Note, however, that this choice still leaves some flexibility when proceeding to the statistical inference to accommodate different levels of variation in the $\alpha_{mark}[i, y]$ and $\alpha_{migr}[j, y]$ from year to year.

All quantities controlling the capture process at trap 2 (eq.2.5) are assumed to vary randomly from year to year. The inverse-logit of $\beta[1, y]$, denoted $logit^{-1}(\beta[1, y])$, is the mean probability of capture under an average environmental condition in any year y, so we use a beta distribution:

$$logit^{-1}(\beta[1, y]) \sim Beta(M_{\beta[1]}, \rho_{\beta[1]}) \tag{2.11}$$

where $M_{\beta[1]}$ is the interannual average capture probability at trap 2 under an average environmental condition, and $\rho_{\beta[1]}$ is the dispersion parameter of the beta distribution (see ρ_μ above).

A normal distributions is used for $\beta[2, y]$:

$$\beta[2, y] \sim Normal(M_{\beta[2]}, \sigma_{\beta[2]}) \tag{2.12}$$

where $M_{\beta[2]}$ is the inter-annual mean effect of the environmental covariate, and and $\sigma_{\beta[2]}$ is the standard deviation of $\beta[2, y]$.

The residual standard deviation of the daily capture probabilities $\sigma_{tr2}[y]$ is assumed to be distributed according to a gamma law with mean M_σ and shape κ_σ:

$$\sigma_{tr2}[y] \sim Gamma(M_\sigma, \kappa_\sigma) \tag{2.13}$$

The over-dispersion parameter $\eta_{tr2}[y]$ (eq. 2.4 and 2.6) of the capture at trap 2 can be expressed as:

$$\eta_{tr2}[y] = \frac{(1 - \rho_{tr2}[y])}{\rho_{tr2}[y]} \tag{2.14}$$

where $\rho_{tr2}[y]$ is a positive correlation coefficient indicating the degree of aggregation of the individuals at capture (Mäntyniemi et al., 2015).

Since $\rho_{tr2}[y]$ is comprised between 0 (i.e. individuals are independent and capture is a binomial process) and 1 (i.e. all individuals behave exactly the same and capture is an all-zero Bernoulli process), we assume that it varies from year to year according to a Beta distribution:

$$\rho_{tr2}[y] \sim Beta(M_\rho, \rho_\rho) \tag{2.15}$$

where M_ρ is the interannual mean of $\rho_{trap2}[y]$ and ρ_ρ is the quantity that controls the dispersion of the beta distribution (as for $logit^{-1}(\beta[1, y])$, eq. 2.12).

Finally, the annual mean of the daily number of unmarked individuals passing at trap 2 $m_N[y]$ is assumed to be log-normally distributed:

$$m_N[y] \sim LogNormal(M_N, \sigma_N) \tag{2.16}$$

where M_N and σ_N are the mean and the standard deviation of the underlying normal distribution (log scale).

A single κ_N irrespective of the year is associated with the annually varying $m_N[y]$ in eq. 2.7. This parsimonious choice is made because this parameter, which controls the shape and the dispersion of the negative-binomial distribution, is difficult to infer from the available capture data while not being of ultimate interest.

2.2.2 Case study of seaward salmon migration in the Scorff river

Study site and data collection

The Scorff is a 78 km long coastal river in southern Brittany, France. Influenced by an oceanic climate, it is rain-fed and flows over a schist and granite bedrock. Its catchment area is 483 km², mainly forested and agricultural. It is colonized by A. salmon and its population has been monitored since 1994 as part of the Observatory for Research on Diadromous Fish in Coastal Rivers program (ORE DiaPFC; Azam et al., 2020).

During their seaward migration from March to June, salmon smolts are first sampled at the Leslé trap (trap1), located in the downstream end of the river. It is checked every morning, and occasionally once more in the afternoon on days of intense migration. Each fish is anaesthetized, marked individually or by batch, with an additional fin clip to detect an eventual mark loss or non-detection, and released shortly after downstream of the facility. The type of mark changed over the years. Visible implants were first applied from 1998 to 2017. Colored elastomers were also used, mainly from 2011 to 2017, for batch marking when large numbers were caught at the Leslé trap. Since 2018, only PIT (passive integrated transponder) tags have been placed. On rare occasions, fin clips have also been used for batch marking. Regardless of the type of mark used, it allows to identify unequivocally the day of marking (with very few exceptions detailed below).

Marked fish are recaptured at the Princes Mill trap (trap 2), located 600 meters downstream from the Leslé trap, just at the limit of tidal action. During the smolt run, it is checked one to three times a day, depending of the migration intensity and the year. The fish caught are counted and examined for the presence of any type of mark. Each mark observed is recorded along with the date of recapture. In the very few instances where a batch was marked at the Leslé trap with the same fin clip as the one used to detect mark loss, we attribute to that batch all the smolts recaptured with only the fin clip on the day of its release and the next two days .

This CMR protocol has been repeated every year since 1998, with the exception of 2020 due to the Covid-19 pandemic. The data consist of the daily numbers of fish marked at trap1, the daily numbers of unmarked fish captured at trap 2, and the daily numbers of marked fish recaptured at trap 2 per day of marking at trap1. For each year, we consider these CMR data between the 74th (i.e. mid-march) and the 158th day of the year (DOY, early June). Juvenile salmon caught at the traps outside of this 85-day window are rare and are considered to be residents rather than seaward migrants.

As the river flow increases, the proportion passing through trap 2 decreases, suggesting its efficiency is influenced by the river discharge. The mean daily discharge is then used as a covariate to explain variations in the probability of capture. We obtained the hourly discharge of the Scorff from 1998 to 2023 from the open database https://data.eaufrance.fr/ (hydrometric gauging station - J510 2210 01). In general, the fish collected at trap 2 on a given day j represent the cumulative catch of fish trapped approximately from noon on day $j-1$ to noon on day j, mostly during the night (see next section for additional details). The mean daily discharge which influences the probability of capture and conditions the observed catch on day j is then calculated over a 24-hour period from noon on day $j-1$ to noon on day j.

Modification to the generic model

We adapted the generic model to accommodate the specifics of the CMR protocol and dataset of our case study on the Scorff. In the generic model, the modeling of both the migration process of marked individuals (eq. 1-3) and the capture process (eq. 4-6) refer to a full calendar day j of passage at trap 2. In practice, however, the observed catch on day j corresponds to the individuals that passed at trap 2 from the last check of trap 2 on day $j-1$ to its last check on day j. Under the field protocol in use on the Scorff, this duration always includes the night of transition from day $j-1$ to j, when most smolts are actively migrating (Thorstad et al., 2012), and the relative contribution of day $j-1$ and j to the observed catch on day j varies. To account for this variable daily offset between the migration process and the recapture data, we modify eq. 3.2 as follows:

$$\begin{aligned}
&j = j, ..., i-1: && \pi[i,j,y] = 0 \\
&j = i: && \pi[i,i,y] = 1 - e^{(-w[i,y] \times \lambda[i,i,y])} \\
&j = i+1, ..., D-1: && \pi[i,j,y] = \left(1 - \sum_{k=1}^{j-1} \pi[i,k,y]\right) \times \left(1 - e^{(-w[j,y] \times \lambda[i,j,y] - (1-w[j-1,y]) \times \lambda[i,j-1,y])}\right) \\
&j = D: && \pi[i,D,y] = 1 - \sum_{k=1}^{D-1} \pi[i,k,y]
\end{aligned} \tag{2.17}$$

where $w[j,y]$ is a weighing factor comprised between 0 and 1.

These weights may reflect daily variations in both the schedule of trap checks and the within-day timing of smolts passage at trap 2. They are assumed to be distributed according to a beta law parameterized as for ρ_{tr2} (eq. 2.18):

$$w[j,y] \sim Beta(M_w, \rho_w) \tag{2.18}$$

where M_w is the overall mean of $w[j,y]$ and ρ_w controls the dispersion of the beta distribution.

The double marking by fin clipping shows that a small but significant fraction of marks are lost or undetected. We therefore modified the recapture process at trap 2 by replacing $p_{tr2}[j,]$ in eq. 2.4 by its product with $(1 - p_{lost})$, where p_{lost} is the probability of a mark being lost (or undetected). In order not to double count the fish that have lost their mark in eq. 2.8, we also replace the $n_{mark}[i, y]$ by the number of marked fish that did not lose their mark, which we model as a binomial draw in the $n_{mark}[i, y]$ with probability $(1 - p_{lost})$.

We used the logarithm of the river discharge as the covariate $X[j, y]$ in eq. 2.5. This transformation ensures both that the support of $X[j, y]$ is the same as that of $logit(p_{tr2}[j, y])$ and that the multiplication or division of the discharge by a factor has a symmetric effect on $logit(p_{tr2}[j, y])$. The covariate $X[j, y]$ is standardized over all observations during the migration period and years (in this case 85×25).

Due to the large number of quantities to be inferred and to the structure of our model, the computations for statistical inference can be cumbersome (see next section). To reduce the computational burden, we introduce a simplification in the model to downsize the set of unknowns. As 97.7% of the recaptures of marked fish occur within the first nine days after tagging, we restrict the multinomial distribution of eq. 3.3, and the associated quantities to ten categories from the day of marking to the 8^{th} day after marking, the last category corresponding to all the fish passing at trap 2 on the 9^{th} day after marking or later. We then use only the capture data (in eq. 2.4) for the first nine days from the day of marking, as the probability of capture of the fish in the 10^{th} category has no straightforward expression.

We consider a period of 85 days for smolt migration on the Scorff. However, the active migration window varies from year to year and is shorter. We define its start date as the first day which is followed by at least two days when the sum of the daily catch at trap1 and trap 2 is not 0. Symmetrically, we define its end date as the first day which is followed by at least two days when the sum of the daily catch at trap1 and trap 2 is 0. We restrict the inference on the $N_{um}[j, y]$ and the $N_{tot}[y]$ to the set of days between these two dates. This removes from the analysis many days with no (or very small) numbers of unmarked migrants, whose "artificial" accumulation could lead to a misfit with the negative-binomial distribution of eq. 7. The impact on the estimates of $N_{tot}[y]$ is expected to be negligible.

2.2.3 Bayesian statistical inference

Statistical inference about all the unknown quantities of our model is performed in the Bayesian framework. It requires completing the model specification already presented by assigning a prior distribution to all unknowns that are not conditionally dependent on any other other quantity in the model. We

then proceed separately and sequentially by inferring first the capture probabilities and then the numbers of unmarked migrants. We use MCMC sampling to approximate the joint posterior of all the model unknowns, combined with a Rao-Blackwell type approach inspiring from Rivot et al. (2001). Finally, we use posterior checking techniques to assess the adequacy between the model and the data at hand.

Prior distribution

Bayesian statistical ecologists must pay attention to the prior distribution they use (Banner et al., 2020). It must be considered and specified in the context of the model and the data at hand (Gelman et al., 2017). Our preference here is for weakly informative priors as presented and advocated by Gelman et al. (2017) and Lemoine (2019), while assuming that all unknowns that are not conditioned by any other quantity are *a priori* independent (see table 2.1).

We use non-classical parameterizations, mainly for the beta and gamma distributions, to facilitate the specification of the "weak information" that we introduce with our priors (Gelman, 2004). For the hyper-parameters that control the yearly variation of some parameters, we ran prior simulations to ensure that the resulting probabilities for the dependent parameter are both, not too contrasted over a range wide enough to allow a posterior updating by the type data we could observe, and not inadvertently giving too much credibility to unplausible values. Finally, we verify how our priors are updated *a posteriori* by our data (see 2.3 section).

We assigned χ^2 distributions with 5 degrees of freedom, rescaled to have a mean of 1, to all standard deviations, i.e. σ_{mark}, σ_{migr}, $\sigma_{\beta[2]}$, σ_N. It ensures that the probability is close to 0 when the standard deviation is very small. This is an important feature, because introducing a source of variation into the model is *a priori* inconsistent with considering that its standard deviation parameter could be negligible. By choosing a low number of degrees of freedom, we aim to have a dispersion that is high enough to allow for a significant updating by the data.

As 97.7% of the marked fish are recaptured within the first nine days, we set $s = 9$, i.e. the upper bound on the variation of the yearly mean duration of the migration of marked fish between the two traps $\mu[y]$. Accordingly, we choose a bounded prior between 0 and 9 for M_μ, the overall mean of the $\mu[y]$. We use a rescaled $Beta(2.5, 2.5)$, under its classical parameterization, to ensure that we have 0 probability on the 0 and 9 extremes, while *a priori* accepting a wide range of values in between.

$M_{\beta[1]}$ is the overall average probability of capture at trap 2 for an average discharge. We use a $Beta(2.5, 2.5)$, as for M_μ, but without rescaling. We then adjust the prior for $\rho_{\beta[1]}$ in order to get a resulting prior for $logit^{-1}(\beta[1, y])$,

i.e. the mean probability of capture under an average discharge in any year y, which is also weakly informative. We used a $Beta(2.5, 47.5)$ for $\rho_{\beta[1]}$, which allows us to get a prior for $logit^{-1}(\beta[1, y])$ that looks intermediate between the uniform distribution between 0 and 1 and the parabolic $Beta(2, 2)$ distribution. The same prior as for $(M_{\beta[1]}, \rho_{\beta[1]})$ is assigned to (M_ρ, ρ_ρ) and to (M_w, ρ_w).

We set a standard normal prior for $M_{\beta[2]}$. Combined with the prior assigned to $\sigma_{\beta[2]}$, this results in a prior for $\beta_2[y]$ with a 0 mean and a standard deviation of 1.55. The covariate $X[j, y]$ being standardized, this slightly less informative than the recommendation of Gelman et al. (2008).

The re-scaled χ^2 distribution with 5 degrees of freedom assigned to the standard deviations is used again for M_σ. For κ_σ, we also set a χ^2 distribution with 5 degrees of freedom, but not rescaled and translated with an offset of $+2$. This ensures that the resulting prior for $\sigma_{tr2}[y]$ has a probability close to 0 when $\sigma_{tr2}[y]$ becomes very small. It also has a mean of 1 and its 95% probability interval is $[0.1, 3.1]$.

We set a log-normal prior for M_N with a standard deviation of 1 for the underlying normal distribution in log scale. This results in a 95% prior probability interval comprised between the median divided by 7 and the median multiplied by 7. It is wide enough to allow *a posteriori* updating by the data, provided that we choose a plausible median (i.e. the exponential of the mean in log-scale), to avoid inadvertently creating a prior *vs* data conflict (Evans et al., 2006; Evans et al., 2020). Thus, we set the median to 28.5, calculated as the overall median number of unmarked fish captured per day (4) divided by the ratio of the cumulative number of marked of fish that we have recaptured (6421) to the cumulative number of fish marked (45715). The associated shape parameter κ_N is assigned a $Gamma(1, 1)$ distribution. This prior slightly favors κ_N values below 1 ($P(\kappa_N < 1) = 63\%$) that leads to negative-binomial distributions of $N_{um}[j, y]$ (eq. 7) that decrease monotonically from 0. This is consistent with the very plausible *a priori* assumption of a majority of days with low $N_{um}[j, y]$ and few days with much larger $N_{um}[j, y]$.

An informative prior is assigned to p_{lost} based on available data not used elsewhere for statistical inference. We use the observations made in the years when only visible implants were used. A $Beta(115, 1775)$ distribution is used because, in those years, among the marked fish recaptured, 115 had lost their visible implant while 1775 had retained it. In the absence of proper data to assess the probability of an elastomer or a PIT tag being lost or undetected, we additionally assume that it is the same as for visible implants.

Sequential inference

Without the numbers of fish marked per day $n_{mark}[i, y]$ and the numbers subsequently recaptured per recapture day $n_{rec}[i, j, y]$, the capture data of un-

Table 2.1 – Symbols, definitions and prior distributions of all the quantities referenced in the model. They are grouped by process and ordered within each process from the top (hyper)parameters, through the intermediate latent layer, down to the data

Symbol	Description	Prior
i	marking day index	
j	recapture day index	
y	year index	
$N_{tot}[y]$	Total number of migrants	
	Migration and timing of passage of marked individuals at trap 2	
M_μ	mean of $\mu[y]$	Beta(2.5,2.5) (rescaled [0,s])
s	upper bound of $\mu[y]$	
ρ_μ	dispersion parameter of $\mu[y]$	Beta(2.5,47.5)
σ_{mark}	standard deviation of $\alpha_{mark}[i,y]$	$\chi^2(5)$ (rescaled, mean = 1)
σ_{migr}	standard deviation of $\alpha_{migr}[j,y]$	$\chi^2(5)$ (rescaled, mean = 1)
M_w	mean of $w[j,y]$	Beta(2.5,2.5)
ρ_w	dispersion parameter of $w[j,y]$	Beta(2.5,47.5)
$\mu[y]$	mean duration of transit between the two traps	
$\alpha_{base}[y]$	mean hazard of passage (log scale)	
$\alpha_{mark}[i,y]$	marking day effect on hazard (log scale)	
$\alpha_{migr}[j,y]$	recapture day effect on hazard (log scale)	
$\lambda[i,j,y]$	hazard of passage	
$w[j,y]$	daily weighing of hazard	
$\pi[i,j,y]$	probability of passage	
$\nu[i,j,y]$	number of marked individuals passing at trap 2	
$n_{mark}[i,y]$	number marked	
p_{lost}	probability of mark loss	Beta(115,1775)
	Recapture of marked individuals at trap 2	
M_ρ	mean of $\rho_{tr2}[y]$	Beta(2.5,2.5)
ρ_ρ	dispersion parameter of $\rho_{tr2}[y]$	Beta(2.5,47.5)
$M_{\beta[1]}$	mean of $\beta[1,y]$ (logit^{-1} scale)	Beta(2.5,2.5)
$\rho_{\beta[1]}$	dispersion of $\beta[1,y]$ (logit^{-1} scale)	Beta(2.5,47.5)
$M_{\beta[2]}$	mean of $\beta[2,y]$	Normal(0,1)
$\sigma_{\beta[2]}$	standard deviation of $\beta[2,y]$	$\chi^2(5)$ (rescaled, mean = 1)
M_σ	mean of $\sigma_{tr2}[y]$	$\chi^2(5)$ (rescaled, mean = 1)
κ_σ	shape of gamma distribution of $\sigma_{tr2}[y]$	$\chi^2(5)$ (translated, offset = 2)
$\rho_{tr2}[y]$	capture overdispersion	
$\beta[1,y]$	mean capture probability (logit scale)	
$\beta[2,y]$	covariate effect on capture probability	
$\sigma_{tr2}[y]$	residual standard deviation of $p_{tr2}[j,y]$ (logit scale)	
$p_{tr2}[j,y]$	capture probability	
$n_{rec}[i,j,y]$	number recaptured	
$X[j,y]$	covariate influencing capture probability (standardized log of discharge)	
	Capture of unmarked individuals at trap 2	
M_N	mean of $m_N[y]$ (log scale)	Normal(log(28.5),1)
σ_N	standard deviation of m_N[y] (log scale)	$\chi^2(5)$ (rescaled, mean = 1)
κ_N	shape of negative-binomial distribution of N_{um}	Gamma(1,1)
m_N[y]	mean number of unmarked individuals passing at trap 2	
$N_{um}[j,y]$	number of unmarked individuals passing at trap 2	
$n_{um}[j,y]$	number of unmarked individuals captured	

marked individuals $n_{um}[j,y]$ alone do not allow estimation of the daily capture probabilities $p_{tr2}[j,y]$ or the daily numbers of migrating fish $N_{um}[j,y]$. On their own, the $n_{um}[j,y]$ are essentially uninformative about the capture probabilities. However, in a Bayesian approach using all available data to infer all unknown quantities of interest, the numbers of unmarked fish caught at trap 2 will contribute to the *a posteriori* updating of the daily capture probabilities. This can be misleading if large, resp. small, numbers of unmarked fish are captured at trap 2 for reasons independent of any increase, resp. decrease, of the capture probability. Indeed, variations of the numbers of unmarked fish caught at trap 2 can be primarily driven by variations of the intensity of smolt migration over

time. This issue can be addressed by adding an explicit modeling of the phenolgy of smolt migration to that of the CMR process (e.g. Mäntyniemi et al., 2002; Bonner et al., 2011; Pulkkinen et al., 2020). Here, we offer an alternative option that does not require modeling of the phenology, while ensuring that the capture data of unmarked fish do not unduly influence the estimation of captures probabilities, hence also of the daily and annual numbers of migrants.

We propose a sequential procedure in which we first proceed to the estimation of the capture probabilities $p_{tr2}[j,y]$, and then to that of the daily and annual numbers of migrants $N_{um}[j,y]$. In the first step, we derive the joint posterior distribution of all the unknown quantities of the CMR model presented at eq. 1-5 and 9-15, what does not require using the data of daily captures of unmarked fish at trap 2 $n_{um}[j,y]$. In the second step, we derive the joint posterior of the $N_{um}[j,y]$ as follows:

$$p(N_{um}|n_{mark},n_{rec},X,n_{um}) = \int p(N_{um}|p_{tr2},\rho_{tr2},n_{um}) \times p(p_{tr2},\rho_{tr2}|n_{mark},n_{rec},X)dp_{tr2}d\rho_{tr2} \tag{2.19}$$

This integral can be easily approximated numerically by a procedure inspired from the Rao-Blackwell technique demonstrated in Rivot et al. (2001). It amounts to first sampling a set of (p_{tr2},ρ_{tr2}) values in $p(p_{tr2},\rho_{tr2}|n_{mark},n_{rec},X)$, i.e. the posterior distribution derived from the first step, and then to average the distribution $p(N_{um}|p_{tr2},\rho_{tr2},n_{um})$ over all the (p_{tr2},ρ_{tr2}) values previously sampled. The distribution $p(N_{um}|p_{tr2},\rho_{tr2},n_{um})$ is obtained by the Bayesian treatment of the model presented at eq. 6-7 and 16 with fixed (p_{tr2},ρ_{tr2}) values. Note that in a Bayesian analysis of our full model using all the data at once we would have:

$$p(N_{um}|n_{mark},n_{rec},X,n_{um}) = \int p(N_{um}|p_{tr2},\rho_{tr2},n_{um}) \times p(p_{tr2},\rho_{tr2}|n_{mark},n_{rec},X,n_{um})dp_{tr2}d\rho_{tr2} \tag{2.20}$$

Hence, with our sequential procedure, we manage to remove the conditioning of the capture probabilities $p_{tr2}[j,y]$ by the capture data of unmarked fish $n_{um}[j,y]$.

In the sequel, the term "sequential procedure" refers to 2.19 and "single-step procedure" refers to 2.20. We compare them to assess their relative consequences. We also provide a comparison of the sequential procedure with a Petersen-type approach that ignores both the daily variations of the capture probabilities at trap 2 and the overdispersion in the capture process (i.e. the capture is modeled by a binomial law). The details of the Petersen-type model are given in the Supplementary material (section2.5.1).

MCMC sampling

For each of the model we use, we approximate the joint posterior distributions of all unknown quantities by Monte Carlo Markov Chain (MCMC) sampling, as implemented by the Nimble software (Valpine et al., 2024) and the R statistical computing environment (R Core Team, 2024). We run 3 parallel chains and retain 5000 iterations from each (after an initial burn-in sequence). Based on this sample of 15000 values, we assess the convergence of the MCMC sampling by checking the stationarity and the mixing of the chains marginally for each quantity (Gelman et al., 2013). We examine the stationarity by means of running quantiles (5%, 50%, 95%). We use the $\hat{R}$ criterion for mixing and verify it is below 1.01 (Vehtari et al., 2021)., 2021. In addition, we ensure the effective sample size is greater than 400 (Vehtari et al., 2021). Model script is provided in appendices A and B (see 4.6 and 4.6).

To implement the Rao-Backwell procedure presented in the previous section, we first subsample 50 (p_{tr2}, ρ_{tr2}) values from the 15000 values used to approximate the joint distribution $p(p_{tr2}, \rho_{tr2}|n_{mark}, n_{rec}, X)$. For each (p_{tr2}, ρ_{tr2}) value, we draw an MCMC sample to approximate $p(N_{um}|p_{tr2}, \rho_{tr2}, n_{um})$, from which we subsample 300 values. We then combine the 50 samples of 300 values to get a sample of 15000 values that approximates $p(N_{um}|n_{mark}, n_{rec}, X, n_{um})$ according to eq. 2.20. We check the convergence by monitoring the evolution of the quantiles (5%, 50%, 95%) of the $N_{um}[j, y]$ and the $N_{tot}[y]$ along the sequential cumulative of the 50 subsamples. We verify that the quantiles stabilize with the cumulative of the subsamples.

Posterior checking

We assess *a posteriori* the adequacy between our model and the available data (Gelman et al., 2013). We use the replication of data approach and we compare the distribution of summary statistics over *a posteriori* replicated datasets with their observed values calculated from the data (Gelman et al., 2013). For the first step of our sequential procedure, we consider for each year the variance of the numbers of marked fish recaptured (per day of marking and of recapture) and the total number of marked fish recaptured at trap 2. For the second step, the same statistics are used but for the unmarked fish. Note that we performed several other posterior checks to guide us during the model building phase which we do not present here. We used the data replications tools of the Nimble software.

2.3 Results

The posterior checks do not reveal any inadequacy between our model and our sequential procedure for Bayesian inference, and the available data. The observed values of the yearly statistics fall within the range of those calculated

from the *a posteriori* replicated data sets. Additional details can be found in the supplementary material.

All the priors assigned to the (hyper)parameters of the model are clearly updated *a posteriori* (see 2.5), except for κ_σ and p_{lost}. This is no surprise for the latter, as there is no information in the CMR data about mark loss. For κ_σ, the quasi absence of posterior updating is associated with a very strong one on M_σ though. For all the other parameters, the posterior updating leads to a significant variance reduction (except for ρ_w) and a displacement of the median (except for and κ_N).

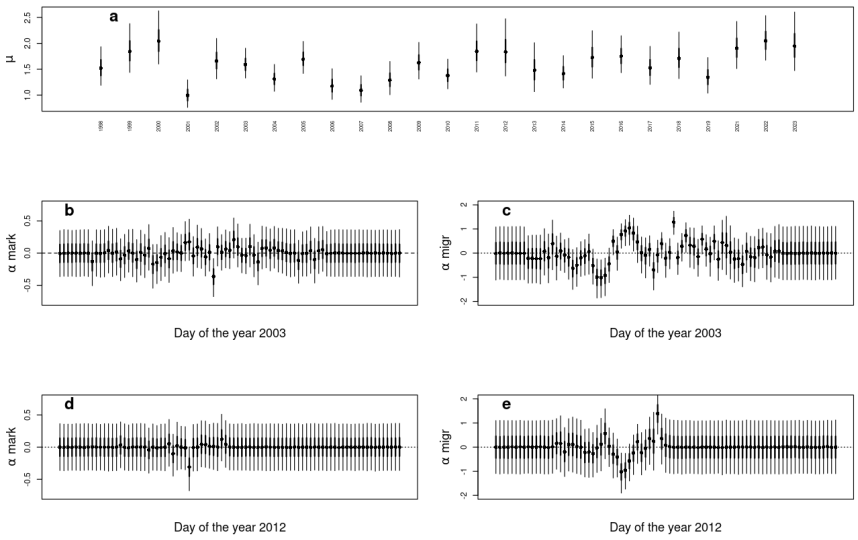


Figure 2.2 – **Posterior distributions of quantities of the migration and timing of passage process.** The plain dot represents the median, the thick line the 50% interval and the thin line the 90% interval. a. Average transit time between the two traps ($\mu[y]$) by year. b & d. Marking day effect ($\alpha_{mark}[i,y]$) for the year 2013 and 2016 respectively. c & e. Migration day effect ($\alpha_{migr}[j,y]$) for the year 2013 and 2016 respectively.

Overall, the mean duration of the migration between the two traps is 1.6 days (posterior median of M_μ). Its variation between years is moderate, with posterior medians of $\mu[y]$ ranging from 0.99 in 2001 to 2.05 in 2022 (Fig. 2.2.a). The effect of the day of marking on the timing of passage at trap 2 is much weaker than that of the day of recapture (posterior medians of $\sigma_{mark} = 0.22$ and $\sigma_{migr} = 0.67$). The $\alpha_{mark}[i,y]$ can be rather pronounced on some days, with posterior medians ranging from-0.36 (on day 39 in 2003) to (0.23 on day 43 in 2004), but only 4 of them have more than 90% posterior probability to be lower or greater than 0 (Fig. 2.2.b and d). In contrast, the posterior medians of the $\alpha_{migr}[j,y]$ vary from -1.09 (on day 33 in 2005) to 1.39 (on day 41 in2012) and they have over 90% posterior probability to be lower or

greater than 0 for 93 days (Fig. 2.2.c and e). Within each year y, the posterior correlations between the $\alpha_{mark}[i, y]$ and the $\alpha_{migr}[j, y]$ are in most instances low (over 99.9% below 0.25 in absolute value; min = -0.56, max = 0.20), showing little confusion between the two sets of daily effects. The highest correlations are negative and concern essentially those corresponding to the same day. The average correlation between $\alpha_{mark}[i, y]$ and $\alpha_{migr}[j, y]$ is -0.05 when $i = j$ (ranging from -0.56 to 0.06) vs. 0 (ranging from -0.31 to 0.09) otherwise (see). The median of M_w is 0.3, indicating that, overall, the marked fish recaptured on day j have passed at trap 2 primarily on day $j - 1$. However, the relative contribution of day $j - 1$ and j is quite variable between days as indicated by the relatively high ρ_w (posterior median = 0.11) and the posterior distributions of the $w[j, y]$ (Fig. 2.4 , see also supplementary material 2.S4).

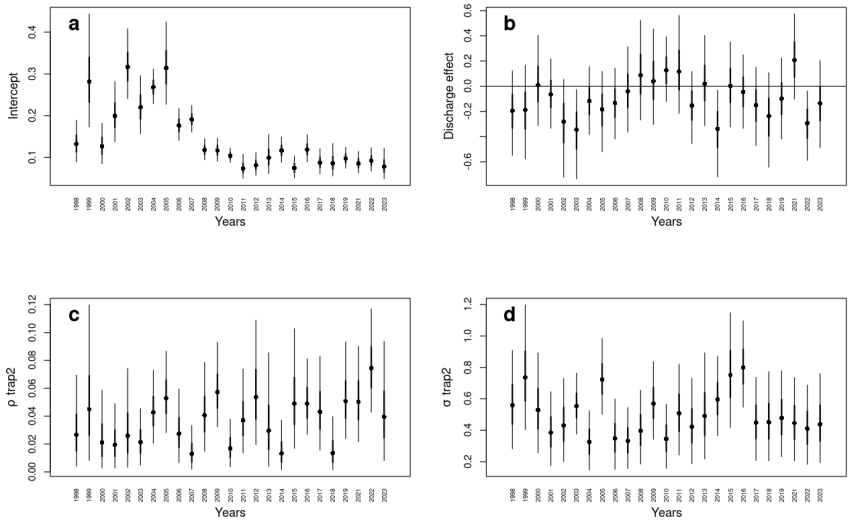


Figure 2.3 – **Posterior distributions of quantities of the (re)capture process at trap 2.** The plain dot represents the median, the thick line the 50% interval and the thin line the 90% interval. a. Average capture probability (for a river discharge equal the mean; $logit^{-1}(\beta[1, y])$). b. River discharge effect on capture probability ($\beta[2, y]$). c. Overdispersion parameter ($\rho_{tr2}[y]$). d. Residual standard deviation of the capture probability ($\sigma_{tr2}[y]$).

The mean capture probability at trap 2 varies widely from year to year (posterior median of $logit^{-1}(\beta[1, y])$ from 0.07 in 2002 to 0.24 in 2011), with generally higher values at the beginning of the study period (Fig. 2.3. a). The overall effect of the discharge on the trap efficiency is rather negative ($P(M_{\beta[2]} < 0) = 0.88$). but the annual effects vary between years. The 90% posterior probability intervals (ppi) of the $\beta[2, y]$ encompass 0 in a number of years, even though the medians are negative in the vast majority of cases (Fig. 2.3. b). The overdispersion of the capture at trap 2 appears to be low on average (posterior median of $M_\rho = 0.04$), with some significant variations of $\rho_{tr2}[y]$ from year to year (Fig. 2.3.c). Among the four quantities characterising

the capture process annually, the standard deviation of the residual variation of the capture probability $\sigma_{tr2}[y]$ seems to be the least variable between years. The variation of the quantities characterizing the capture process, together with those of the discharge regime, lead to contrasted temporal profiles of daily capture probability between years, as shown at Fig. 2.4 (see also supplementary material2.S4).

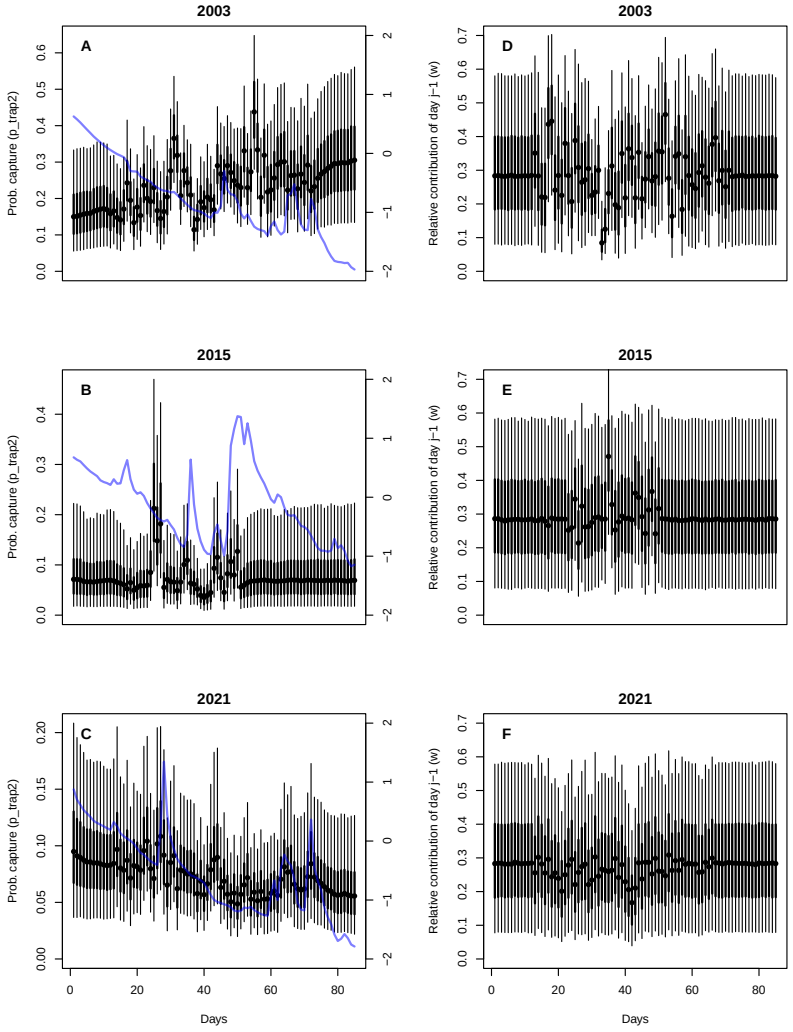


Figure 2.4 – **Posterior distributions of the daily probabilities of capture at trap 2 (a-c) and daily weighted factors w measuring the relative contribution of the fish passing at trp2 on day j to the capture on the same day (d-f) for years 2003, 2015 and 2021.** The plain dots represent the medians, the thick lines the 50% intervals and the thin lines the 90% intervals. The blue line indicates the standardized daily discharge (log scale).

The posterior probability that $\kappa_N < 1$ is 1, so the yearly distributions of the $N_{um}[j, y]$ (eq. 2.7) are monotonically decreasing from 0. The intra-annual

temporal profile of the $N_{um}[j,y]$ are characterized by the presence of one to several peaks and frequently large variations from one day to the next (see supplementary material 2.S5). The precision of the daily $N_{um}[j,y]$ estimates are relatively poor (average posterior CV $= 1.22$, see 2.S5), as is that of the daily capture probabilities (Fig. 2.4). The annual estimates of the total number of migrating smolts $N_{tot}[y]$ are much more precise (average posterior CV $= 0.14$) and quite variable between years (Fig. 2.5).

The estimates of the $N_{tot}[y]$ derived from our sequential procedure are overall fairly consistent with those obtain by the single step procedure, which updates *a posteriori* the joint distribution of all the unknown quantities using all the available data at once. There is no systematic difference regarding their position or their uncertainty. However, there is a slight tendency for the median of the posterior $N_{tot}[y]$ distributions to be higher with our sequential procedure (17 out of 25; Fig. 2.5) and the difference can be noticeable in some years (e.g. $+12.5\%$ in 2001 or $+23.3\%$ in 2023). The uncertainty of the $N_{tot}[y]$ posterior estimates is also slightly larger on average with the sequential procedure (mean posterior CV: 0.14 vs 0.13 with the single-step procedure). There is strong evidence that the capture data of unmarked fish $n_{um}[j,y]$ contribute significantly to the *a posteriori* updating of the capture process at trap 2 when used jointly with data on marked individuals. In particular, the estimates of the effects of discharge are generally greater, and the overall negative effect of the river discharge becomes clearly positive ($P(M_{\beta[2]} > 0) = 0.97$), and the mean capture probabilities are generally smaller, when compared to the sequential approach (see). There is a tendency to associate low, resp. high, $n_{um}[j,y]$ with low, resp. high, capture probabilities $p_{tr2}[j,y]$, a pattern that does not appear with the sequential procedure (see).

The Petersen-type model produces posterior estimates of $N_{tot}[y]$ that are rather consistent with those derived from our sequential procedure, which rely on a more complex model accounting for both daily variation in the probability of capture and overdispersion in the capture process (Fig. 2.5). However, the uncertainty from the Petersen-type model is systematically lower: the average posterior CV of the $N_{tot}[y]$ is 0.07, a reduction of 51% compared to our approach (0.14). At the same time, the medians of the posterior distributions of the $N_{tot}[y]$ tend to be lower with the Petersen-type model (18 out of 25), the difference being substantial in some years (e.g. -20.9% in 1999, -17% in 2013 or -18.1% in 2017).

2.4 Discussion

The approach presented here meets the challenges identified in the introduction and is potentially applicable to any taxon that undergoes unidirectional displacement along a migratory corridor. Based on a CMR protocol using a sequential double trapping, it allows the estimation of daily capture probabilities,

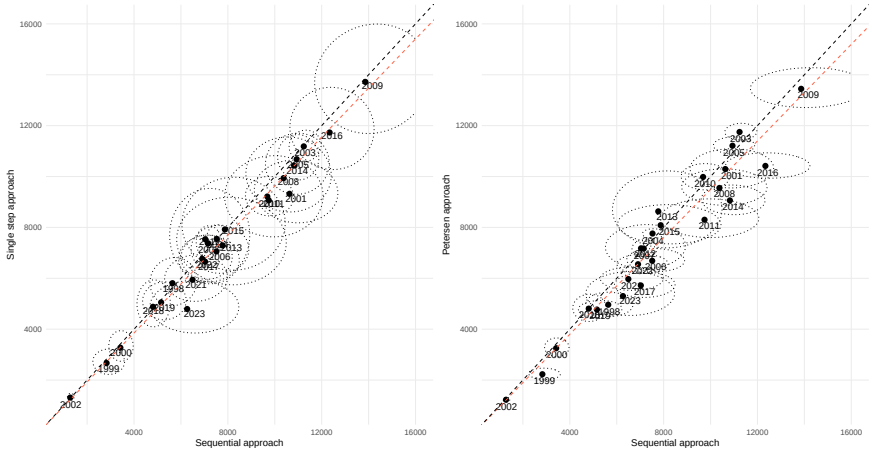


Figure 2.5 – **Comparisons of the posterior distributions of the annual total number of migrating fish between the sequential and the single-step procedures with our model (left panel) and between a Petersen-type approach and our model with the sequential procedure (right panel).** The plain dots represent the medians, the widths and heights of the dotted ellipses are proportional to the standard deviations of the posterior distributions (confidence level = 0.5). The black line is for $X = Y$ and the red one is the linear relationship between the medians (with 0 intercept).

daily numbers of unmarked fish passing at trap 2 and total annual numbers of migrants, without having to resort to modelling the migration phenology. A sequential Bayesian procedure is proposed for estimating all of these unknown quantities, which prevents from any undue influence of the numbers of unmarked fish caught at trap 2 on the estimates of capture probabilities. The model is based on an expression of the daily passage probabilities of marked fish at trap 2 that takes into account the time elapsed since marking together with a combination of three main effects corresponding to the year, the day of marking and the day of passage. A possible overdispersion of the capture at trap 2 (relative to a binomial process) is also included. All of this is implemented in a multi-year hierarchical framework that allows for the joint analysis of a series of years of observations (25 in our case).

Our approach has several notable and original features. The first is the use of a discrete- time point process formulation. Hance et al. (2020) present a general approach in discrete time for estimating capture and survival probabilities at a series of capture devices along a migration corridor. In an application to the downstream migration of Chinook salmon juveniles, Hance et al. (2024) propose an extension of Hance et al. (2020) approach that additionally allows estimation of the numbers of migrating juveniles, but in a specific context where marked fish are of hatchery origin only. These models are not unrelated to ours, which might be seen as a special case with only two capture devices and no mortality of marked fish in between. However, despite potentially opening the door to many options for modeling of the timing of passage at the capture device(s), neither Hance et al. (2020) nor Hance et al. (2024) suggest anything

similar to our approach based on point process modelling with a piecewise constant hazard function and the combination of year, day of marking and day of passage effects. They also do not consider the joint treatment of a series of years of observations with the same CMR protocol and the overdispersion of the capture data.

The conditioning of the intensity of passage at trap 2 by the day of passage itself is a second originality of our approach. The value of this modeling choice is validated *a posteriori* in our case study by the demonstration of a stronger effect of the day of passage than of the day of marking on the passage rate of marked individuals at trap 2. The marking day effect is so weak that we could even consider removing it from the model, but we prefer to keep it in order to maintain a more general formulation of our model. This result was expected, as the same standard CMR protocol is applied day after day and year after year, in order to minimize the effects of marking day. In contrast, smolt migration activity is known to be highly variable over time, particularly under the influence of environmental conditions (McCormick et al., 1998; Thorstad et al., 2012; Pulkkinen et al., 2020). We have not introduced an explicit conditioning of daily effects by observed environmental covariates (as this is not of primary interest in our case study), or by time (with increasing or decreasing passage intensities over time), but this would be a possible extension and fairly easy to implement.

A third originality of our approach is the sequential procedure we propose for performing the statistical inferences. As our case study illustrates, the single step procedure, i.e. the Bayesian treatment of the full model at once, can lead to an updating of the capture probabilities by the numbers of unmarked fish caught at trap 2, with estimates of capture probabilities positively correlated with the catches of unmarked fish. This may seem reasonable at first sight and cannot be ruled out *a priori*. However, it must be critically examined, as the number of unmarked fish caught at trap 2 can reflect the intensity of the migration in the first place. To separate the potentially confounded effects of trap efficiency and migratory activity on the catch at trap 2, several authors rightly proposed to extend the model to include an explicit representation of the migration phenology (e.g. Mäntyniemi et al., 2002; Bonner et al., 2011; Pulkkinen et al., 2020). But this comes at the cost of a significant increase of the model complexity, with associated difficulties and limitations (see 3.1). We propose another option that keeps the modeling of the daily numbers of migrants fairly simple, while ensuring that the unmarked fish data do not affect our inference of captures probabilities (and dependent quantities). Considering the numbers of unmarked fish caught at trap 2 alone are not sufficient to estimate the capture probabilities, our sequential procedure is particularly relevant when the data on marked vs unmarked fish appear to carry conflicting information, and when there is additional evidence that the number of unmarked fish caught at trap 2 is strongly influenced by migratory activity. Indeed, in such configuration, there is a risk of getting misleading estimates of capture probabilities and numbers of migrants by the single step procedure, and we contend that it is safer to apply our sequential procedure

to rely on the marked fish data only to estimate the captures probabilities.

This is in line with our case study. Our initial expectation was that, if the smolts are to follow the river flow, trap 2 would become less attractive when the river discharge increases, as the proportion of the discharge flowing through the trap decreases. This is confirmed *a posteriori* by the overall tendency for a negative effect of river discharge on daily capture probabilities evidenced on the basis of the marked fish data only (Fig. 2.3. b). At the same time, a positive relationship between the river discharge and the numbers unmarked individuals caught at trap 2 is observed almost every year (see supplementary materials 2.5). In the context of the model, this leads to infer an opposite positive relationship between the river discharge and the capture probabilities. As a result, the overall influence of river discharge on the capture probabilities becomes clearly positive when we allow their estimation to be influenced by both the marked and the unmarked fish data using the single-step procedure. This is misleading, because the river discharge is known to have a strong and positive influence on the smolt migration activity (McCormick et al., 1998; Thorstad et al., 2012; Pulkkinen et al., 2020), and thus potentially on the number of unmarked smolts caught at trap 2. In absence of such a phenological relationship explicitly accounted for in our model, the positive association between the river discharge and the numbers of migrating smolts is erroneously taken to indicate an increase in the capture probabilities with the river discharge. For the practitioner wanting to keep the advantage of the fairly simple modelling of the daily numbers of migrants we propose, compared to an additional modeling of the migration phenology, we recommend the use of our sequential procedure for statistical inference.

Overall, the model is well updated *a posteriori* by the available data in our case study. The only unknown quantity that shows little updating is κ_σ (along with p_{lost} which is assigned a strongly informative prior based an ancillary data). This is not due to a confusion with other model parameters (see the posterior correlation matrix of the (hyper)parameters in the supplementary material), so there is most likely not enough information in the data to modify our prior through the likelihood. To the extent that this is considered an issue, one could modify the model by using a single σ_{tr2} irrespective of the year, since the $\sigma_{tr2}[y]$ are not very different and the mean parameter M_σ is well estimated. For the sake of consistency we prefer to let all the parameters of the recapture process at trap 2 to vary between years and to use our weakly informative prior on κ_σ as a way to regularize the estimates of all other unknowns by averaging over a wide range of plausible values of κ_σ.

The overall median transit time between the two traps is 1.6 days. This duration varies among individuals and years and it may take several days to some individuals to reach trap 2. Considering the short distance between the two traps and the literature on smolt migration speed (Fängstam, 1993; Aarestrup et al., 2002; Lothian et al., 2018), this seems relatively long for fish that were actively migrating when caught at trap1. It reminds us that capture and marking is not neutral with respect to the behaviour of smolts and that the assumption that the marked fish behave as their unmarked counterparts is

always questionable (but see also Sortland et al., 2024), although it is required in CMR models.

The effects of the year, the day of marking and the day of passage are fairly well identified *a posteriori* in our case study. While remaining moderate, the highest potential confusion is detected between the $\alpha_{mark}[i, y]$ and $\alpha_{migr}[j, y]$ when $i = j$. This is most likely related to the fact that, in days with high $\alpha_{migr}[j, y]$, a high proportion of fish marked on day $i = j$ pass at trap 2 on their day of marking. But in such a case, a high proportion of fish passing at trap 2 on their day of marking could also be explained by a high $\alpha_{mark}[i, y]$. Taking this line of reasoning to its logical conclusion, in the limit case where all fish pass at trap 2 on their day of marking, there would be no way to distinguish the effect of the day of marking from that of the day of passage. Note however that the relative confusion between the $\alpha_{mark}[i, y]$ and $\alpha_{migr}[j, y]$ when $i = j$ in no way invalidates the introduction of a day of passage effect in our model because its larger magnitude (i.e. variance) could not be compensated for by the weak marking day effect.

The capture process of marked individuals shows *a posteriori* obvious variations between years. There are potentially several reasons for this, such as changes in personnel, in the configuration of the river in the vicinity of trap 2, or in the way the proportion of the river flow passing through trap 2 is regulated. However, the exact reasons in our case study remain elusive and could not be precisely determined from field information. Nevertheless, the accounting for these annual variations remains relevant because they affect the estimates of other unknown quantities of interest, the $N_{tot}[y]$ in the first place.

In our model, the use of the daily weights $w[j, y]$ allows the synchronization of the capture process with the timing of passage at trap 2. Their introduction in the model is validated by their clear *a posteriori* updating which shows that they can vary strongly from day to day. They also proved to be crucial for demonstrating the effect of the environmental covariate (river discharge) on the capture probability, avoiding a mismatch of the capture data relative to the timing of passage at trap 2, which would otherwise be attributed to the dispersion of the capture process and/or of the migration between the two traps. The variations of the $w[j, y]$ are not only caused by the environment, through its influence on the migration of the marked individuals, but most likely by the daily variations in the field work, especially in the timing and the number of checks at the two traps. These short term variations play a significant role in structuring the variability of the CMR observations when dealing with daily time steps. This is even more important in our case study, where the two traps are very close and the travel from trap1 to trap 2 is short and can be of less than a day.

Following Mäntyniemi et al. (2002), we use a beta-binomial distribution for the capture process at trap 2 to account for the overdispersion in the CMR data due to the propensity of the smolts to migrate and be caught in batches (eq.2.4 and 2.6). Along the same line, we could have replaced the multinomial distribution (eq. 3.3) by its overdispersed version, a Dirichlet-multinomial, for the timing of passage at trap 2. The use of the multinomial distribution seems

somewhat inconsistent, but implementing a Dirichlet-multinomial distribution for the latent migration process is not straightforward with the Bayesian modeling tools we used (Nimble software; Valpine et al., 2024). More fundamentally, separating of the overdispersion due to the migration process from that due to the capture process would be difficult. This is even more true in the context of our model, where the timing of passage at trap 2 is modeled with two daily random effects, $\alpha_{mark}[i, y]$ and $\alpha_{migr}[j, y]$ which already account for the variability of the latent numbers of marked fish passing at trap 2 $\nu[i, j, y]$. Thus, we prefer to keep a multinomial distribution for the $\nu[i, j, y]$, even though the overdispersion we then estimate for the capture process only may at least partially reflect that of the migration process.

The overdispersion of the capture process may seem small, but it results in catches that are significantly more dispersed than under the assumption of binomial process (i.e. $\rho_{tr2}[y] = 0$), especially on days when large number of fish pass at trap 2. Indeed, with a capture probability of 0.13 and an overdispersion of 0.04, i.e. similar to the averages we estimated in our case study, the standard deviation of the number captured is increased by 17% for a draw from 10 fish, by 172% for 50 fish, 331% for 250 fish and by 458% for a draw from 500 fish, compared to a binomial process. Hence, if only for this reason, it is not surprising that the Petersen-type estimates of the $N_{tot}[y]$ are more precise. In addition, accounting for the variability of the capture probability also plays a role. In the context where the overriding priority is on the conservation of Atlantic salmon populations (NASCO, 2019; Darwall, 2023), it is important not to be overly confident in the estimates we produce and we prefer to err on the side of caution by using a model that produces less precise estimates while being more comprehensive and realistic about the sources of variability affecting the CMR data at hand. The same applies to the posterior updating of the full model using all the available data at once, which tends to produce slightly more precise $N_{tot}[y]$ estimates than the sequential procedure we recommend (see above).

There is a tendency for the Petersen-type estimates of $N_{tot}[y]$ to be lower than those derived with our more detailed model. The differences between the posterior medians are not systematic, but they can be substantial in some years (e.g. 1999, 2013, 2017; Fig. 2.5). The magnitude and the sign of the difference depend on the temporal distributions of the numbers of marked individuals released at trap1, of the daily capture probabilities, and of the numbers of unmarked individuals caught at trap 2. If small, resp. large, numbers of marked individuals are available for recapture on days when the capture probability at trap 2 is low, resp. high, the $N_{tot}[y]$ median tends to be smaller, resp. smaller, with the Petersen-type model, because the average probability of capture estimated with that model is then higher, resp. lower. At the same time, if large numbers of unmarked individuals are caught at trap 2 when the capture probability is low, resp. high, the $N_{tot}[y]$ median tends to be larger, resp. lower, with our approach. Although the simpler Petersen-type model may provide reasonable estimates of the annual total numbers of migrating smolts in our case study, we recommend the use of our more complex model

which accounts more realistically of the intricacies of the temporal dynamics of our CMR protocol.

It is now increasingly recognized that not accounting explicitly for the observation process by which data are collected in ecological studies, exposes to the risk of making misleading statistical inferences about the ecological process of ultimate interest (Chadwick et al., 2023). When studying the phenology of migration by a CMR protocol, the data collected result from an observation process by trapping, which in turn is conditioned by the phenological process of interest. To analyze the latter, estimating the temporal profile of daily capture probabilities is key. When a double sequential trapping is operated (or a single trap with marked individuals released back upstream of the trap), our approach allows to estimate annually these profiles together with those of the daily numbers of unmarked migrating individuals at trap 2. However, the migration phenology cannot be properly inferred at trap 2, especially when the number of marked individuals is a significant fraction of the total number of migrants per year, as in our case study of salmon smolt migration in the Scorff. Indeed, the timing of passage of the marked individuals at trap 2 is altered by marking. Therefore, it is most preferable to examine the phenology of migration through the timing of passage at trap1. This requires an additional modeling effort, including the explicit representation some meaningful ecological mechanism for the phenological process, as in Pulkkinen et al. (2020). It is clearly an exciting avenue of future research that is opened up by the modeling exercise presented in this paper.

Acknowledgments

We would like to thank the Scorff technical team and the other people involved in collecting the data and managing the facilities. In particular, we would like to thank N. Jeannot and F. Quendo (INRAE, Pont-Scorff) for checking and completing the data.

2.5 Supplementary Material

2.5.1 Estimation of annual abundance using the Petersen approach

We present a simplified model based on the Petersen approach, also known as the Lincoln-Petersen method, which is more commonly used for estimating population abundance from capture-mark-recapture data. This method relies on the total number of individuals captured and marked, as well as the number of recaptured individuals, both marked and unmarked.

We used the same CMR protocol and data as described in section Methods. However, this standard model only takes into account the recapture process of marked fish and the process of capturing unmarked individuals. It combines all captures and recaptures over the migration period rather than representing the migration process on a daily time step. It allows the estimation of the capture probability at a second trap (p_{trap2}), while accounting for the effect of average discharge during the migration window and the probability of mark loss. Below, we provide a detailed description of each part of the model.

Recapture process

Every year, we capture a certain number of fish during their migration $n_{marked}[y]$ and they are all individually marked. However, some of them may lose their mark after release. The total number of fish marked that can be identified at trap 2 n_{marked} is then the result of a binomial draw which depends on the total number of individuals marked in trap 1 $n_{trap1}[y]$ and the probability of not losing their mark $(1 - p_{lost})$:

$$n_{marked}[y] \sim \text{Binomial}(1 - p_{\text{lost}}, n_{trap1}[y]) \tag{2.S1}$$

We model the recapture of those marked individuals for each year $n_{rec}[y]$ with a binomial distribution depending of the probability of capture at trap 2 $p_{tr2}[y]$ and the number of marked individuals who did not lose their marks ($n_{marked}[y]$):

$$n_{rec}[y] \sim \text{Binomial}(p_{tr2}[y], n_{marked}[y]) \tag{2.S2}$$

We model $p_{tr2}[y]$ in logit scale according to a linear relationship depending on the log-transformed and standardized discharge over the migration period ($StdLogQ$) :

$$logit(p_{tr2}[y]) = \beta[1] + \beta[2] \times StdLogQ[y] + \epsilon_{tr2}[y] \tag{2.S3}$$

with $\beta[1]$ the mean capture probability (logit scale), $\beta[2]$ the effect of discharge, and $\epsilon_{tr2}[y]$ a residual iid term, with mean 0 and standard deviation σ_{tr2} accounting for variations in the probability of capture due to unknown causes.

Capture process of unmarked individuals

The number of unmarked fish captured at trap 2 $n_{um}[y]$ is also draw in a binomial distribution depending of the number of fish not captured and marked at trap 1 $N_{um}[y]$ and the probability of capture at trap 2 $p_{tr2}[y]$:

$$n_{um}[y] \sim \text{Binomial}(p_{tr2}[y], N_{um}[y]) \tag{2.S4}$$

Note that the total number of unmarked fish is a combination of individuals not caught in trap 1 and individuals that were caught but lost their tags $(n_{trap1} - n_{marked})$. Thus, the total number of unmarked fish per year $N_{um}[y]$ are the total number of fish each year $(N_{tot}[y])$ minus the fish still marked $n_{marked}[y]$:

$$N_{um}[y] = N_{tot}[y] - n_{marked}[y] \tag{2.S5}$$

Population Process

The total number of fish each year (N_{tot}) is modeled using a Poisson distribution with a Gamma-distributed rate parameter (λ) with shape parameter κ_λ and rate parameter θ_λ :

$$\begin{aligned} N_{tot}[y] &\sim \text{Poisson}(\lambda[y]) \\ \lambda[y] &\sim \Gamma(\kappa_\lambda, \theta_\lambda) \end{aligned} \tag{2.S6}$$

Prior distribution

The trapping efficiency is modeled with a logistic regression where the intercept and slope (with respect to discharge) are assigned uniform priors. The variability in the trapping efficiency is modeled using a precision parameter re-scaled to assigned a uniform prior distribution on the standard deviation :

$$\begin{aligned} \beta_1 &\sim \text{Uniform}(-10, 10) \\ \beta_2 &\sim \text{Uniform}(-10, 10) \\ \sigma_p &\sim \text{Uniform}(0, 30) \end{aligned} \tag{2.S7}$$

We assigned gamma distribution to the parameters of the Gamma-distributed rate parameter (λ):

$$\begin{aligned} \kappa_\lambda &\sim \text{Gamma}(0.001, 0.001) \\ \theta_\lambda &\sim \text{Gamma}(0.001, 0.001) \end{aligned} \tag{2.S8}$$

The probability of losing marks is modeled using a Beta distribution using the same values as the sequential model, i.e. a $Beta(115, 1775)$ distribution.

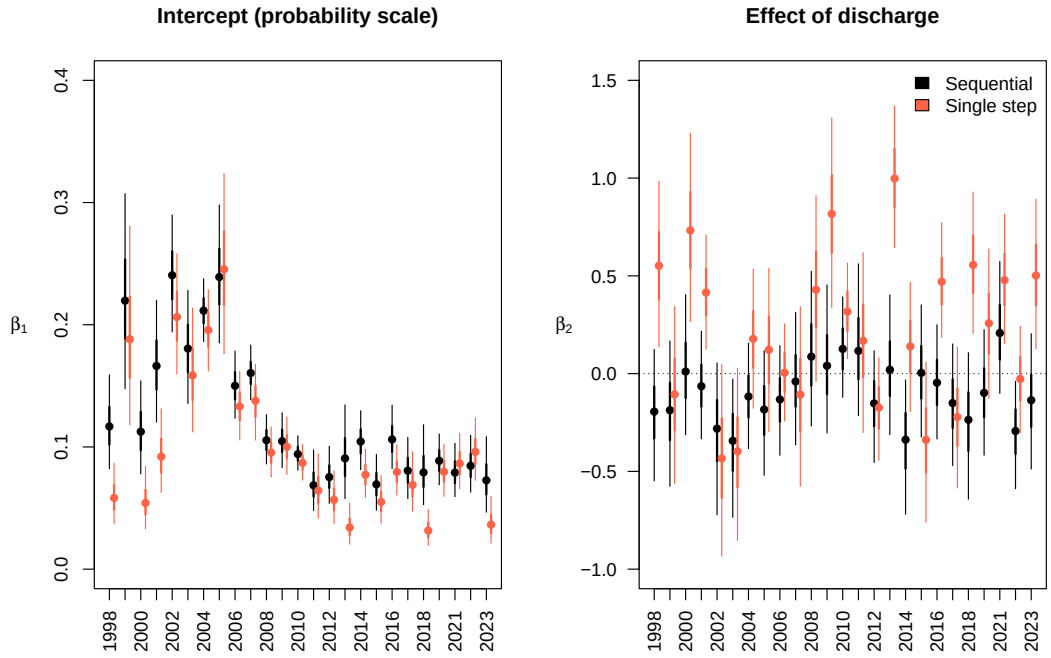


Figure 2.S1 – **Posterior distributions of the intercept (probability scale) and slope (effect of discharge) on the trapping efficiency (p_{tr2}) for each years.** The plain dot represents the median, the thick line the 50% interval and the thin line the 90% interval. The results from the sequential approach are in black and those from the single step approach in red.

2.5.2 Additional figures

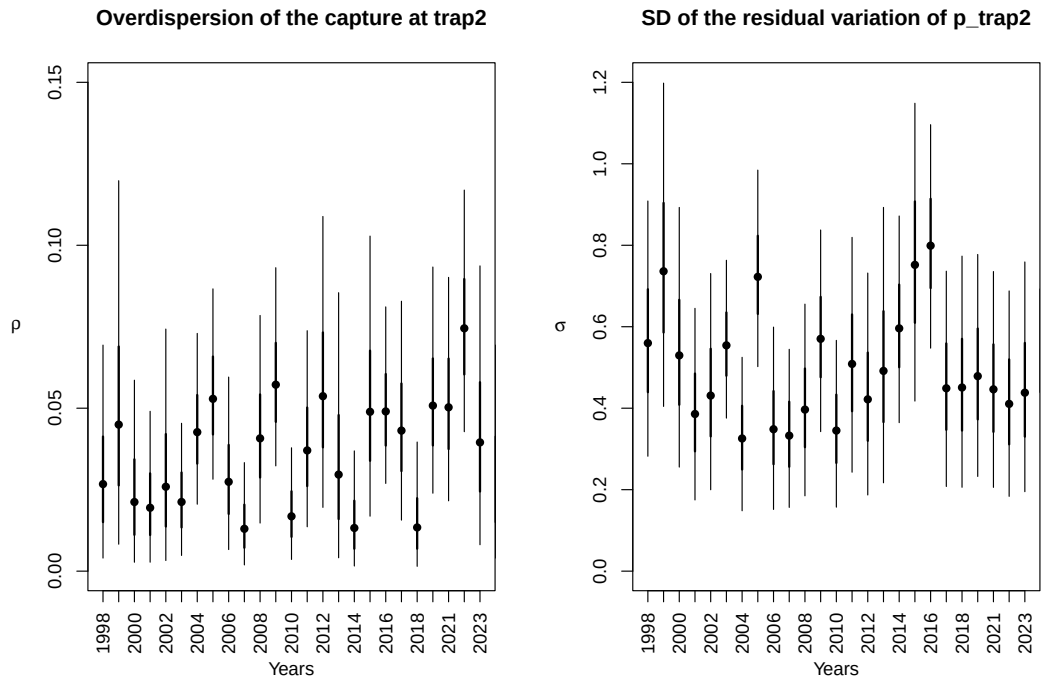


Figure 2.S2 – **Posterior distributions of the overdispersion of the capture at trap 2 (ρ_{tr2}) and standard deviation of the residual variation at trap 2 (σ_{tr2}, right panel) for each years.** The plain dot represents the median, the thick line the 50% interval and the thin line the 90% interval.

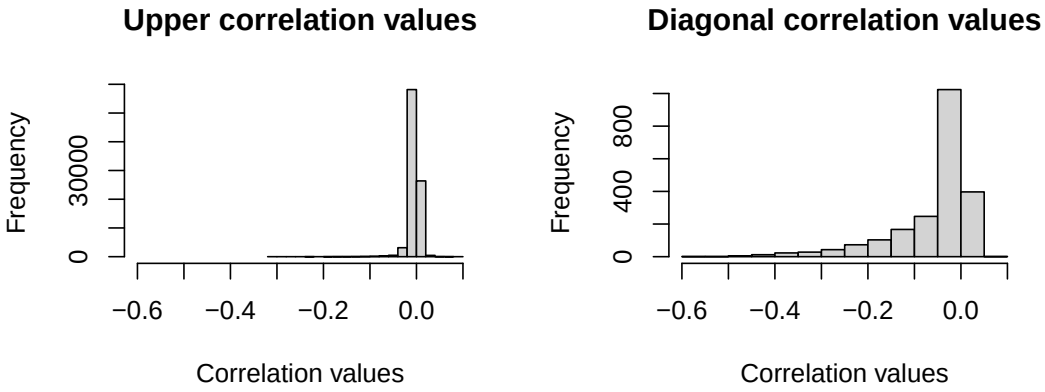
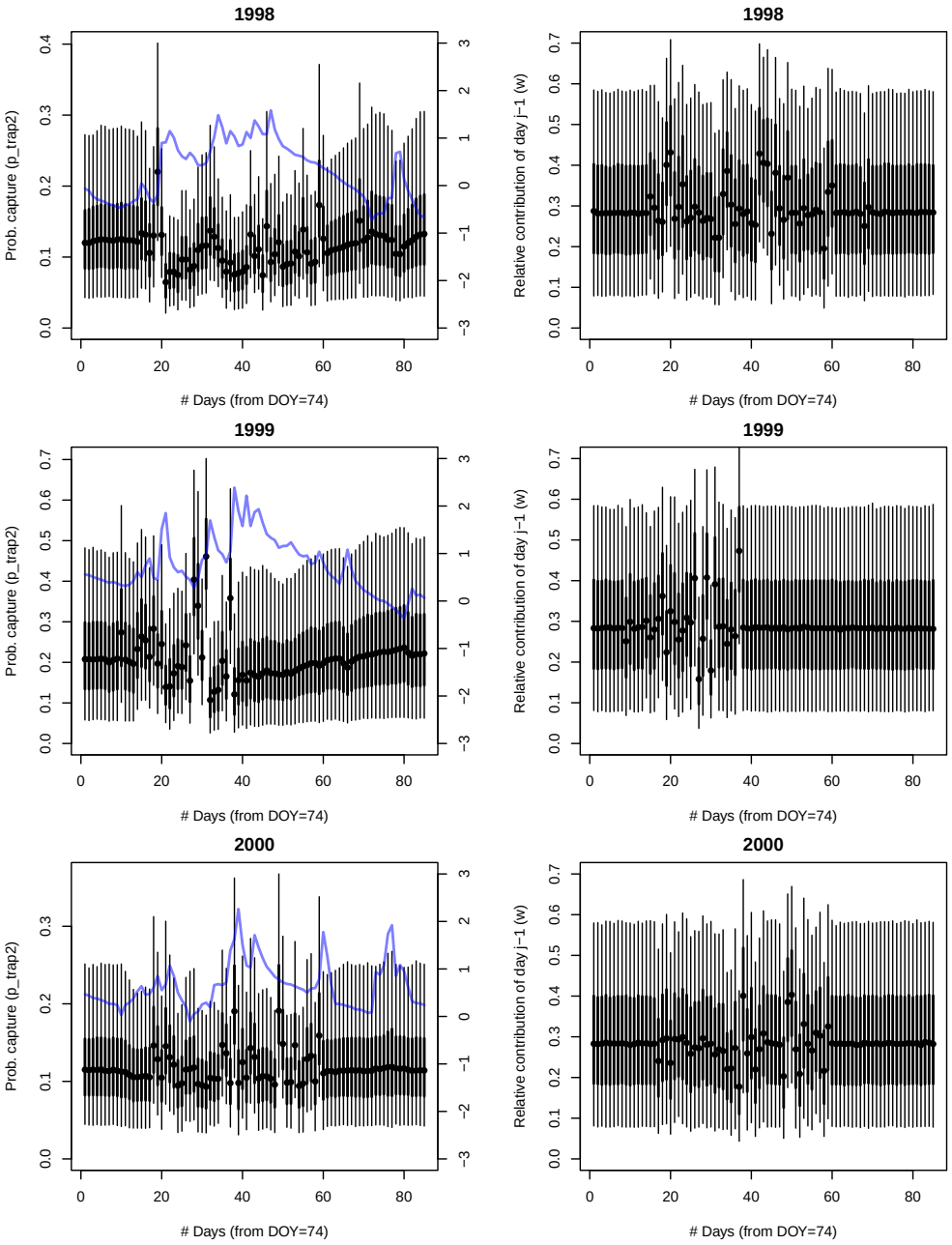
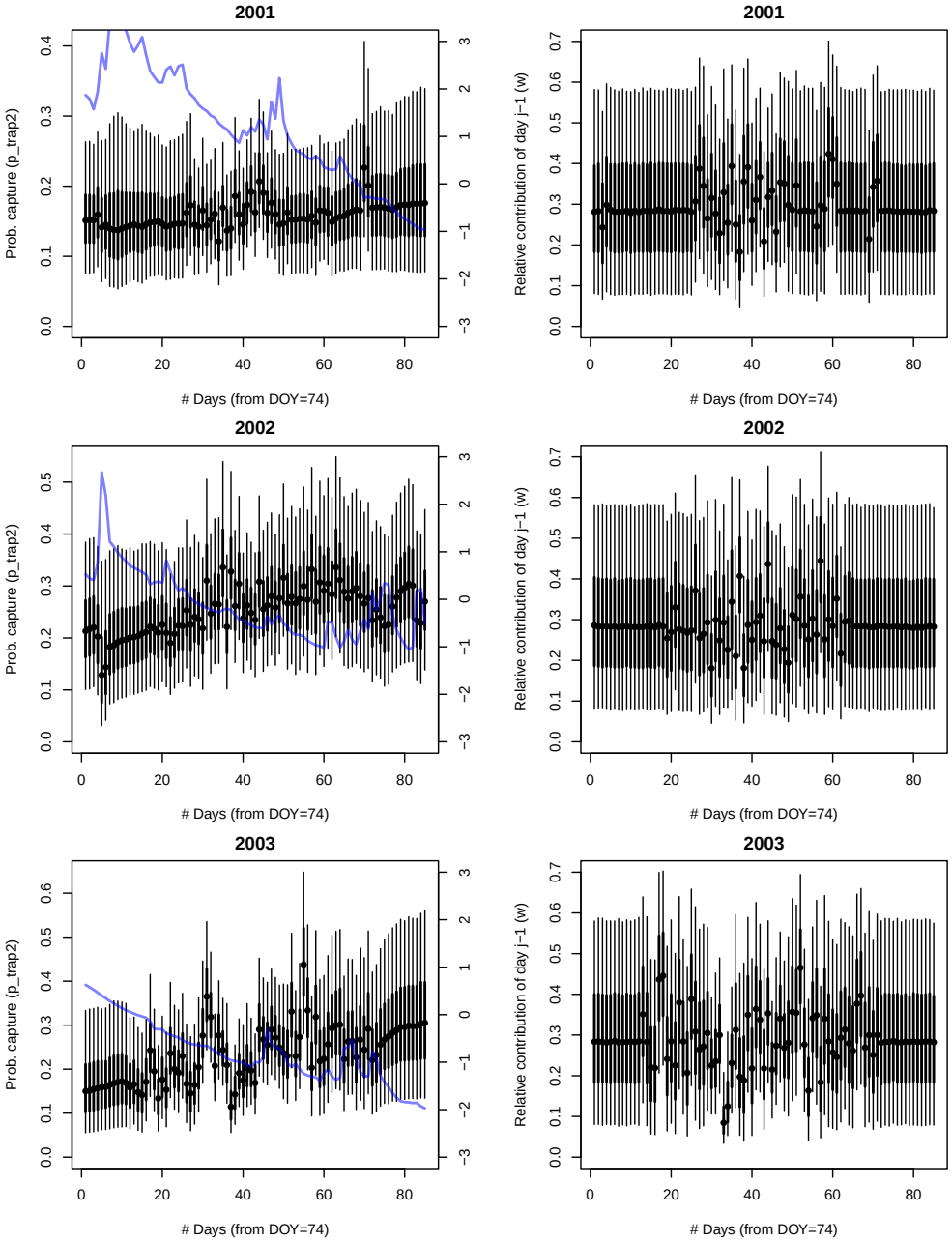
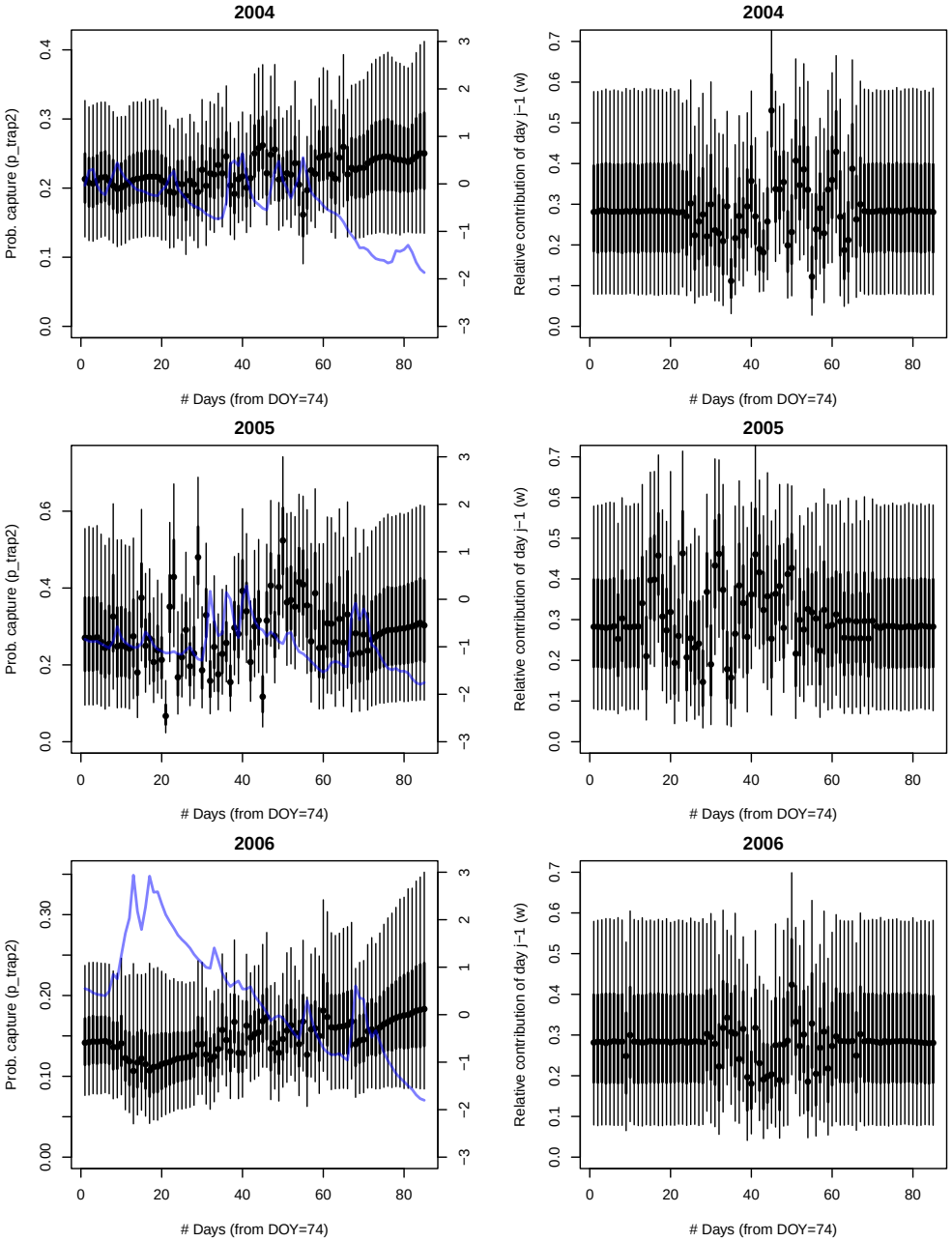
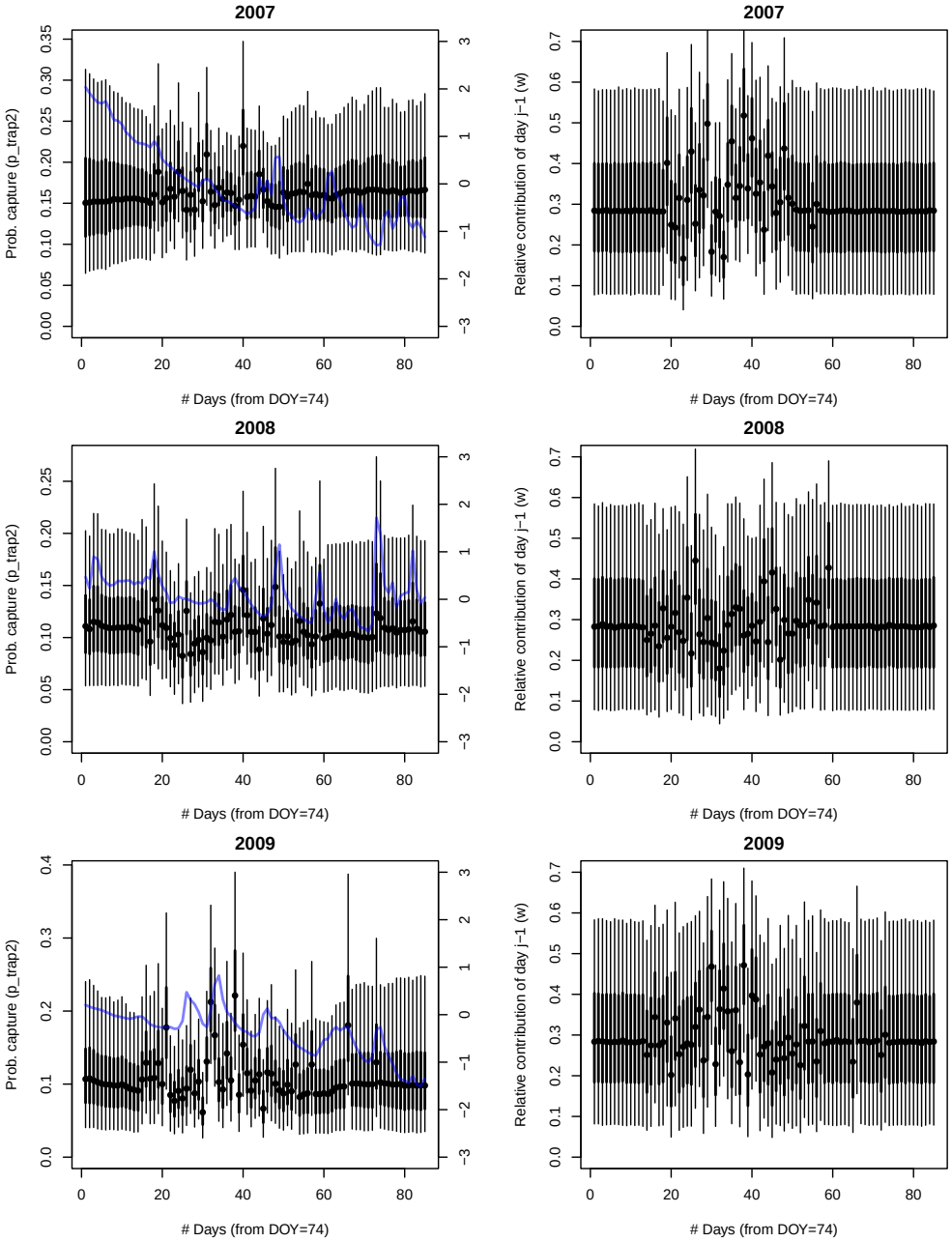


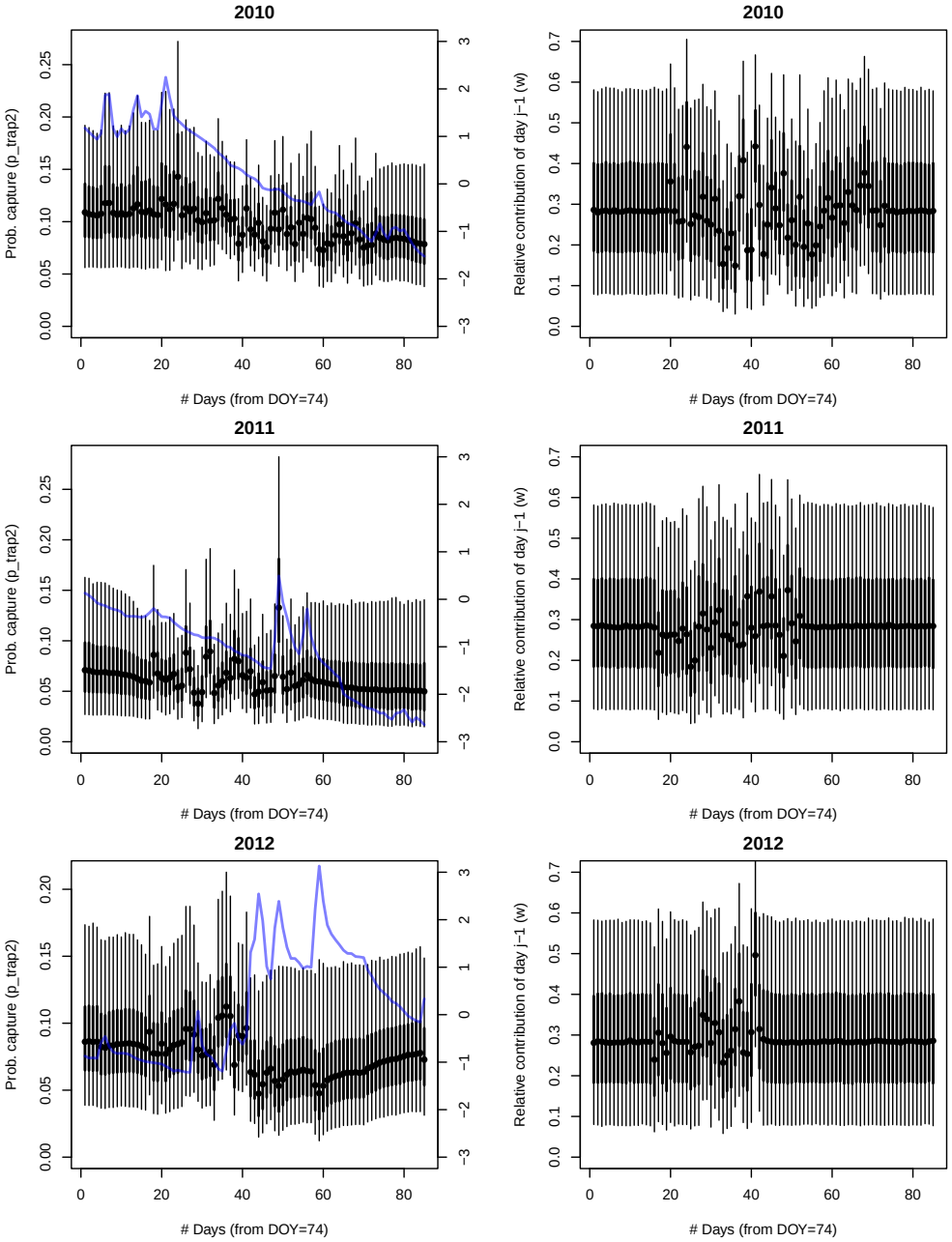
Figure 2.S3 – **Distributions of correlation values between α_{mark} and α_{migr} on the upper side only (left panel) and diagonal only (right panel) over all years.**

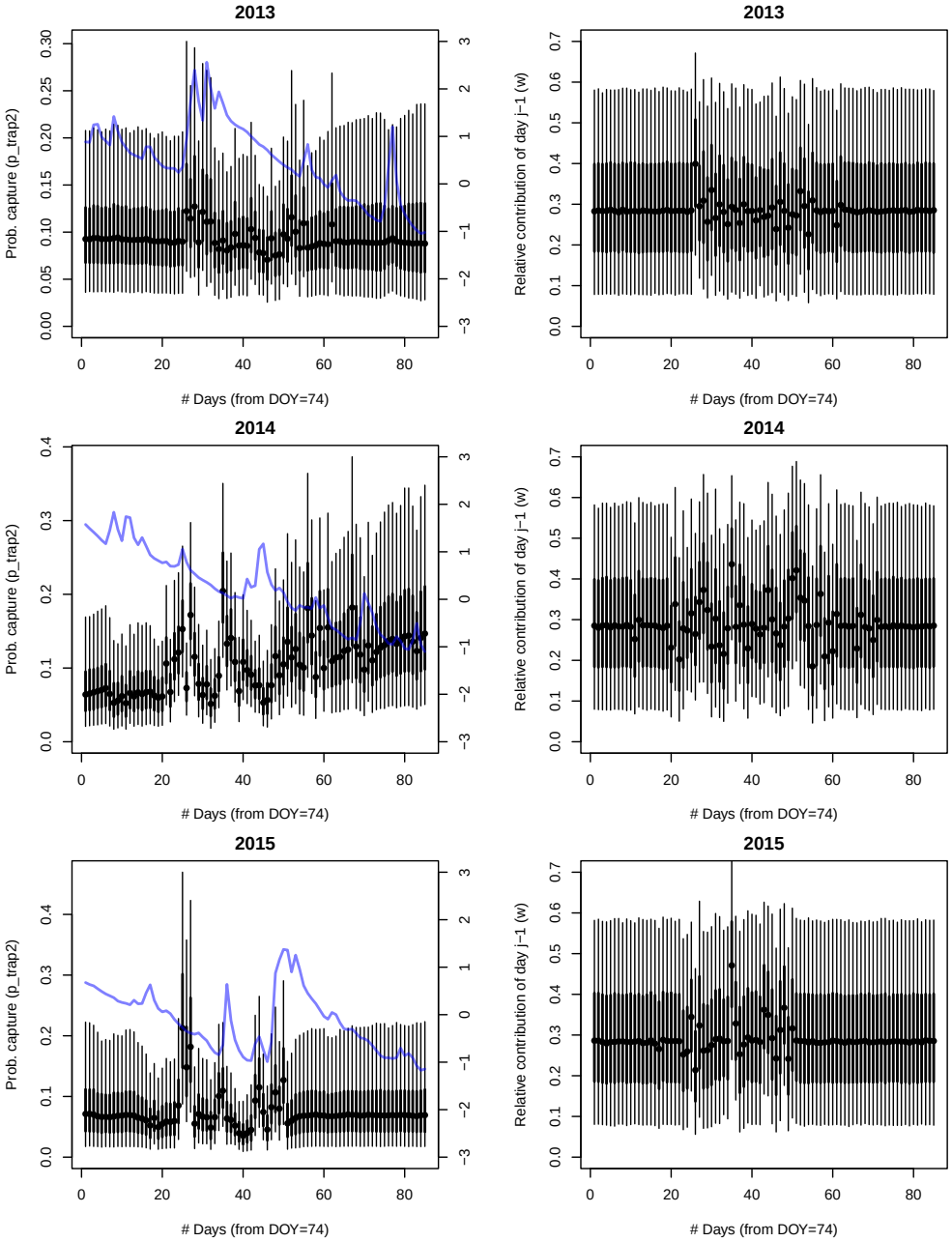

1998
Prob. capture (p_trap2)
Relative contribution of day j−1 (w)
Days (from DOY=74)
1999
2000

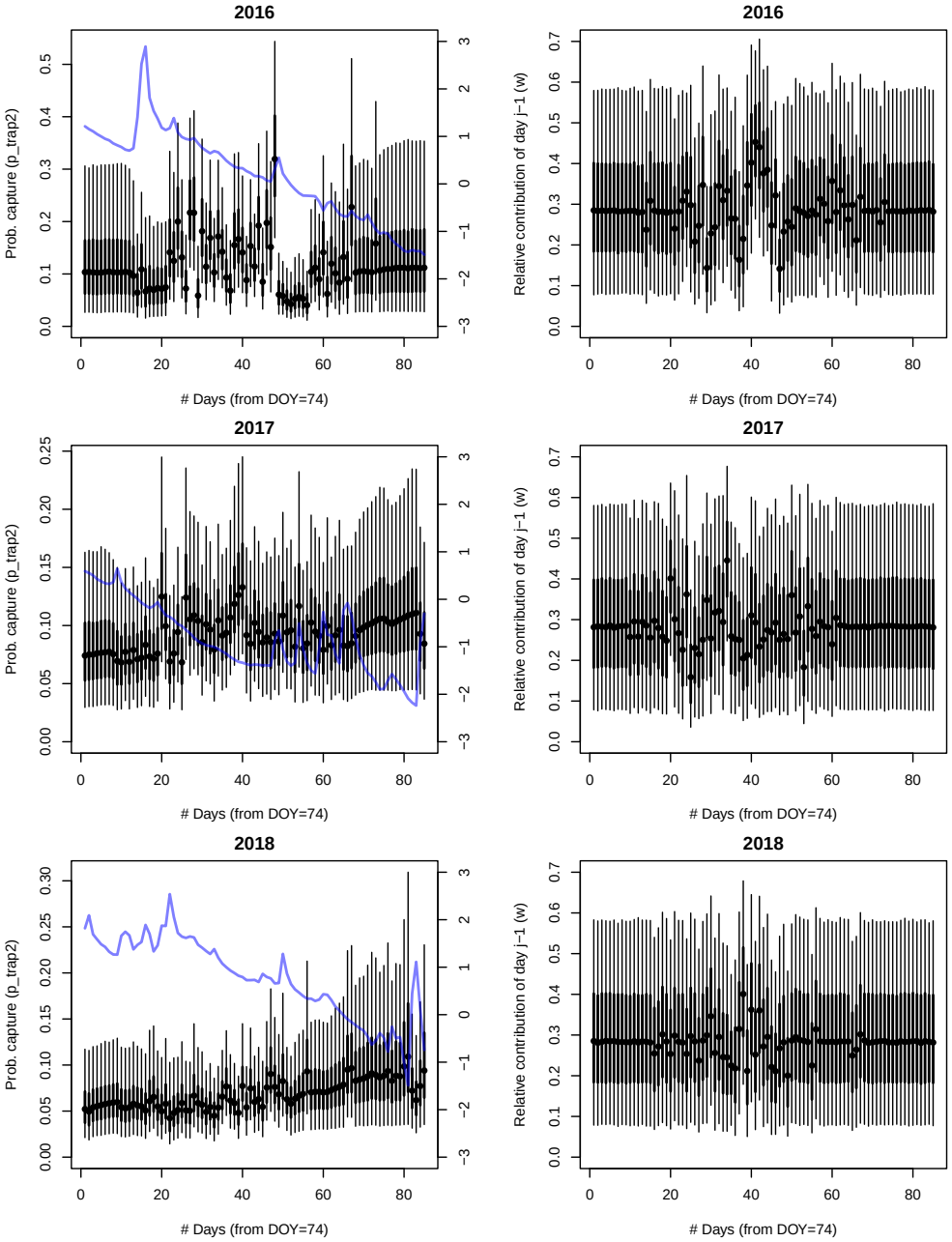

2001
Prob. capture (p_trap2)
Days (from DOY=74)
2001
Relative contribution of day j−1 (w)
Days (from DOY=74)
2002
Prob. capture (p_trap2)
Days (from DOY=74)
2002
Relative contribution of day j−1 (w)
Days (from DOY=74)
2003
Prob. capture (p_trap2)
Days (from DOY=74)
2003
Relative contribution of day j−1 (w)
Days (from DOY=74)

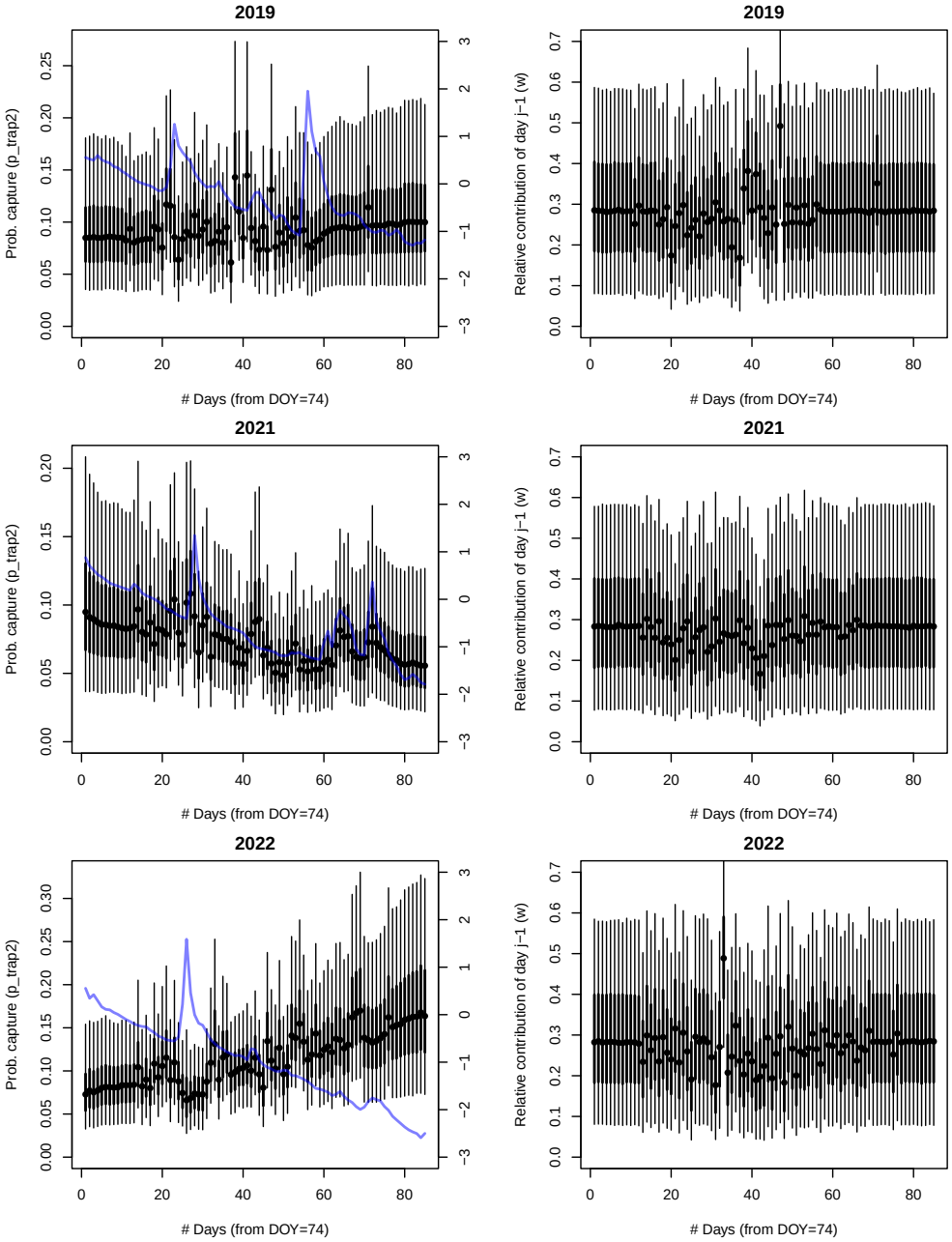

2004
Prob. capture (p_trap2)
Relative contribution of day j−1 (w)
Days (from DOY=74)
2005
2006


2007
Prob. capture (p_trap2)
Relative contribution of day j−1 (w)
Days (from DOY=74)
2008
2009


2010
Prob. capture (p_trap2)
Relative contribution of day j−1 (w)
Days (from DOY=74)
2011
2012


2013
Prob. capture (p_trap2)
Days (from DOY=74)
2013
Relative contribution of day j−1 (w)
Days (from DOY=74)
2014
Prob. capture (p_trap2)
Days (from DOY=74)
2014
Relative contribution of day j−1 (w)
Days (from DOY=74)
2015
Prob. capture (p_trap2)
Days (from DOY=74)
2015
Relative contribution of day j−1 (w)
Days (from DOY=74)


2016
Prob. capture (p_trap2)
Days (from DOY=74)
2016
Relative contribution of day j−1 (w)
Days (from DOY=74)
2017
Prob. capture (p_trap2)
Days (from DOY=74)
2017
Relative contribution of day j−1 (w)
Days (from DOY=74)
2018
Prob. capture (p_trap2)
Days (from DOY=74)
2018
Relative contribution of day j−1 (w)
Days (from DOY=74)


2019
Prob. capture (p_trap2)
Days (from DOY=74)
2019
Relative contribution of day j−1 (w)
Days (from DOY=74)
2021
Prob. capture (p_trap2)
Days (from DOY=74)
2021
Relative contribution of day j−1 (w)
Days (from DOY=74)
2022
Prob. capture (p_trap2)
Days (from DOY=74)
2022
Relative contribution of day j−1 (w)
Days (from DOY=74)

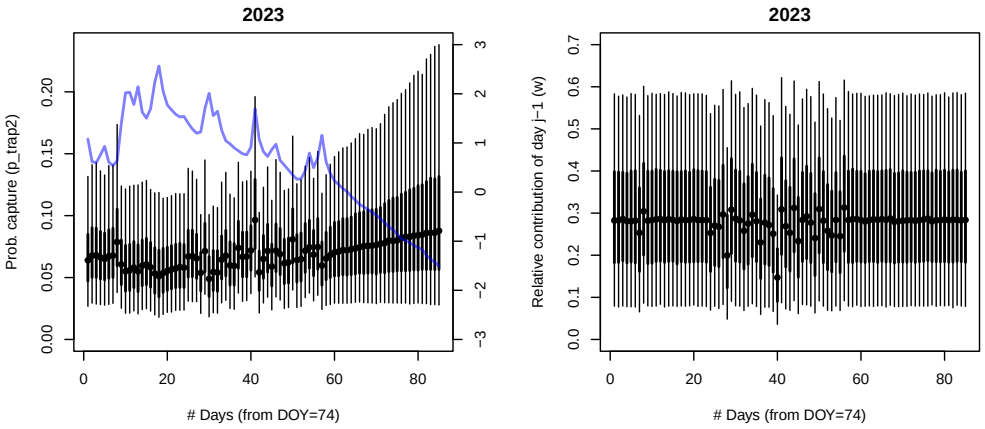
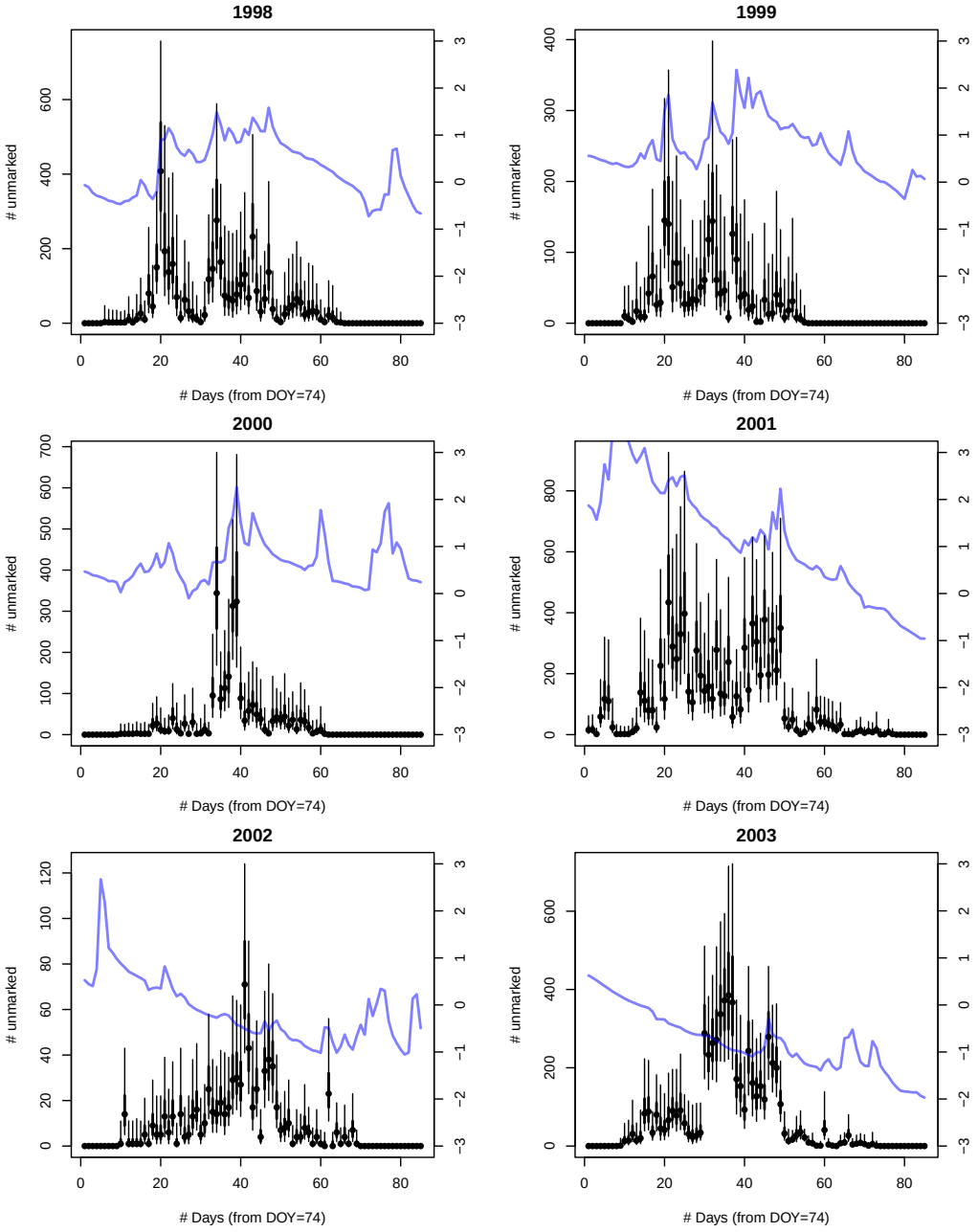
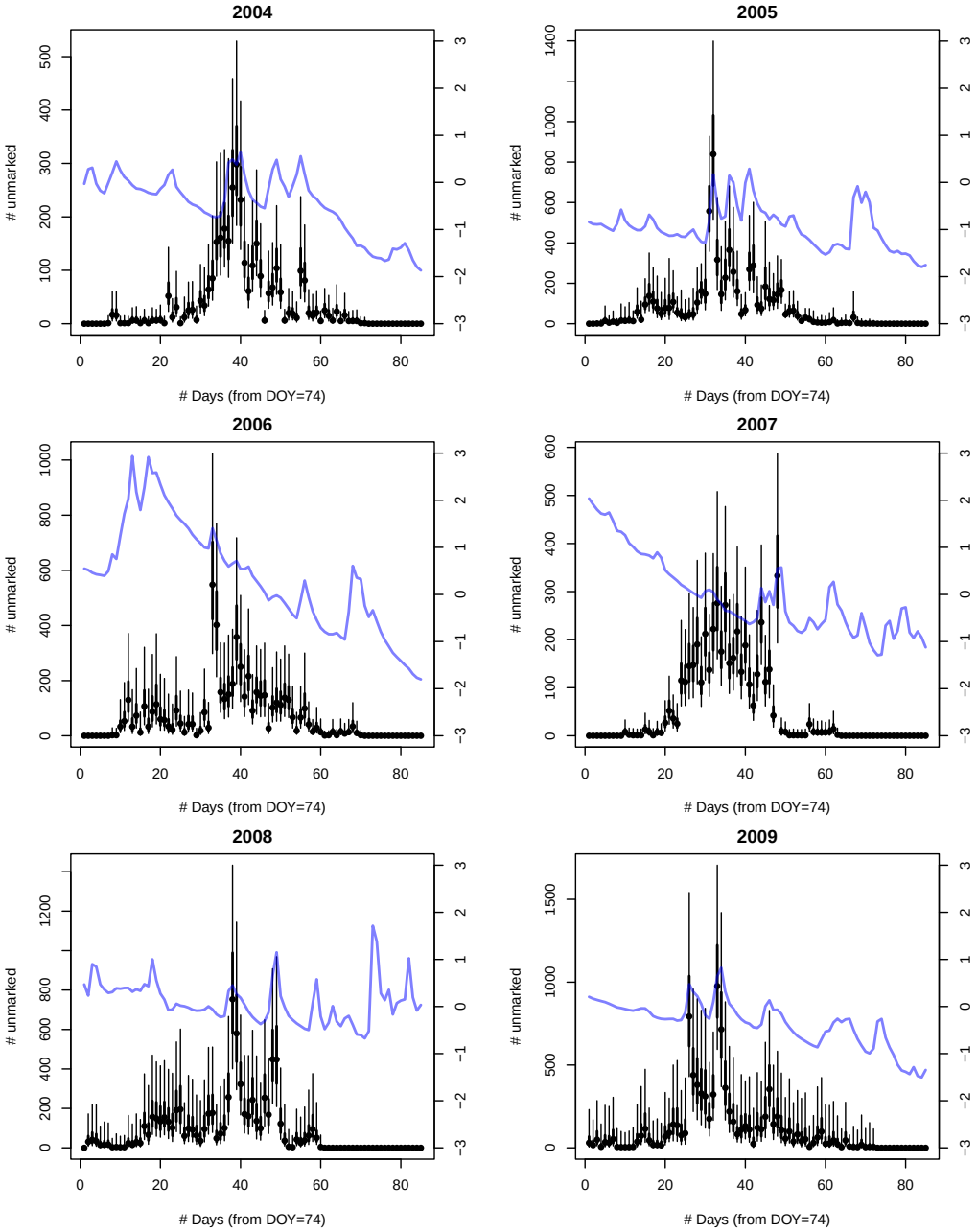
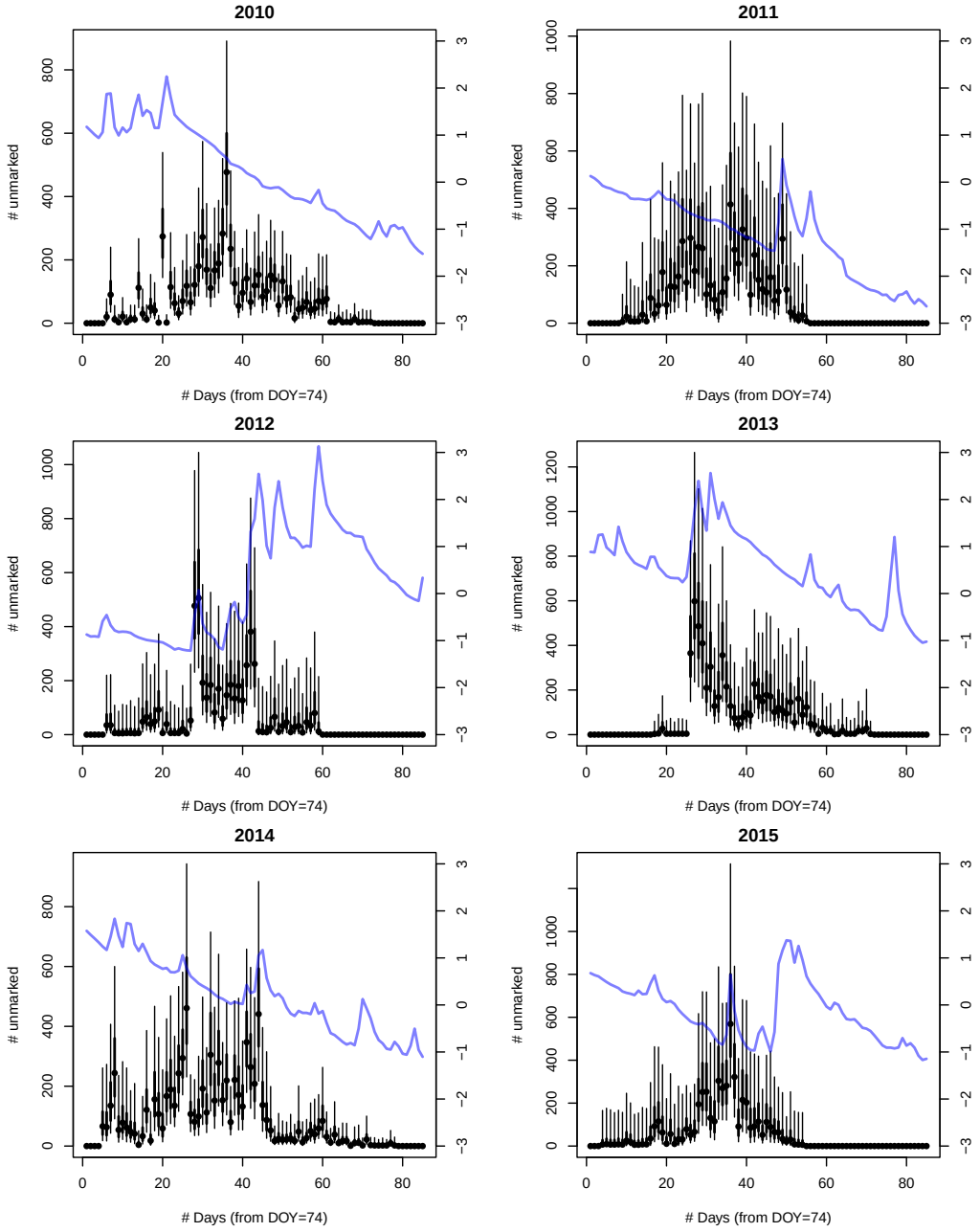
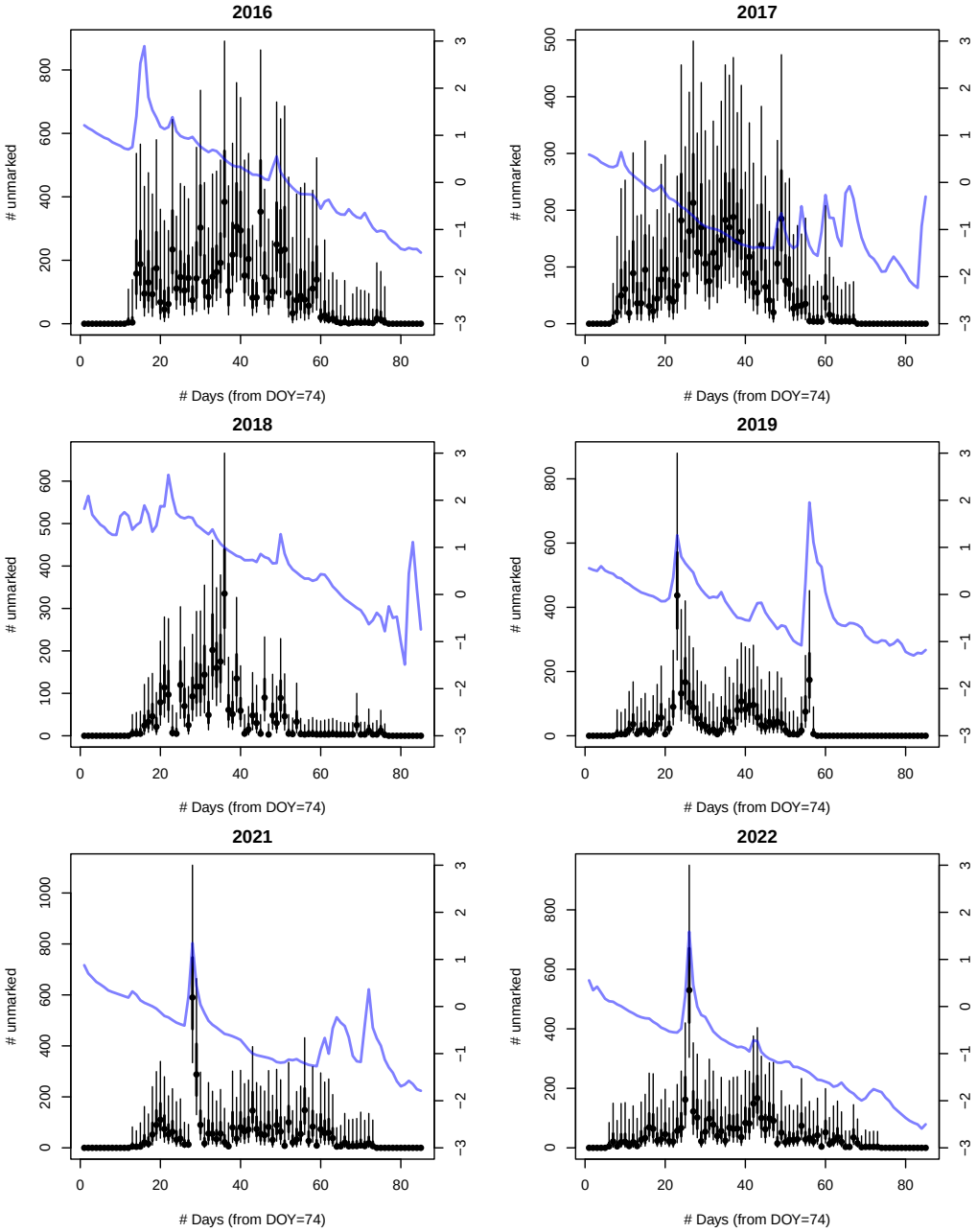


Figure 2.S4 – **Posterior distributions of the daily probabilities of capture at trap 2 (left panel) and daily weighted factors w measuring the relative contribution of the fish passing at trap 2 on day j to the capture on the same day (right panel) for all years.** The plain dots represent the medians, the thick lines the 50% intervals and the thin lines the 90% intervals. The blue line indicates the standardized daily discharge (log scale).


1998
1999
2000
2001
2002
2003
unmarked
Days (from DOY=74)


2004
2005
2006
2007
2008
2009
unmarked
Days (from DOY=74)


2010
2011
2012
2013
2014
2015
unmarked
Days (from DOY=74)


2016
2017
2018
2019
2021
2022
unmarked
Days (from DOY=74)

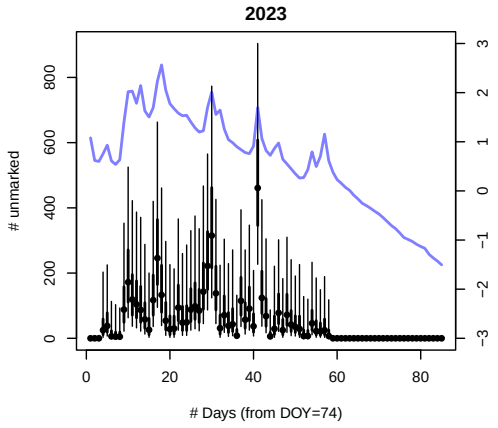


Figure 2.S5 – **Posterior distributions of the daily capture of unmarked fish at trap 2 ($N_{unmarked}$) by years.** The plain dots represent the medians, the thick lines the 50% intervals and the thin lines the 90% intervals. The blue line indicates the standardized daily discharge (log scale).

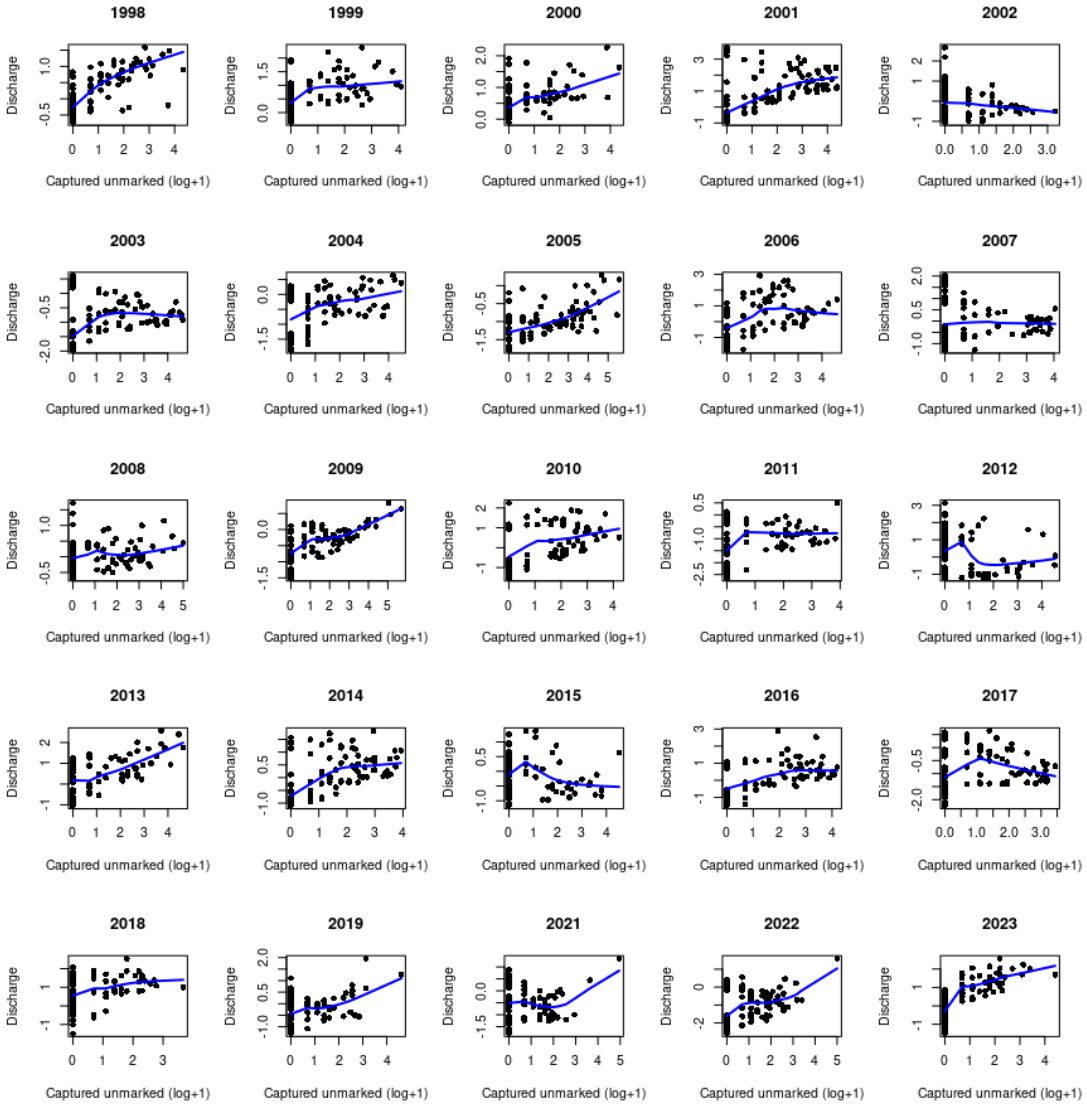


Figure 2.S6 – Medians of daily capture of unmarked fish (log1p scale) vs daily discharge (log-transformed) for each years.

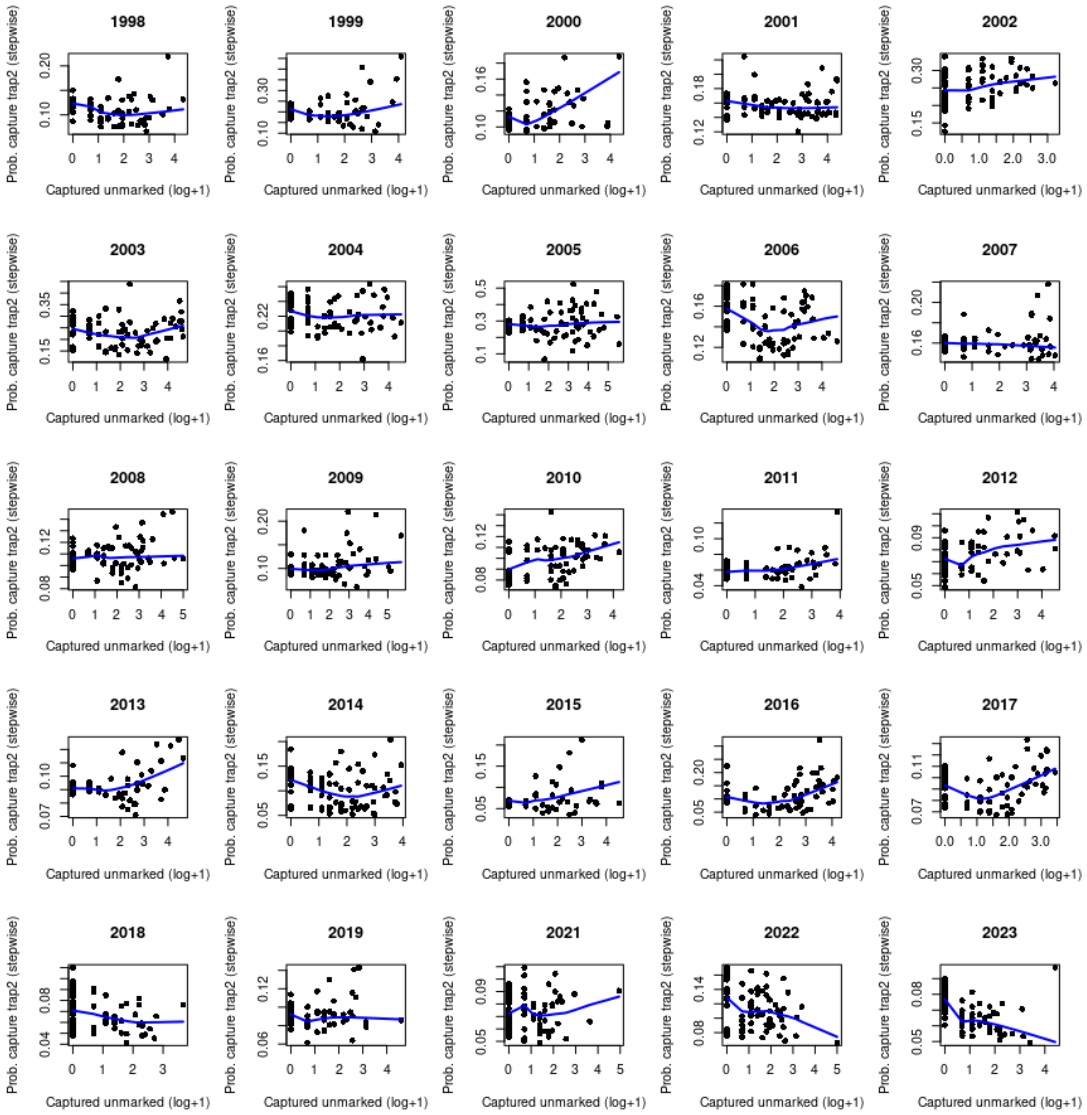


Figure 2.S7 – Medians of daily capture of unmarked fish (log1p scale) vs daily probability of capture at trap 2 for each years from the sequential approach.

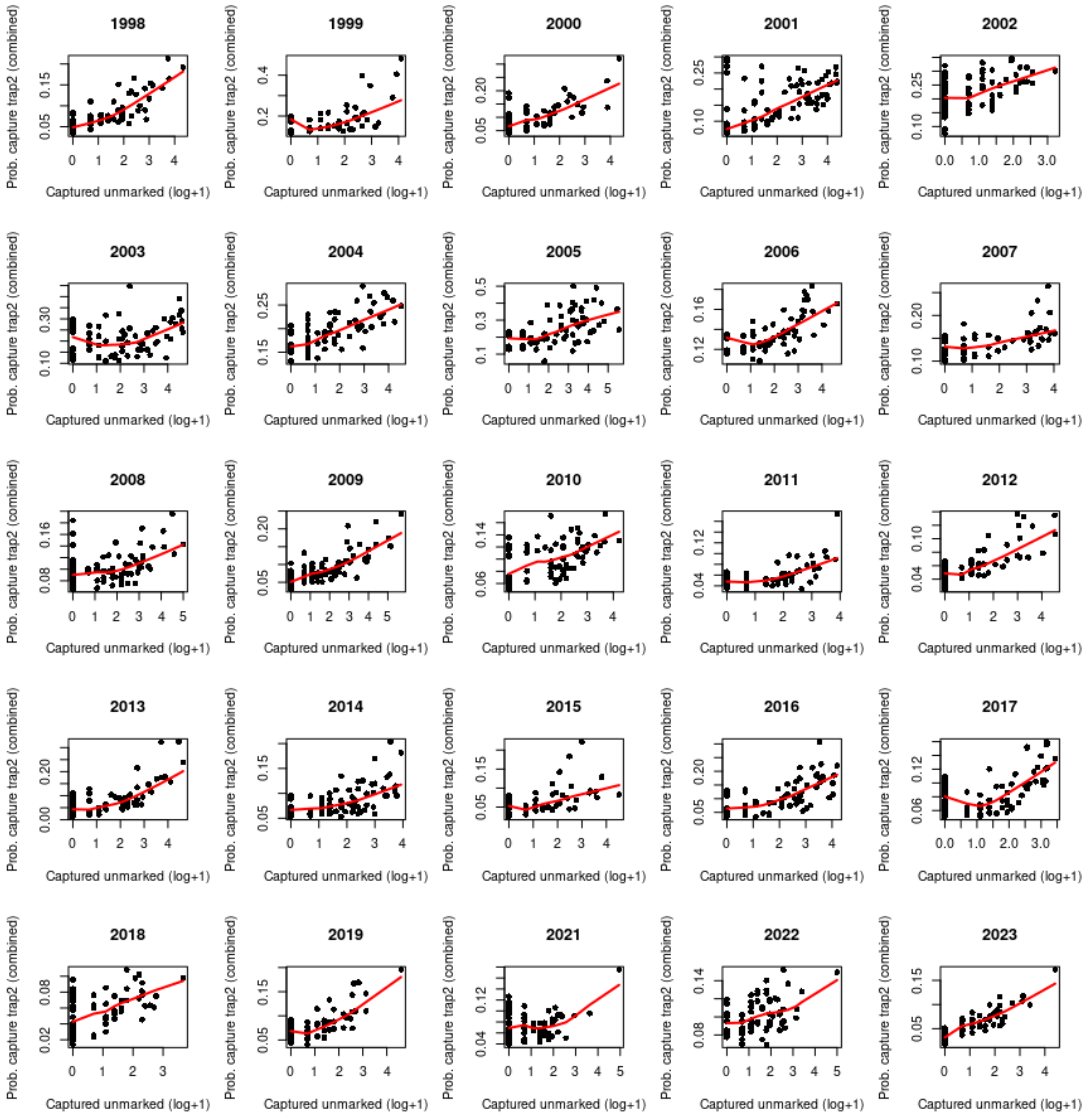


Figure 2.S8 – Medians of daily capture of unmarked fish (log1p scale) vs daily probability of capture at trap 2 for each years from the SingleStep approach.

Chapter 3

Bayesian mechanistic approach to modelling the phenology of smolt migration: disentangling the observation process from the underlying ecological mechanisms

In the previous chapter, we pointed out that the observation process of the system we are studying is influenced by environmental factors: the efficiency of the trap is influenced by the discharge. On the basis of this understanding of the observation process, we will now focus on the biological process of interest: the phenology of Atlantic salmon migration. This section corresponds to an article under preparation that will be submitted for publication in ***Canadian Journal of Fisheries and Aquatic Sciences***.

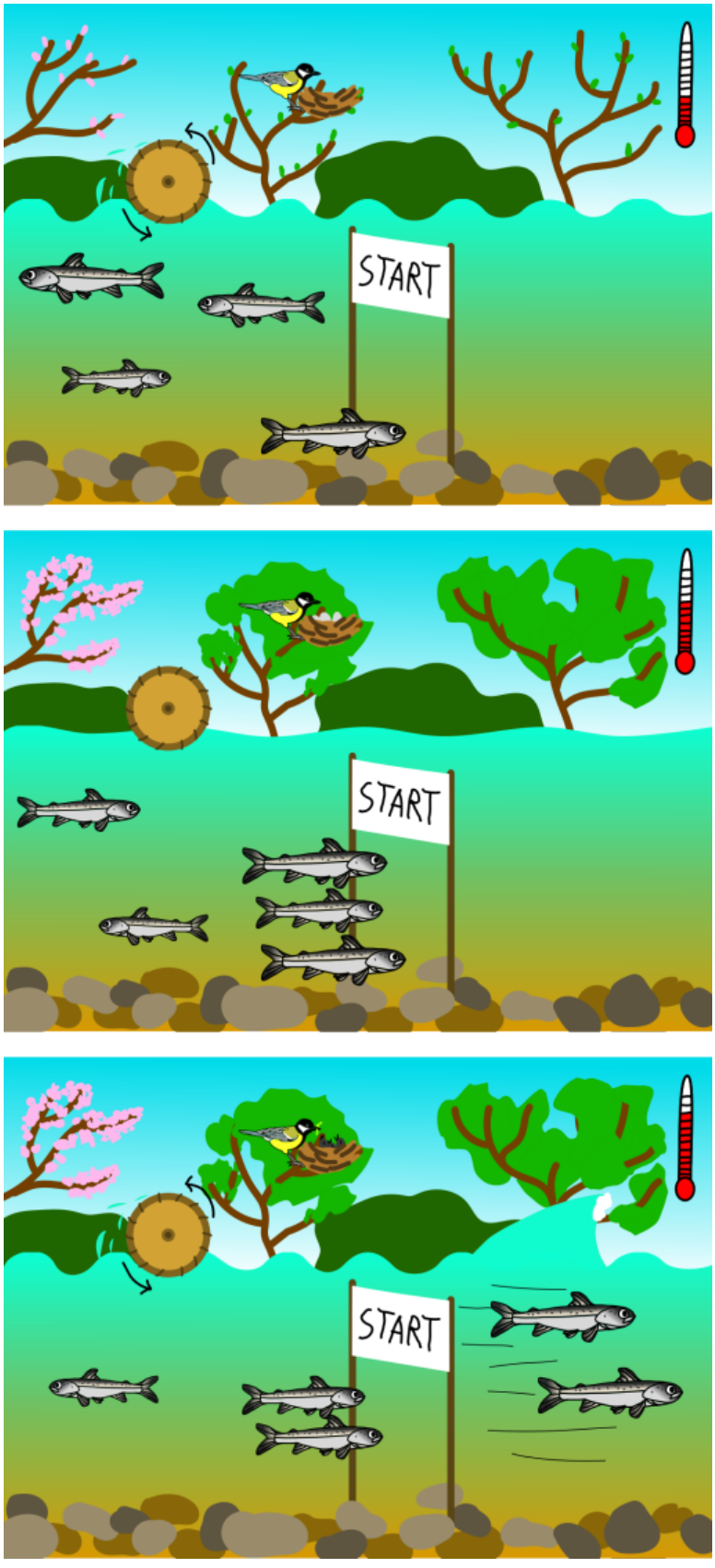


Figure 3.1 – **Two sub-processes of migration: preparation and departure**

Bayesian mechanistic approach to modelling the phenology of smolt migration: disentangling the observation process from the underlying ecological mechanisms.

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Abstract

Climate change can significantly disrupt the phenology of many species, i.e. the time at which a species completes an event in its life cycle. This is particularly the case for migratory species, such as Atlantic salmon (*Salmo salar*, A. salmon), as it alters the life history traits and environmental factors that trigger migration, which can affect their fitness. Understanding the mechanisms underlying phenological changes is essential for predicting the impact of these disturbances on species. However, these mechanisms remain poorly understood due to incomplete data and/or inappropriate approaches to their statistical analysis. In addition, data collected in the natural environment are subject to variations in the observation process that can mask or bias our understanding of the underlying biological processes. This study proposes a Bayesian mechanistic model that aims to disentangle the effects of the environment on biological and observational processes, and mechanically describe the phenology of A. salmon smolt migration in the Scorff, Brittany. The model distinguishes two sub-processes of migration phenology: preparation and departure. This makes it possible to introduce sufficient flexibility into the more realistic phenology distributions. These distributions vary from one year to the next, depending on the preparation process, which is more or less rapid, and on the environmental conditions (temperature, discharge, discharge variation) that trigger migration. This method that can be extended to model the migration phenology of other anadromous fish, which could eventually help to adapt management measures.

Keywords: Mechanistic model, Migration phenology, Atlantic salmon, Bayesian, modeling, Hierarchical modeling

3.1 Introduction

Migration is an hazardous stage of the life-cycle (Newton, 2024a). The phenology of migration, i.e. the timing at which individuals migrate, can help the species to reduce the overall cost of this stage by synchronising their migration with the best environmental conditions (Alerstam, 2011). But climate change disturb the species phenology (Visser, 2022), which can have consequences for the fitness and the demography of the species. For instance, anadromous fish such as Atlantic salmon (*Salmo salar*) show earlier seaward migration (Otero et al., 2013). This can lead to a mismatch between the arrival of Atlantic salmon at sea and the conditions necessary for their growth and survival, such as sea temperature and the abundance of prey (Kennedy et al., 2010; Teichert et al., 2020; Thorstad et al., 2012; Wilson et al., 2021).

Understanding the causes and the mechanisms of phenological change would enable us to make forecasts and eventually adapt management measures. For example, forecasting the phenology of salmon migration can enable controls on hydroelectric turbines and dams to be adapted to facilitate the passage of salmon during this critical period (Teichert et al., 2020). However, we lack a real understanding of the mechanism underlying the migration timing (Chmura et al., 2019) because phenological analyses are often only correlative. For A.salmon migration, most studies are descriptive, with some including explanatory variables in their analyses (e.g. Antonsson et al., 2010; Carr-Harris et al., 2018; Simmonds et al., 2020; Teichert et al., 2020; Otero et al., 2013). However, they do not explicitly describe the underlying process. Mechanistic biological modelling is an approach based on biological knowledge and hypotheses about the actual process (Pulkkinen et al., 2020). By explicitly representing the underlying mechanism, these models provide a better understanding of the real process (Craver, 2006; Pulkkinen et al., 2020). Applying this approach to the phenology of species enable us to better understand the causes of its observed or potential changes (Chuine et al., 2017). For instance, while salmon migration most often appears to be multimodal (Bjerck et al., 2021), the reasons for this pattern are not well understood. The mechanistic model developed by Pulkkinen et al. (2020) helps to explain this pattern. They describe the mechanism in terms of two sub-processes, the departure decision and the travel time. This allows greater flexibility in the shape of the distribution of smolt arrivals, enabling multimodality. However, this model is partly based on expert judgement, instead of observation data. The problem is that for one part of the model, the expert judgement is updated and partially contradicted by the data. For the rest of the model, in particular the observation process, the parameters are not updated, i.e. the model relies on expert judgements that were wrong for the other part of the model. This may raise questions about the reliability of the model. The aim of this study is to use a similar approach with observation data, i.e. to write the biological processes explicitly, leaving sufficient flexibility to explain the multimodal shape of migration phenology. In particular, we describe the phenology of salmon in two

sub-processes: preparation for migration and departure.

Collected data in natural environments come often with variation in the observation process, which can blur or bias our understanding of the biological process of interest (Chadwick et al., 2023). This is especially important when an environmental factor influences both the observation (e.g. trap efficiency) and the biological process (triggering migration decision) potentially leading to misinterpretation. This is true for capture-mark-recapture (CMR) protocols which are often used to study the migration phenology of anadromous fish and where the environment such as the discharge can have an effect on both the migration decision (e.g. Bjerck et al., 2021; Kennedy et al., 2010; Stich et al., 2015a; Simmonds et al., 2020 for the A.salmon) and on the trap efficiency (Lheureux et al., submitted). In this study, we want to better understand the factors that determine the phenology of the seaward migration of the Atlantic salmon, using long term CMR data. The discharge is assumed to have an impact on both the observation process, the probability of capture at the two traps, and on the biological process, the departure on migration. This dual influence can create confusion, as variations of the number of migrants captured at traps can results either from variations of the trapping efficiency or of the number of migrants. We therefore need to take careful account of the role of the observation process, as done in Lheureux et al. (submitted), but without phenological model. In contrast, Pulkkinen et al. (2020) proposes a phenological model with an observational model that relies mainly on expert judgements, as parameters controlling this process are poorly updated.

The long-term daily capture-recapture protocol on the river Scorff in Brittany, France, makes it possible to closely monitor migratory dynamics and to study possible changes in salmon phenology over time. These protocols, based on double trapping, can also be used to assess temporal fluctuations in capture probabilities. In this study, we aim to 1) disentangle the effects of the environment on biological and observational processes, and 2) mechanically describe the phenology of smolt migration. To this end, we propose a Bayesian mechanistic model that explicitly separates the observational (trap capture) and biological (migration) processes, as well as the different effects of environmental factors.

3.2 Methods

3.2.1 Generic model description

We first present our generic phenological model which can be applied to any organism during an unidirectional migration with two consecutive traps and a series of years repeating the same capture protocol. Individuals are captured in two traps, the first (trap 1) and the second (trap 2), but for simplicity the model is first described with a single trap z. Time is discretized in 24h time

step. For convenience, and because data at the start of the process is often unreliable (Moussus et al., 2010), the data is considered to be left-censored, with the starting point being a date t_1 at which we are sure that the process has begun. The day of the start of the biological process t_0 is estimated, with the first time step from time t_0 to time t_1. The following time steps are daily steps, and the total duration of the migration period is the sum of the first time step and the following D days.

The aim here is to analyse the phenology distribution and not to estimate the number of migrants. Then, the model represents the process that generates the capture data: the daily number of individuals captured at trap 1 and at trap 2. To do this, we use multinomial distributions on the total number of fish caught at each trap over the full migration period, with the probability of being caught in trap z on days 1 to D. These probabilities depends on both the phenology and the capture probability. The phenology of these captured individuals are assumed to be representative of the phenology of all migrants. Individuals caught in the first trap are marked, so they are not taken into account in the analysis if they are recaptured at the second trap. For any given year y, we describe the phenological processes: the migration of individuals, itself separated into two processes, the accumulation of ready individual and the effective migration. Then, we describe the specificity of the case of studies, and particularly the other process of importance that shapes data: the capture of the individual at each trap. The way in which these processes vary between years is then presented.

The individuals trapped are assumed to be migrating, and to have triggered this migration due to the environmental factors of the 24h-time step in which they are captured.

Migration process

To generate the phenology of the captured individuals, i.e. p_{phen}, two processes are considered. Not all individuals are ready at the start of the migration period. The first process is therefore the accumulation of ready individuals that have not yet migrated, p_r. It represents the accumulation of 'ready' fish in the vicinity of the trap (less than 24 hours travel time), waiting for the right conditions to migrate. It is an approximation of the migration preparation process. The ready individual becomes sensitive to the environmental signals that trigger migration. The second process is therefore the effect of environmental factors on the probability of departing on migration, p_{migr}.

Thus, $p_{phen}[i, y]$, the probability to being migrating the time step i the year y, that is mean the probability to be in the stock of ready individual that have not migrated yet and to migrate at the time step i, is:

$$
\begin{aligned}
&i = 0 && p_{phen}[0,y] = p_r[0,y]) \times p_{migr}[0,y] \\
&i = 1,...,D && p_{phen}[i,y] = (\sum_{k=0}^{i-1}(p_r[k] \times (1 - p_{migr}[k])) + p_r[i,y]) \times p_{migr}[i,y]
\end{aligned}
\tag{3.1}
$$

We modeled the accumulation of the stock as a time-to-event process, an approach classically used for survival or reliability analyses (Congdon, 2014). Individuals, during each time step, have a chance of becoming ready which depends on a probability distribution. This distribution is characterised by its hazard function, which represents the instantaneous rate at which the individual becomes ready (see Congdon, 2014, p. 459). We have chosen to use a piecewise constant hazard function with daily time steps. Such an approach, also known as a piecewise exponential model, offers more flexibility than standard parametric models (e.g. lognormal as in Schwarz et al. (1994), while remaining simple. To allow greater flexibility in the hazard distribution, we have chosen to express it in terms of a Weibull distribution, which is a generalization of the exponential distribution (Congdon, 2014). Unlike an exponential distribution, the hazard of a Weibull distribution can be increasing or decreasing, depending on the shape parameter value. If the shape is inferior to 1, the hazard is decreasing, if it is superior to 1, it is increasing (Congdon, 2014).

Then, the probability to be ready $p_r[i,y]$ at a time i the year y is the probability of being ready at a given time i knowing that you were not ready before. The probability to be ready p_r at a time i, is:

$$
\begin{aligned}
&i = 1 && p_r[1] = 1 - e^{(-\lambda[0,y])} \\
&i = 2,...,D-1: && p_r[i,y] = \left(1 - e^{-\lambda[i,y]}\right) \times e^{-\sum_{k=0}^{i-1}\lambda[k,y]} \\
&i = D: && p_r[D,y] = 1 - \sum_{k=0}^{D-1} p_r[k,y]
\end{aligned}
\tag{3.2}
$$

where $\lambda[i,y]$ is the constant hazard on day i, expressed as a Weibull hazard function following a log normal distribution, allowing more flexibility:

$$
\begin{aligned}
&i = 0 && \lambda[i,y] \sim logNormal(\log(\frac{\log(2)}{m[y]^{k[y]}} \times (-0.5 - t_0[y]^{k[y]}, 0.1) \\
&i = 1,...,D && \lambda[i,y] \sim logNormal(\log(\frac{\log(2)}{m[y]^{k[y]}} \times ((i - 0.5 - t_0[y])^{k[y]} \\
& && \quad - (i - 1.5 - t_0[y])^{k[y]})), 0.1)
\end{aligned}
\tag{3.3}
$$

with m the median and k the shape of the Weibull distribution. We fixed the standard deviation at the value 0.1. On the one hand for the sake of parsi-

mony, and on the other hand because we hypothesize the process of preparation for migration is essentially smooth, with only limited day to day variations. Indeed, this preparation process is dependent on a temporally smooth environmental conditions, i.e. the photoperiod (McCormick et al., 2011), and it also depends on the past history of the fish in the months preceding migration (Jonsson et al., 2016; Simmons et al., 2021a). Time is not only i as it is shifted according to the starting date of the process t_0. This parameter is negative: it is the number of days elapsed between the start of the process and 1st April. Note that we have to subtract 0.5 to take account of a specificity of the protocol, namely that we are observing approximately the smolts that migrated between noon on the day $i-1$ and noon on day i.

Once individuals are ready, they are sensitive to the environmental factors that trigger migration. This process, p_{migr}, is related to environmental parameters X_j through the equation:

$$\begin{aligned} logit(p_{migr}[i,y]) = \beta_{migr}[1] + \beta_{migr}[2] \times X_1[i,y] + \beta_{migr}[3] \times X_2[i,y] \\ + \beta_{migr}[4] \times X_3[i,y] + \epsilon_{phen}[i,y] \end{aligned} \tag{3.4}$$

where $\beta[1]$ is the mean migration probability in logit scale, and the subsequent β are the coefficients of each environmental covariate X_j. The $\epsilon_{phen}[i,y]$ are the residuals, they are identically and independently distributed and account for the unknown causes of variation of the migration probability per day.

As the probability to migrate during the time step 0 is a mixture of migration probability during several days, we model $p_{migr}[0,y]$ differently, by assigning it an independent prior.

Multinomial distribution

The captures we get depend on the phenology of the individuals p_{phen}. However, most of the time in ecology, the capture process is imperfect (Chadwick et al., 2023). This means that the number of captures per day depends not only on the number of individuals migrating but also on the proportion captured each day.

So we can calculate the probability to be migrating and captured for each day and for the trap z as:

$$p_{phen,trz}[i] = p_{phen}[i] \times p_{trz}[i] \tag{3.5}$$

The methods used to determine the capture probabilities depend on each installation and are therefore explained in the paragraph 3.2.2.

Then, to make the inference, we use these probabilities in multinomial distributions, one per trap, with, for each time step i, a probability of being a migrant and captured at trap 1 or of being a migrant and being captured at trap 2. As we are only interested in the phenological process, and not to estimate the total migrants number, we do not consider untrapped individuals. This also facilitates the computing calculations. To account for the overdispersion of the capture due to the schooling behaviour of salmon smolts (Davidsen et al., 2005; McCormick et al., 1998), we used Dirichlet-multinomial distributions. The numbers of captured individuals at each trap per day $n_{trz}[i, y]$ are:

$$n_{trz}[i, y] \sim DirichletMultinomial(p_{phen,trz}[1, y] \times \eta_{trz}, ..., p_{phen,trz}[D, y] \times \eta_{trz}, N_{trz,tot}[y]) \tag{3.6}$$

With η_{trz} the overdispersion parameter for the trap z, and $N_{trz,tot}[y]$ the total number of captured individuals at the trap z and the year y. As the data are left-censored, the individuals captured during the first time step are not used in the inference.

Annual variations of the processes

We hierarchically model the year to year variation in the phenological process using random effects, in particular for the accumulation of ready individuals. The accumulation of ready individuals process depends on the three parameters of the 3-parameters-Weibull distribution, the shape, the scale, and on the location parameter. In what follows, this last parameter is called the starting date, as it is the date on which the preparation process begins. In order to facilitate the later assignment of priors (see section 3.2.3), we use another parametrization than the classical. In fact, we reparameterize the scale and the shape in the median $m[y]$ and the 90% quantile $q90[y]$.

Then the median $m[y]$ follow a beta distribution :

$$\frac{(m[y] + t_0[y])}{30} \sim Beta(M_m, \rho_m) \tag{3.7}$$

with M_m the interannual mean of $m[y]$ and ρ_m the quantity that control the overdispersion of the beta distribution. $m[y]$ is rescaled between 0 and 30 as April is the month of most active migration, so we assume the median of the accumulation stock occurs during this month. We then checked the posterior to be sure that this prior was large enough (see section 3.2.3).

The shape $k[y]$ is calculated through:

$$k[y] = log(log(10)/log(2))/log(q90[y]/(m[y])) \tag{3.8}$$

and $q90[y]$:

$$\frac{q90[y] - m[y] - 5}{((m[y]) \times log(10)/log(2) - (m[y] + 5))} \sim Beta(M_{q90}, \rho_{q90}) \tag{3.9}$$

with M_{q90} the interannual mean of $q90[y]$ and ρ_{q90} the quantity that controls the overdispersion of the beta distribution. $q90[y]$ is rescaled to be comprised after the median date to which we add 5, as we assume there are at least five time steps between the median and the quantile 90%. The posterior distributions were checked also check to verify that this prior was not too constraining.

The starting date parameter $t_0[y]$ is not reparameterized and is expressed as :

$$t_0[y] \sim Beta(M_{t_0}, \rho_{t_0}) * 30 - 30.5 \tag{3.10}$$

with M_{t_0} the interannual mean of $t_0[y]$ and ρ_{t_0} the quantity that controls the overdispersion of the beta distribution. The rescalling between $[-30.5, -0.5]$ constrains $t_0[y]$ to occur during the month before the 1st April, which seems reasonable and sufficiently large with the date of first capture of migrating smolt we usually observe.

For the sake of identifiability and parsimony, no other quantity controlling the biological process is explicitly modeled as varying from year to year. Especially, the parameter of the first time step $p_r[0]$ and $p_{migr}[0]$, as they are not linked with data, are modeled as constant over the years.

The observation process can also be variable with the day and the year, so the capture process is also hierarchically modeled. See section 3.2.2 for more information.

3.2.2 Case study of the seaward salmon migration in the Scorff river

Study site and data collection

The Scorff is a 78 km long coastal river in southern Brittany, France. Influenced by an oceanic climate, it is rain-fed and flows over a schist and granite bedrock. Its catchment area is 483 km², mainly forested and agricultural. It is colonized by A. salmon and its population has been monitored since 1994 as part of the Observatory for Research on Diadromous Fish in Coastal Rivers program (ORE DiaPFC; Azam et al., 2020).

During their seaward migration from March to June, salmon smolts are first sampled at the Leslé trap (trap 1), located in the downstream end of the river, and then at the Prince Mill trap (trap 2) (Fig. 3.2), located 600 meters downstream from the Leslé trap, just at the limit of tidal action. Both traps are checked every morning, and occasionally once more in the afternoon on days

Figure 3.2 – The Leslé trap, i.e. trap 1 (a.) and the Prince Mill trap i.e. trap 2 (b.)

of intense migration. At the trap 1, most of the fish are anaesthetized, marked individually or by batch, with an additional fin clip to detect an eventual mark loss or non-detection, and released shortly after downstream of the facility. Then, marked fish can be recaptured at the Princes Mill trap (trap 2). These data can be used to estimate the probability of capture of the second trap, which has been done in another analysis (Lheureux et al. submitted, Chapter 2). Since marked and recaptured fish are not indicative of phenology, recaptures of these marked fish in the second trap are disregarded. Here, only the daily numbers of unmarked fish caught in trap 1 and in trap 2 are taken into account.

This CMR protocol has been repeated every year since 1998, with the exception of 2020 due to the Covid-19 pandemic. For each year, we consider these CMR data between the 91th (i.e. 1st April for non-leap years) and the 158th julian day (early June). As the date of the beginning migration is uncertain, the data are considered as left-censored. Juvenile salmon caught at the traps after of this window are rare and are considered to be residents rather than seaward migrants.

As the river flow increases, the proportion passing through trap 1 and trap 2 decreases, suggesting their efficiency is influenced by the river discharge. The discharge is also assumed to provoke migration pulse (Bjerck et al., 2021; Kennedy et al., 2010; Stich et al., 2015a). The mean daily discharge is then used as a covariate to explain variations in the probability of capture and migration probability. We obtained the hourly discharge of the Scorff from 1998 to 2023 from the open database https://data.eaufrance.fr/ (hydrometric gauging station - J510 2210 01). The temperature is assumed to increase the migration probability as well (Jonsson, 1991; Zydlewski et al., 2005; Kennedy et al., 2010; Spence et al., 2014; Simmons et al., 2021a; Vollset et al., 2021; Bjerck et al., 2021; Arevalo et al., 2021). We obtained the water temperatures from a thermometer located at the second trap. Some temperature data were missing, these water temperature data were estimated from a model that used air temperature. This model estimates the relationship between water temperature and both air temperature and discharge using a multiple regression approach. For more information, see supplementary materials 3.5.1.

In general, the fish collected at both traps on a given day j represent the cumulative catch of fish trapped approximately from noon on day $j-1$ to noon on day j, mostly during the night. The mean daily discharge and mean daily water temperature, which influences the probability of capture and the migration probability the observed catch on day j, are then calculated over a 24-hour period from noon on day $j-1$ to noon on day j. The discharge variations, which are also assumed to impact the migration behaviour (Bjerck et al., 2021; Simmons et al., 2021a) are calculated using the mean discharge on these 24-hour time step. These three covariates are standardised over all years.

Capture process

The capture system is composed of two consecutive traps. Trap efficiency is often influenced by environmental conditions, some of which can be measured and used as covariates to explain daily variations of the capture probability (e.g. river discharge for salmon smolts; Mäntyniemi and Romakkaniemi, 2002). We assume both trap were influenced by the environment and model $p_{trz}[i,y]$ in logit scale according to a linear relationship:

$$logit(p_{trz}[j,y]) = \beta_{trz}[1,y] + \beta_{trz}[2,y] \times X[j,y] + \epsilon_{trz}[j] \tag{3.11}$$

with:

- $X[j,y]$ a standardized environmental covariate,
- $\beta_{trz}[1,y]$ the mean capture probability in year y (logit scale),
- $\beta_{trz}[2,y]$ the effect of the environmental covariate $X[j,y]$,
- and $\epsilon_{trz}[j]$ a residual iid term, with mean 0 and standard deviation σ_{trz} accounting for daily variations in the probability of capture due to unknown causes.

$\beta_{trz}[1,y]$ and $\beta_{trz}[2,y]$ are assumed to vary randomly from year to year. $logit^{-1}(\beta[1,y])$ follows a beta distribution with parameters $M_{\beta_{tr1}[1]}$ and $\rho_{\beta_{tr1}[1]}$, and $\beta_{tr1}[2,y]$ follows a normal distribution with parameters $M_{\beta_{tr1}[2]}$ and $\sigma_{\beta_{tr1}[2]}$. The case of the second trap is different as we use informative prior on the annual parameters (see 3.2.3).

Modification to the generic model

We adapted the generic model to accommodate the specifics of the CMR protocol and dataset of our case study on the Scorff. The individuals captured at the first trap are marked and released, and can be recaptured at the second trap. Here, we have two consecutive traps, each with its own capture probability, p_{tr1} and p_{tr2}. Some of the migrating individuals are caught in the first trap. Then, among those that were not caught, some are caught in the second trap. Marking makes it possible to identify those caught in both the first and the second trap, allowing them to be counted only once. To infer the phenology, only the first capture matters. Then, thanks to the marking, the recaptured individual are discarded from the analysis. However, because of protocol variations, some individuals have not been marked, or have lost their mark. As a result, these individuals may be recaptured in the second trap and counted as individuals that have never been caught. This could lead to an overestimation of p_{phen}. In order to correct for the unmarked fish, we calculate the ratio of unmarked fish r_{unm} among the fish caught in the first trap. Thanks to a previous analysis, we had an idea of the probability of losing a mark, p_{lost}, and so we account for this probability too. These probabilities and this ratio are used to correct the probability of capture in the first trap when modelling the phenology in the second trap.

Smolts can swim pretty fast (Fängstam, 1993; Aarestrup et al., 2002; Lothian et al., 2018), so, giving the short distance between the two traps, they may pass through the first and second trap on the same day. Nevertheless, we discretised the time into 24h time steps. For this reason, and for any other reason that might slow down their speed, they can also pass through the first trap at time $i-1$ and through the second at time step i. So the fish caught in trap 2 at time i are made up of fish that passed through trap 1 at time step $i-1$ and at time step i. Thus, we adjust the probability to be a migrant and trapped at the second trap by adding a parameter ψ, which represents the proportion of individual passing through the first trap and the second trap at the same time step. Then, the proportion $1-\psi$ represents the individual that passed through the trap 1 during the time step $i-1$ and through the trap 2 during the time step i. We assume this proportion was similar over the migration period and the years, with the exception of the first time step. This time step is of a different nature since it is a mixture of several days, so we estimated the parameter $\psi[0]$ independently.

With these three modifications, the equation 3.12 remains the same for the first trap, and for the second trap becomes:

$$\begin{aligned} p_{phen,tr2}[i] = p_{phen}[i] \times p_{tr2}[i] \times (1 - p_{tr1}[i] + p_{tr1}[i] \times p_{lost} + p_{tr1}[i] \times r_{unm}[i]) \times \psi \\ + p_{phen}[i-1] \times p_{tr2}[i] \times (1 - p_{tr1}[i-1] + p_{tr1}[i] \times p_{lost} + p_{tr1}[i-1] \times r_{unm}[i-1]) \times \psi \end{aligned} \tag{3.12}$$

The first term of the sum is the migrating individuals that have passed through trap 1 on time step i which were:

— not captured
— or captured but unmarked
— or captured and marked but with loss of mark

The second term if the sum is the same but for the individuals that pass through the first trap the day before.

The last modification is due to the fact that the trap 1 were sometimes closed. Whether for reasons of accessibility to the trap or inefficiency, if the flow rate was too high ($> 14 m.s^{-1}$), the trap 1 no longer worked. To avoid any confusion explaining the zero captures, we added an index taking the value of 0 when the trap was closed, and 1 when the trap was open. This index multiplies the probability $p_{phen,tr1}[i]$ in the multinomial.

3.2.3 Bayesian statistical inference

Prior distribution

Bayesian statistical ecologists must pay attention to the prior distribution they use (Banner et al., 2020). It must be considered and specified in the

context of the model and the data at hand (Gelman et al., 2017).

In our model, we use non-classical parameterizations, mainly for the Beta distribution, to facilitate the specification of the "weak information" that we introduce with our priors (Gelman, 2004). For the hyper-parameters that control the yearly variation of some parameters, we ran prior simulations to ensure that the resulting probabilities for the dependent parameter are both, not too contrasted over a range wide enough to allow a posterior updating by the type data we could observe, and not inadvertently giving too much credibility to unplausible values. Finally, we verify how our priors are updated a posteriori by our data (see section 3.3).

We use a $Beta(2.5, 2.5)$ for M_{t_0}, M_{q90} and M_m. We used a $Beta(2.5, 47.5)$ for ρ_{t_0} , ρ_{q90} and ρ_m, which allows us to get priors for t_0, $q90$ and m that looks intermediate between the uniform distribution between 0 and 1 and the parabolic $Beta(2, 2)$ distribution.

We also use the weakly informative $Beta(2.5, 2.5)$ for ψ, $\psi[0]$ and $p_{migr}[0]$.

We set a standard normal prior for $\beta_{migr}[1]$, $\beta_{migr}[2]$, $\beta_{migr}[3]$ and $\beta_{migr}[4]$, which seems little informative.

We assigned χ^2 distributions with 5 degrees of freedom, rescaled to have a mean of 1, to the standard deviations of the migration probability, i.e. σ_{migr}. It ensures that the probability is close to 0 when the standard deviation is very small. This is an important feature, because introducing a source of variation into the model is *a priori* inconsistent with considering that its standard deviation parameter could be negligible. By choosing a low number of degrees of freedom, we aim to have a dispersion that is high enough to allow for a significant updating by the data.

The capture probability of the trap 2 has been estimated in a preceding analysis, thanks to a CMR model (Lheureux et al. submitted, 2). As the data used in the phenological model are not very informative about these capture probabilities, we have reused these estimations. These capture probabilities are assumed to be similar for the unmarked fish. Thanks to this former analysis, we know the capture probability at the trap 2 is dependant on the discharge: the discharge have a negative effect on the capture probability, so we use informative prior from the previous CMR analysis.

The previous analysis was carried out on the trap 2. The same expression has been used for the capture process as in the model of the current study, with the exception of the variability and the overdispersion that were hierarchical. As the present data set was less informative on the capture process than during the previous analysis, and this parameter was not very variable from year to

year, we have opted for parsimony. Then we used a unique parameter over the period for both the variability (standard deviation σ_{tr2}) of the capture probability at the trap 2 and for the over-dispersion parameter (ρ_{tr2}) at the trap 2.

For the linear coefficient of trap 2, $\beta_{tr2}[1, y]$ and $\beta_{tr2}[2, y]$, we used a multi-normal distribution for each year. The parameters of these multi-normal distributions, the mean matrix and the covariance matrix, are derived from the posteriors samples of the CMR model. The standard deviation and overdispersion parameters are not hierarchical in this model, unlike in the CMR model. We extracted, respectively, the logarithm and the logit of the mean standard deviation and the mean overdispersion parameter of the posterior samples of the CMR model to obtain another mean matrix and another covariance matrix. We use these parameters in another single multinormal distribution, checking that the *a posteriori* correlation between these two parameters and the annual coefficients was low. For the mean and covariance matrix, we used the posteriors of the hyper-parameters of σ_{tr2} and ρ_{tr2}, i.e. we used the mean of the two hierarchical parameters.

We assume the capture probability of trap 1 is also dependant on the discharge. As we have little information for the trap 1 efficiency, we used informative prior derived form the CMR analysis on the trap 2 for the $\beta_{tr1}[2, y]$ hyper-parameters, $M_{\beta_{tr2}[2]}$ and $\sigma_{\beta_{tr2}[2]}$, the standard deviation σ_{tr1} and over-dispersion ρ_{tr1} parameters. We used again a single multi-normal distribution with the mean matrix and the covariance matrix derived from the posteriors of the CMR model, as for the second trap. The annual values $\beta_{tr1}[2, y]$ were then drawn in a normal distribution with the hyper-parameters $M_{\beta_{tr1}[2]}$ and $\sigma_{\beta_{tr1}[2]}$, as we assume the annual discharge effects at the trap 1 are independent from the annual discharge effect at the second trap. The intercept $\beta_{tr1}[1, y]$ is the overall average probability of capture at trap 1 for an average discharge. There was no reason to assume it was similar to the average probability of capture at trap 2 as these traps are different, so we use a weakly informative prior such as in the CMR analysis. We use a $Beta(2.5, 2.5)$, for $M_{\beta_{tr1}[1]}$ and then adjust the prior for $\rho_{\beta_{tr1}[1]}$ in order to get a resulting prior for $logit^{-1}(\beta[1, y])$, i.e. the mean probability of capture under an average discharge in any year y, which is also weakly informative.

An informative prior is assigned to p_{lost} based on available data. We use the observations made in the years when only visible implants were used. A $Beta(115, 1775)$ distribution is used because, in those years, among the marked fish recaptured, 115 had lost their visible implant while 1775 had retained it. In the absence of proper data to assess the probability of an elastomer or a PIT tag being lost or undetected, we additionally assume that it is the same as for visible implants.

Table 3.1 – Symbols, definitions and prior distributions of all the quantities referenced in the model. They are grouped by process and ordered within each process from the top (hyper)parameters, through the intermediate latent layer, down to the data

Symbol	Description	Prior
i	migration day index	
y	year index	
	Phenological process	
M_{t_0}	mean of t_0	$Beta(2.5, 2.5)$
ρ_{t_0}	dispersion parameter of t_0	$Beta(2.5, 47.5)$
t_0	starting date parameter of the 3-parameters Weibull distribution	
M_m	mean of m	$Beta(2.5, 2.5)$
ρ_m	dispersion parameter of m	$Beta(2.5, 47.5)$
m	median of the 3-parameters Weibull distribution	
M_{q90}	mean of $q90$	$Beta(2.5, 2.5)$
ρ_{q90}	dispersion parameter of $q90$	$Beta(2.5, 47.5)$
$q90$	quantile 90% of the 3-parameters Weibull distribution	
$\beta_{migr}[1]$	mean probability to migrate (logit scale)	$Normal(0, 1)$
$\beta_{migr}[2]$	covariates effect on the probability to migrate (discharge effect)	$Normal(0, 1)$
$\beta_{migr}[3]$	covariates effect on the probability to migrate (discharge variation effect)	$Normal(0, 1)$
$\beta_{migr}[4]$	covariates effect on the probability to migrate (temperature effect)	$Normal(0, 1)$
σ_{migr}	standard deviation of the probability to migrate	$\chi^2(5)$ (rescaled, mean = 1)
$p_{migr}[0]$	probability to migrate on the first time step	$Beta(2.5, 2.5)$
$X_1[i, y]$	covariate influencing capture probability (standardized log of discharge)	
$X_2[i, y]$	covariate influencing capture probability (standardized log of variation of the discharge)	
$X_3[i, y]$	covariate influencing capture probability (standardized log of temperature)	
$p_r[i, y]$	probability to be in the stock of "ready" individuals	
$p_{migr}[i, y]$	probability to migrate through the trap	
$p_{phen}[i, y]$	phenological probability: probability of being migrating	
	Capture process	
$M_{\beta_{tr1}[1]}$	mean of $\beta_{tr1}[1, y]$ (logit^{-1} scale)	$Beta(2.5, 2.5)$
$\rho_{\beta_{tr1}[1]}$	dispersion de $\beta_{tr1}[1, y]$ (logit^{-1} scale)	$Beta(2.5, 47.5)$
$\beta_{tr1}[1, y]$	mean capture probability of the trap 1 (logit scale)	
$M_{\beta_{tr1}[2]}$	mean of $\beta_{tr1}[2, y]$	
$\sigma_{\beta_{tr1}[2]}$	standard deviation of $\beta_{tr1}[2, y]$	$MultiNormal(M_{ip}[1:4], cov_{ip}[1:4])$
ρ_{tr1}	capture overdispersion at trap 1	
σ_{tr1}	residual standard deviation of p_{tr1} (logit scale)	
$\beta_{tr1}[2, y]$	covariate effect on the trap 1 capture probability	
ρ_{tr2}	capture overdispersion at trap 2	$MultiNormal(M_{ip}[1:2], cov_{ip}[1:2])$
σ_{tr2}	residual standard deviation of p_{tr2} (logit scale)	
$\beta_{tr2}[1, y]$	mean capture probability at trap 2(logit scale)	$MultiNormal(M_{ip}[1:2, y], cov_{ip}[1:2, y])$
$\beta_{tr2}[2, y]$	covariate effect on capture probability at trap 2	
M_{ip}	mean matrix for the informative priors	
cov_{ip}	covariance matrix for the informative priors	
$X[i, y]$	covariate influencing capture probability (standardized log of discharge)	
p_{lost}	probability of mark loss	$Beta(115, 1775)$
ψ	time lag from one trap to the next	$Beta(2.5, 2.5)$
$\psi[0]$	time lag from one trap to the next at the first time step	$Beta(2.5, 2.5)$
$p_{trx}[i, y]$	capture probability at trap X	
$n_{trx}[i, y]$	number captured at trap X	
$r_{unm}[i, y]$	ratio of unmarked fish at trap 1	
$N_{trx,tot}[y]$	Total number of capture at trap X	

MCMC sampling

For each of the model we use, we approximate the joint posterior distributions of all unknown quantities by Monte Carlo Markov Chain (MCMC) sampling, as implemented by the Nimble software (Valpine et al., 2024) and the R statistical computing environment (R Core Team, 2024). We run 3 parallel chains and retain 5000 iterations from each (after an initial burn-in sequence). Based on this sample of 15000 values, we assess the convergence of the MCMC sampling by checking the stationarity and the mixing of the chains marginally for each quantity (Gelman et al., 2013). We examine stationarity by means of running quantiles (5%, 50%, 95%). We use the $\hat{R}$ criterion for mixing and verify it is below 1.01 (Vehtari et al., 2021). In addition, we ensure the effective sample size is greater than 400 (Vehtari et al., 2021). Model script is provided in appendix C (see 4.6).

Posterior checking

We assess *a posteriori* the adequacy between our model and the available data (Gelman et al., 2013). We use the replication of data approach and we compare the distribution of the capture per day over a posteriori replicated datasets with the observed values in the original data (Gelman et al., 2013).

We verified the correlation matrices of all parameters to check the confusion between the parameters. Uncertainties in model parameters were reported using 90% posterior probability intervals (ppi). The statistical significance of covariate effects (e.g., discharge, discharge variation, temperature) was assessed by ensuring that the $ppi_{90\%}$ did not overlap with 0.

3.3 Results

The posterior checks do not reveal any inadequacy between our model and the available data, with the exception of a slight underestimate of the number of migrants caught at peak times. In the data replication approach, we could not detect any temporal patterns in the residuals between the observed data and the replicated data set. Additional details can be found in the supplementary material (3.5).

All the priors assigned to the (hyper)parameters of the model are clearly updated *a posteriori*, except for ρ_{t_0} and p_{lost}. This is no surprise for the latter, as there is no information in the data about mark loss. For ρ_{t_0}, the quasi absence of posterior updating is associated with a posterior update for M_{t_0}. For all the other parameters, the posterior updating leads to a significant displacement of the median.

3.3.1 Capture process

The mean capture probability at trap 1 has a mean $M_{\beta_{tr1}[1]} = 0.32$ (posterior probability intervals (ppi): $[0.19, 0.47]$). It varies from year to year (posterior median of $logit^{-1}(\beta_{tr1}[1, y])$ from 0.16 in 2015 to 0.41 in 2021), with no apparent temporal trend (Fig. 3.3.a.). The overall discharge effect is negative (median: -0.20, ppi: $[-0.31, -0.09]$), but with a lot of variations from year to year (median $\sigma_{beta_{tr1}[2]}$: 0.51, i.e. 0.62 in natural scale)(Fig. 3.3.b.). For some years, the discharge effect is negative, not exceeding 0. However, for some years, $\beta_{tr1}[2, y]$ encompasses 0 and can even be positive (positive median for 2002, 2004, 2011 and 2017). The overdispersion of the capture at trap 1 ρ_{tr1} is low (median: 0.0026, ppi: $[0.0022, 0.0032]$), and the median of the standard deviation σ_{tr1} is 0.41 (ppi: $[0.36, 0.47]$). These parameters lead to variable profile of p_{tr1}, with some years where p_{tr1} strongly increase within the period, while the discharge decreases, whereas others years present a p_{tr1} profile rather flat (Fig. 3.3).

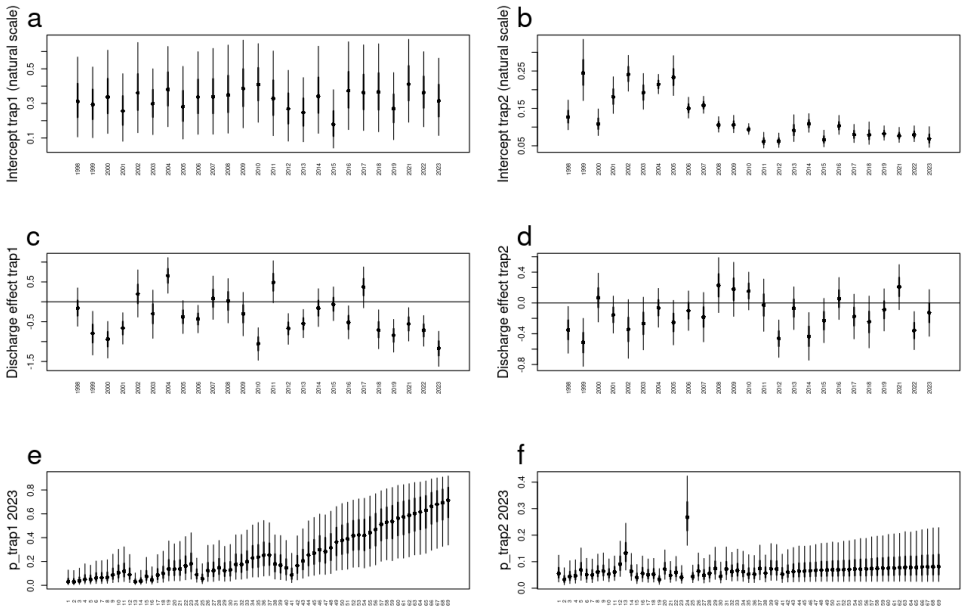


Figure 3.3 – **Marginal posterior distributions of quantities of the capture process at the two traps**. The plain dot represents the median, the thick line the 50% interval and the thin line the 90% interval. a. Mean capture probability at trap 1 (for a river discharge equal the mean; $logit^{-1}(\beta_{trz}[1, y])$) and b. at trap 2. c. River discharge effect on capture probability ($\beta_{trz}[2, y]$) at trap 1 and d. at trap 2. e. Profile of the p_{tr1} for 1999 and f. of p_{tr2} the same year.

The mean capture probability at trap 2 is lower and varies more from year to year than the mean probability at trap 1 (posterior median of $logit^{-1}(\beta_{tr2}[1, y])$ from 0.06 in 2011 to 0.24 in 1999), with generally higher values at the beginning of the study period (Fig. 3.3.b.). The mean capture probability posterior is quite similar to the informative prior. The correlation of the joint distribution for each year of mean capture probability in the two traps $logit^{-1}(\beta_{tr1}[1, y])$ and $logit^{-1}(\beta_{tr2}[1, y])$ is weak (integer value of the Pearson correlation < 0.1). The discharge effect is generally negative, with variation from year to year, and some years with a positive effect (median positive for 2000, 2008, 2009, 2010, 2016 and 2021) (Fig. 3.3.d.). The discharge effect posterior is quite similar to the informative prior, except for 1999, 2012 and 2015, for which the discharge effect is less negative and overlap 0. The variability of this effect is weaker than for the first trap (median of the sample variance for trap 1: 0.30 and for trap 2: 0.08). The discharge effect for the two traps does not show the same pattern of variations and the joint distributions for each year are weakly correlated (integer value of the Pearson correlation between $\beta_{tr1}[1, y]$ and $\beta_{tr2}[1, y] < 0.5$). The overdispersion of the capture at trap 2 is of the same order of magnitude than trap 1 : 0.029 (ppi:[0.023, 0.035]). The standard deviation of the residual variation of the capture probability is larger than trap 1, $\sigma_{tr2} = 0.57$ (ppi : $[0.51, 0.66]$). These parameters together with those of the discharge regime, lead to contrasted temporal profiles of daily capture probability p_{tr2} between years.

The parameter that controls the time lag from one trap to the next ψ is quite high (0.83, ppi: $[0.77, 0.88]$), meaning that most of the fish pass through the two traps during the same time step. The parameter that controls the time lag from one trap to the next for the first time step ψ_0 is smaller, more uncertain (0.27, ppi: $[0.07, 0.67]$) and a bit correlated with $p_{migrate}[0]$ (Pearson correlation $:-0.65$), which reflects a slight confusion between the two parameters.

3.3.2 Migration process

The starting date parameter of the Weibull distribution, i.e. the starting day of the process, t_0, is at the beginning of March, with $M_{t_0} = 0.25$ (ppi: $[0.09, 0.48]$), i.e. 23 time step before the 1st of April (Fig.3.4. a.). The annual values of t_0 are quite similar, the posterior median vary between -24.0 and -22.7, and the ppi for each year include the values $[-28.9, -16.5]$, i.e. all the t_0 are approximately estimated between 3 March and 15 March.

On the other hand, the median date of the accumulation of the stock, is quite variable and better estimated, with a mean $M_m = 0.40$, (ppi: $[0.36, 0.44]$) (Fig.3.4. b.), i.e. the 12 April. The median annual values before rescaling, i.e. before adding $-t_0$, are between 8.3 in 1999 and $17,0$ in 2004, i.e. between the second week to the third week of April. After translation (adding t_0), the median m represents the time spent between t_0 and the date when the

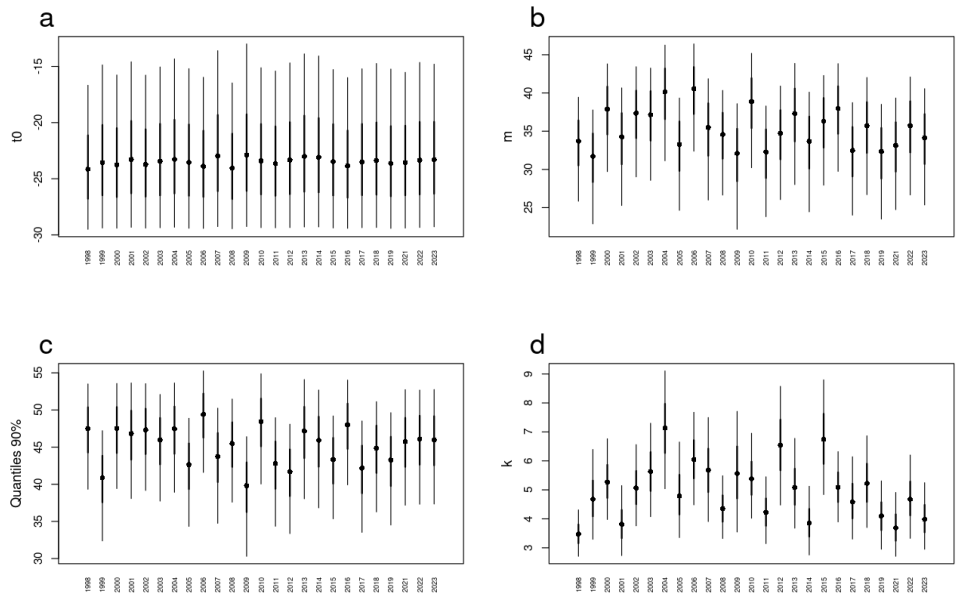


Figure 3.4 – **Posterior distributions of quantities of the accumulation process**. The plain dot represents the median, the thick line the 50% interval and the thin line the 90% interval. a. Starting date parameter of the Weibull distribution of the preparation process, i.e. starting day of the process, t_0, b. Median of the Weibull distribution, m. c. Quantile 90% of the Weibull distribution, $q90$. d. Shape of the Weibull distribution.

probability to accumulate, waiting to migrate, reach 50%. These median annual values vary between 31.4 in 1999 and 40.4 in 2006.

The quantile 90% is also variable and better estimated, with a mean $M_{q90} = 0.12$ (Fig.3.4. c.). The median annual values before rescaling are between 17.1 in 2009 and 25.6 in 2006, meaning that probabilities to accumulate, waiting to migrate, reach 90% between mid-April and the last week of April. After rescaling, the $q90$ parameter are between 39.7 in 2009 and 49.0 in 2006.

The variability of these parameters is the source of a diversity of p_r profiles, with some wider or narrower (Example: Fig. 3.5a. b.). The hazard of the first time step $\lambda[0, y]$, calculated with the three Weibull parameters, is also variable, leading to median $p_r[0]$ between 0.01 in 2004 and 0.20 in 1998, i.e. between 1% and 20% of the smolts were ready to migrate during March. In any case, the median values of p_r values are all below 10^{-4} after 40 time steps.

The mean probability to migrate is -1.80 (ppi: $[-1.88, -1.71]$), i.e. 0.14 (ppi: $[0.13, 0.15]$) in natural scale. All three environmental effect coefficients are positive and significantly different from 0. The discharge effect β_1 is 0.24 (ppi: $[0.15, 0.34]$), the variation of discharge effect β_2 is 0.37 (ppi: $[0.32, 0.41]$), and the temperature effect β_3 is 0.50 (ppi: $[0.44, 0.56]$). Then the temperature is the parameter that presents the biggest effect. The standard deviation of the probability to migrate σ_{migr} is 0.57 (ppi: $[0.52, 0.61]$). The probability to migrate during the first time step $p_{migr}[0]$ is rather low, being less than the mean probability to migrate, at 0.08 (ppi:$[0.02, 0.23]$).

This lead to very different and noisy p_{migr} profiles, some showing that probabilities increase on average over the period, and other showing little temporal trend (Fig.3.5. b. c.). Then, contrary to p_r, p_{migr} can be high at the end of the period. The pairwise correlations between the parameters of p_r and p_{migr}, (M_{t_0}, ρ_{t_0}, M_m, ρ_m, M_{q90}, ρ_{q90}, $\beta_{migr}[1]$, $\beta_{migr}[2]$, $\beta_{migr}[3]$, $\beta_{migr}[4]$, σ_{migr} and $p_{migr}[0]$) remain low (Pearson correlation < 0.46), showing that the model succeed in disentangling the two processes.

3.3.3 Phenology

The p_{phen}, which are the combination of p_r and p_{migr}, are very different from year to year. The profiles vary in width, with one or multiple peaks (Fig. 3.5e. f. and Fig.3.6). The probability are low at the end of the period, but contrary to p_r, there are still superior to 10^{-4} after the 40^{th} time step for some years. Probabilities of being migrating during the first time step $p_{phen}[0]$ are rather low and uncertain, with the median annual values between 0.092% and 1.4% of migrants during this period, but none of these values show any significant difference from the others. The main migration window, i.e. the date on which the cumulative probability of p_{phen} is between 25% and 75% (Fig.3.6) does not

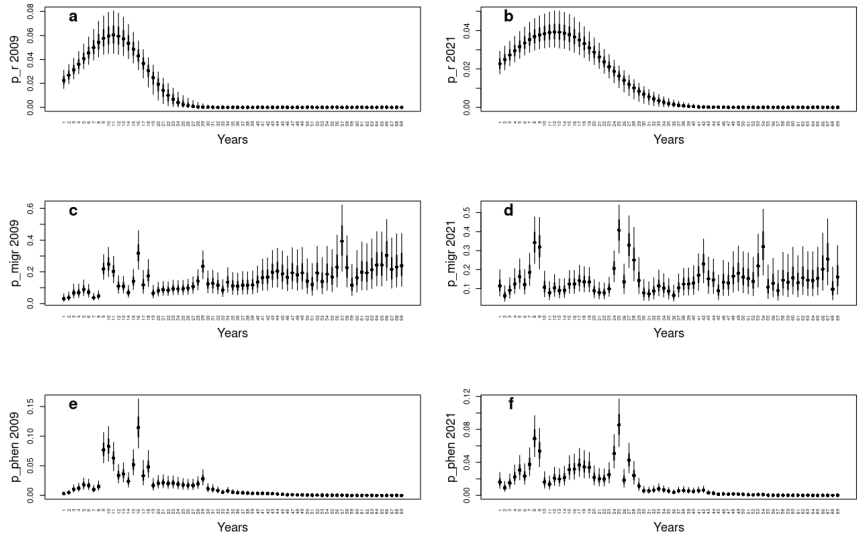


Figure 3.5 – **Comparison of the posterior distributions of the probability p_r, p_{migr} and p_{pheno} for two years.** The plain dot represents the median, the thick line the 50% interval and the thin line the 90% interval. a. p_r in 2009 and b. 2021 c. p_{migr} in 2009 and d. 2021 e. p_{pheno} in 2009 f. and 2021.

show particular temporal trend, except maybe for the first few years. From 1998 to 2004, the main migration window seems to get later.

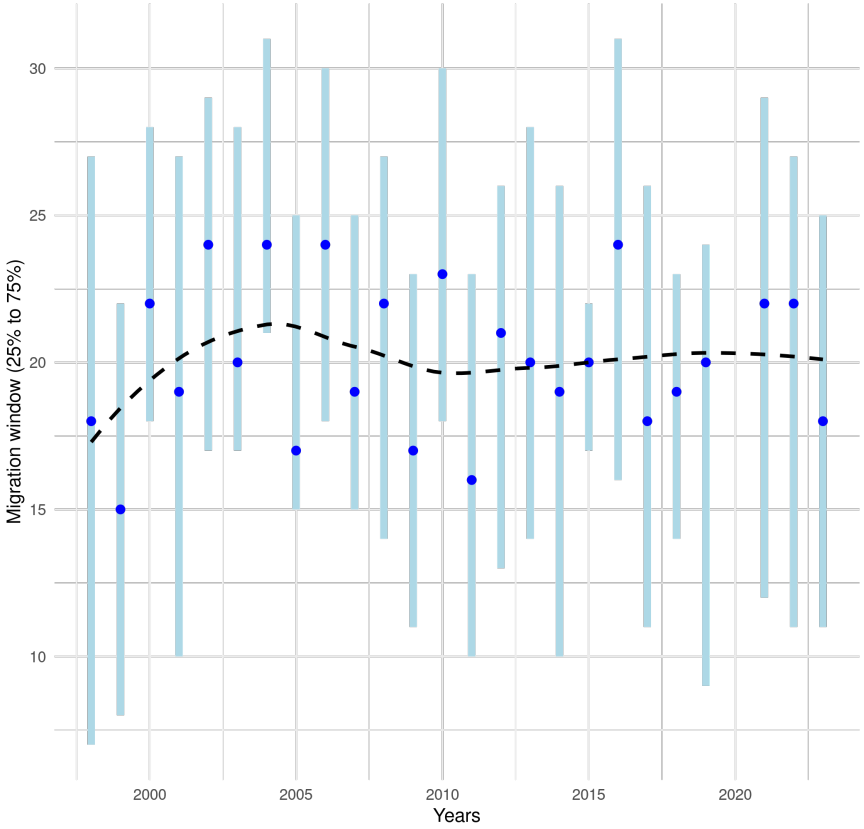


Figure 3.6 – **Migration window variability.** The plain dot represents the median, the solid line represents the distribution of p_{pheno} between 25% and 75%.

3.4 Discussion

Through this model, we describe the two main process, the observation process, and the biological process of interest: the migration phenology of the A.salmon. We have separated the migration phenology process into two sub-mechanisms: the accumulation of the stock of fish ready to migrate, and the decision to migrate. This makes it possible to stagger the migration of individuals: only those individuals in the stock of ready individuals can actually migrate when conditions are good. In line with our hypotheses, we found that discharge, discharge variations and temperature have a positive effect to trigger the migration. The explicit formulation of the process allowed us to disentangle the effect of the environment on both the trap efficiency and the decision to migrate. Our model allows great flexibility in the distribution of phenology, which is more plausible than a uni-modal distribution (Bjerck et al., 2021;

Inouye et al., 2019). This gives profiles that vary from one year to the next, both in shape (number of peak, asymmetries) and extent (Fig. 3.6).

The two traps show different variation profiles of their efficiency, with the first trap presenting higher mean capture probability but also high variations due to the discharge regimes (example: Fig. 3.3.e.). The second trap show slightly weaker dependence with the discharge but with higher standard deviation leading to noisier profile (Example: Fig. 3.3.f.).

The discharge has an overall negative effect on both trap 1 and trap 2 which is consistent with our initial expectations. For the trap 1, the higher the discharge, the more the trap is submerged, with fish able to escape from the cage, which has been observed *in situ* (N. Jeannot, pers.com.). In addition, the higher the flow rate, the lower the proportion of water that passes through the channel leading to the trap, which can reduce the attractiveness of the trap. Indeed, fish are sensitive to hydraulic conditions, they prefer to follow the main flow but they also seem to avoid high turbulence (Silva et al., 2020), so more fish might prefer to follow the less turbulent, faster current in the middle of the river. The installation of the trap 2 is different, but also on the edge of the river following a channel, so that the flow rate can influence the attractiveness of the trap for the same reason.

However, some annual values of the effect discharge are positive or not significant: the discharge increases or does not impact the trap efficiency. The years when it happens are not the same for the two traps, which is not surprising given that the two traps are different installations. The discharge profile of these years does not appear to be drastically different from the other years. The data may not be sufficiently informative for these years to sort out the confusion between the effect of discharge on the trap and that of migration cue, particularly for the first trap, as there is less information for it. In addition, many unrecorded factors can influence the attractiveness of the trap. For example, the sandbanks and vegetation in the channel leading to the trap change each year (N. Jeannot, pers. comm.), settings at nearby private dams can alter the hydraulic system, and turbidity can also affect the decision of smolts to pass an obstacle (Kemp et al., 2006). In addition, the trap settings may have changed over the years, particularly at the start of the study period. This could explain the higher capture probability for the first few years.

In any cases, these variations show the importance of taking into account the capture probability. Taking a constant probability, while in reality the efficiency fluctuates a lot, could lead to underestimating or overestimating the number of individuals per day, and therefore give an erroneous view of phenology. This can be even worst when the environment has a contradictory effect on the phenological process and on the observation process. In the preceding analysis (Lheureux et al. submitted, chapter 2), when trying to estimate the

number of migrants while explicitly modeling the observation process, the discharge effect on the trap 2 becomes positive, which is in contradiction with the CMR alone analysis that show the effect is overall negative. This is because the discharge increases the number of migrants, leading to a confusion that increases the capture probability. Here, modeling explicitly the phenological process and informing the observation process with informative prior helped the model to disentangle the confusion between the positive effect of the discharge on the phenology and the negative effect of the discharge on the trap.

The high value of the parameter ψ, that controls the time lag from one trap to the next, shows that most of the fish migrate rapidly from one trap to another. In the preceding CMR analysis, we found that the mean time to pass from one trap to another is mostly between 1 and 2 time steps, which is a bit longer. Nevertheless, the fish in the CMR analysis endured trapping and marking. This can stress them and delay their migration, so that more fish take more than a time step to make the distance between the two traps. Then, this is not surprising that for this analysis, most of the fish seem to pass from one trap to the next in one time step. The parameter $\psi[0]$ is much smaller. The parameter $p_{migrate}[0]$ is also weak, and correlated to $\psi[0]$. This shows confusion between these two parameters. However, we estimate the product of the two parameters fairly well, which indicates that a small proportion of the fish ready before 1 April actually migrated before that date. This is easily explained by the temperature: the average temperature in March over the study period was between 7.5 and 11°C, while the average temperature in April was between 11 and 14°C (except for 2013: the average temperature in April was 10°C). As the model shows that temperature is a cue for migration, it is possible that temperatures are too low in March to trigger migration. This is consistent with our data as few smolts are captured in March. It is also consistent with the literature, as it has been found that fish migrate more slowly at the start of the migration window (Stich et al., 2015a).

The first sub-mechanism that we included in the model is the accumulation of a stock of smolts "ready" to migrate, i.e. to be triggered by the environment to migrate. This mechanism is not exactly the preparation before the departure on migration, because we do not have information on the behaviour of the fish upstream, therefore we do not know when the smolt effectively began its migration. When the conditions are good, they pass through the trap in the 24h time step that follows. This is an approximation, but as the river is rather short, and smolts can travel up to several tens km per day (Thorstad et al., 2012), this does not seem to be too strong a hypothesis. Nevertheless, this sub-mechanism and its annual variation can have biological explanation.

In a same population, individuals can present variations in the timing they are ready to migrate. In the present case, salmon undertake smoltification, that make them able to survive in the marine environment. The gill Na^+,

K^+-ATPase activity, which is involved in the sea tolerance and sea survival (Stich et al., 2015b), can be used as a marker of physiological readiness (Zydlewski et al., 2005; Stich et al., 2015b). It has been shown that high or low gill Na+, K+-ATPase activity can delay the migration (Stich et al., 2015b), showing the importance of physiological readiness. Then, because of difference in life-history trait, environment, etc., some smolts can be ready at different times, making them sensitive to the environmental cue at different timings. By breaking down migration phenology into two processes, our model takes into account these biological requirements. The interannual variation can be explain by the different conditions smolts endure during the period before migrating, i.e. the winter. For example, discharge and water temperature are factors that can impact the growth rate during winter (Simmons et al., 2020), which can then advance or delay the preparation to migrate.

The migration is triggered by high discharge, increasing discharge and high temperature, which is consistent with the literature (Arevalo et al., 2021; Bjerck et al., 2021; Jonsson, 1991; Kennedy et al., 2010; Simmonds et al., 2020; Stich et al., 2015a; Spence et al., 2014; Zydlewski et al., 2005; Vollset et al., 2021). High discharge limits the energy expenditure of fish during their journey, as smolts use the current to swim, whether they are actively swimming or not (Persson et al., 2018; Davidsen et al., 2005; Thorstad et al., 2012). Then migrating at higher discharge benefits the smolt by saving energy that can be allocated to predators avoidance or foraging, in both the river and the sea. It can also permit them to maintain higher body conditions that is advantageous at sea (Jonsson et al., 2014; Gregory et al., 2019; Simmons et al., 2021b; Wilson et al., 2021). For the same reason, positive variation of the discharge is a cue for higher discharge, i.e. better swimming conditions, so the smolts that are ready to migrate prefer increasing discharge. The temperature, in synergy with the photoperiod, is known to trigger smoltification and migration (Spence et al., 2014; Simmonds et al., 2020; Simmons et al., 2021a). We did not take photoperiod as an explicit covariate, however, the shape k is (Fig.3.4. d), indicating that the hazard increases with time (Congdon, 2014). This implicitly includes a positive effect of time, i.e. of the photoperiod. The use of temperature (and photoperiod) as a migration trigger may have been selected because they are a cue of season and seawater temperature, and therefore an indicator of good marine conditions for migration (**spence_geographic_2014** ; Antonsson et al., 2002; Hvidsten et al., 1998).

We did not found earlier migration throughout the year, contrary to Otero et al., 2013. However, contrary to Otero et al., 2013, we focus on one specific area and on 25 years contrary to 50 years. The local variations in the weather over the last 26 years may, for the moment, be hiding a signal of climate change.

3.4.1 Limits and perspectives

Censorship of our data is a source of uncertainty, since the parameters linked to the first time step ($psi[0]$ and $p_{migrate}[0]$) are fairly uncertain and correlated, showing the inefficiency of estimating them. Furthermore, t_0 are uncertain and their marginal distributions are very similar, with ρ_{t_0} poorly updated. This is not due to a confusion with other model parameters, so there is most likely not enough information in the data to modify our prior through the likelihood. We believe that it is biologically more plausible for us to have different t_0 rather than a constant t_0 throughout the years. This is why we have chosen to keep annual t_0. In addition, the other parameter of t_0, M_{t_0}, is well updated and estimated.

To reduce the uncertainty of the start of the process, it would be beneficial to add more information for this period. The date of 1 April was set for censure, as a date on which we were sure that the process had begun. However, it may be too late to represent the process correctly, as we can see from the p_r profiles that the process has sometimes largely begun (Fig. 3.5). One solution would therefore be to try other dates for the censoring and analyse the effect this may have on the estimates.

Because of the lack of upstream information, we could not include other factor such as the initial distance from the trap. Indeed, it has been suggested that there are local phenological adaptation of sub-population into the same river depending on the distance to the sea (Stewart et al., 2006). The further upstream the fish are from the sea, the earlier is their departure, allowing them to arrive around the same period. Nevertheless, distance can delay there arrival (Simmonds et al., 2020). For the same reason, we could not model the preparation period and the departure decision from their initial habitat, but rather, their departure decision close to the trap. Telemetry is often used to follow the behaviour of smolt in the river (e.g. Stich et al., 2015a; Silva et al., 2020). As some smolts of the study were marked as parrs, using telemetry antenna could help provide information on behaviour upstream of the traps.

3.4.2 Conclusion

Our results show the variability of the phenological window from year to year. Climate change is altering the migration phenology of many species (Visser, 2022). In this context, understanding phenological changes can be difficult because of the many confounding effects. Modelling the phenological mechanism could help in this respect. We believe that the model we propose, by explicitly modeling the mechanism that creates the migration pulse, can achieve this goal better than a simple correlation analysis. We believe that we provide a method that can be extended to model the migration phenology of other anadromous fish.

Acknowledgments

We would like to thank the Scorff technical team and the other people involved in collecting the data and managing the facilities. In particular, we would like to thank N. Jeannot and F. Quendo (INRAE, Pont-Scorff) for checking and completing the data.

3.5 Supplementary Material

3.5.1 Estimation of missing water temperatures

The following model is a version of the model used in (Lamarins et al., 2022), adapted for this article. This model estimates the relationship between water temperature (T_{water}, lagged i.e. from noon of day $i-1$ to noon day i) and both air temperature (T_{air}) and water discharge (Q) (also lagged from noon of day $i-1$ to noon day i) using a multiple regression approach.

For each year y and time step i (here, only over the time period of interest: Julian days 60 to 160), the water temperature (T_{water}) is modeled as a normally distributed random variable with a mean ($\mu_{T_{water}}$) and precision ($\tau_{T_{water}}$).

$$T_{water}[i,y] \sim \text{Normal}(\mu_{T_{water}}[i,y], \tau_{T_{water}}) \tag{3.S1}$$

T_{water} is truncated to be greater than 0, indicating that water temperature cannot be negative.

The mean water temperature ($\mu_{T_{water}}[i,y]$) is modelled using a linear relationship involving the previous air temperatures (T_{air}) and the air temperatures at time step i as well as the discharge at time step i in logarithmic scale $log(Q)$:

$$\mu_{Teau}[i,y] = \theta[y] + a_1 \cdot T_{air}[i,y] + a_2 \cdot T_{air}[i-1,y] + \ldots + a_6 \cdot T_{air}[i-5,y] + b \cdot \log(Q[i,y]) + c \cdot i \tag{3.S2}$$

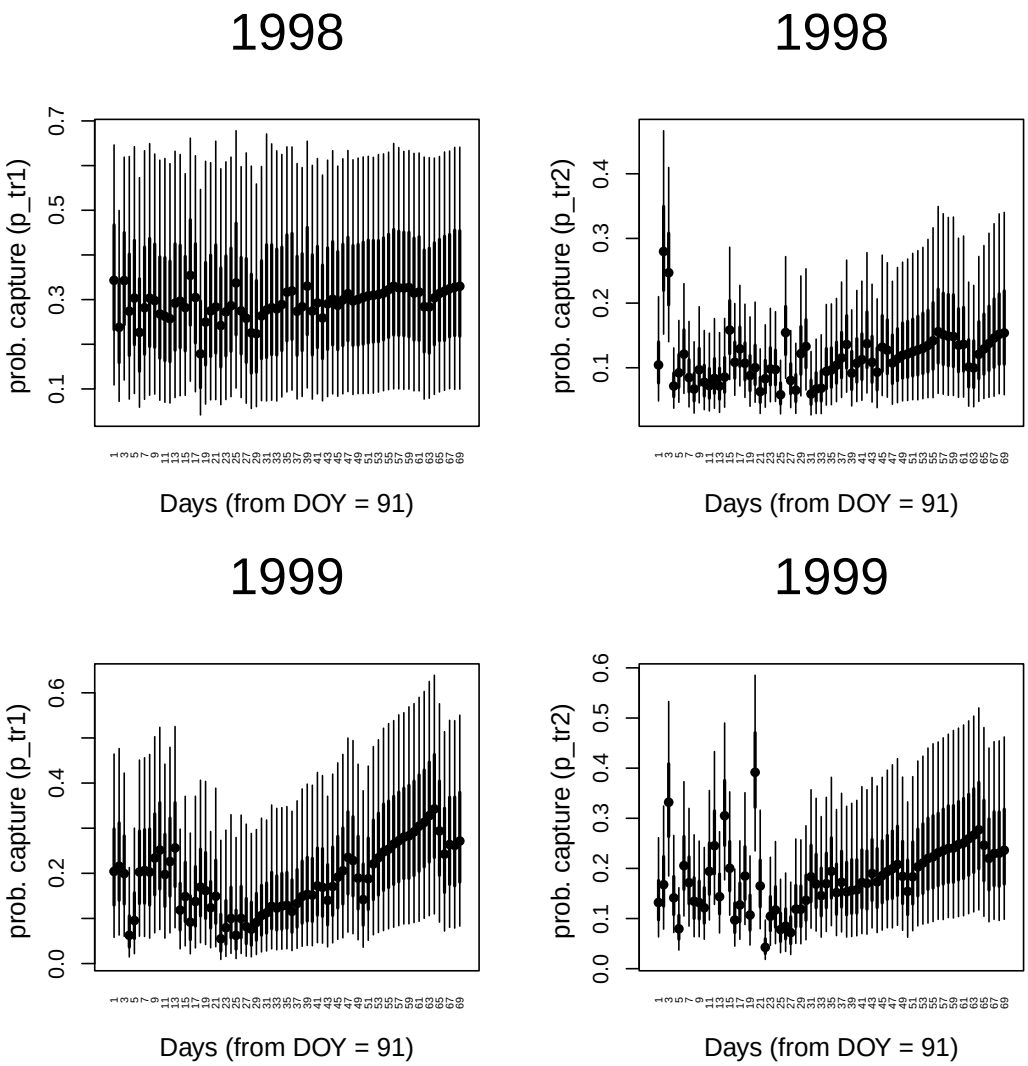
with $theta[y]$ that represents the baseline temperature for year y, the coefficients a_1 to a_6 correspond to the effects of current and last 5 days of air temperatures on water temperature, b is the coefficient for the effect of discharge $log(Q)$ on water temperature and $c \cdot i$ represents a potential time trend within the year.

For each year y and time step i, a predicted water temperature ($T_{water,pred}[i,y]$) is generated from the same normal distribution used for the actual water temperature:

$$T_{water,pred}[i,y] \sim \text{Normal}(\mu_{T_{water}}[i,y], \tau_{T_{water}}) \tag{3.S3}$$

This allows for the generation of new data sets at each MCMC iteration, which can be used for posterior predictive checks.

3.5.2 Additional figures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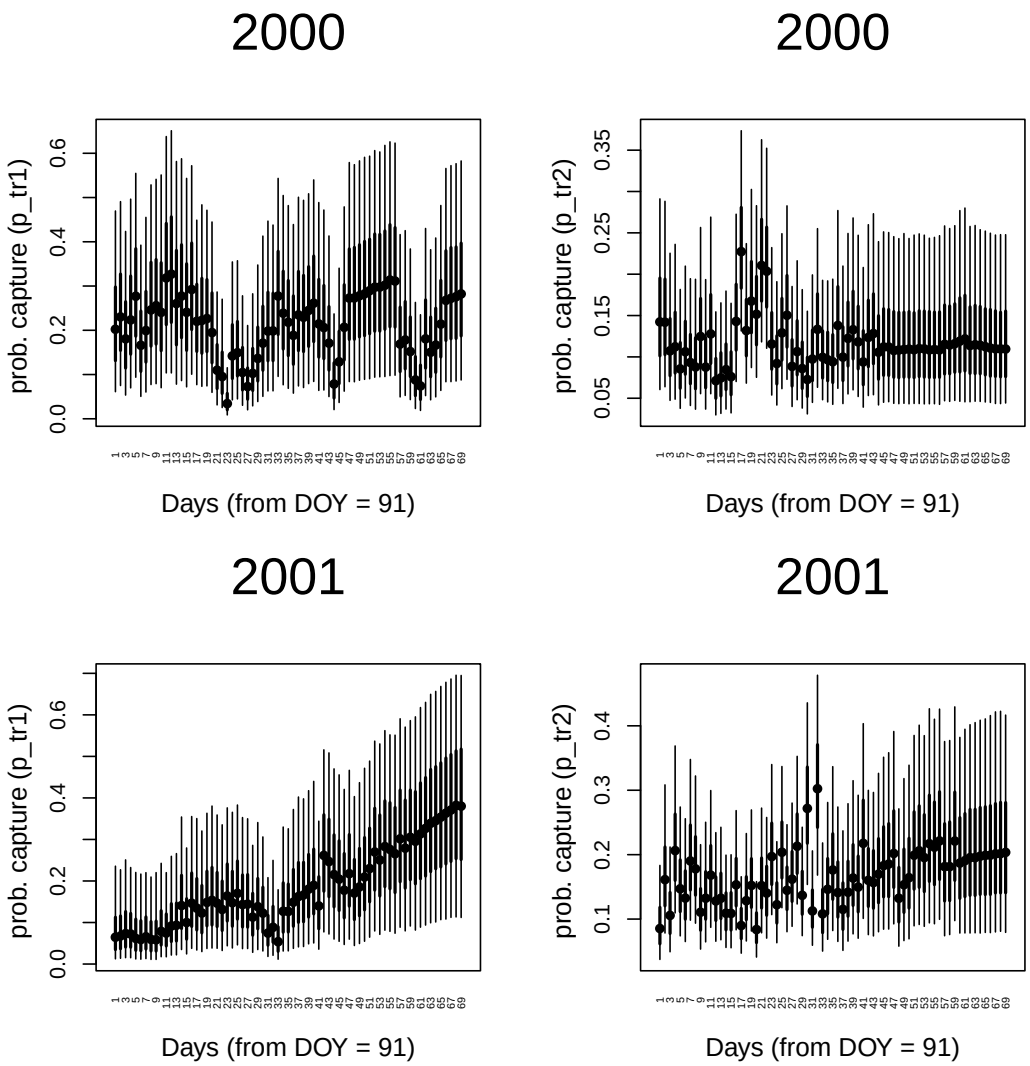
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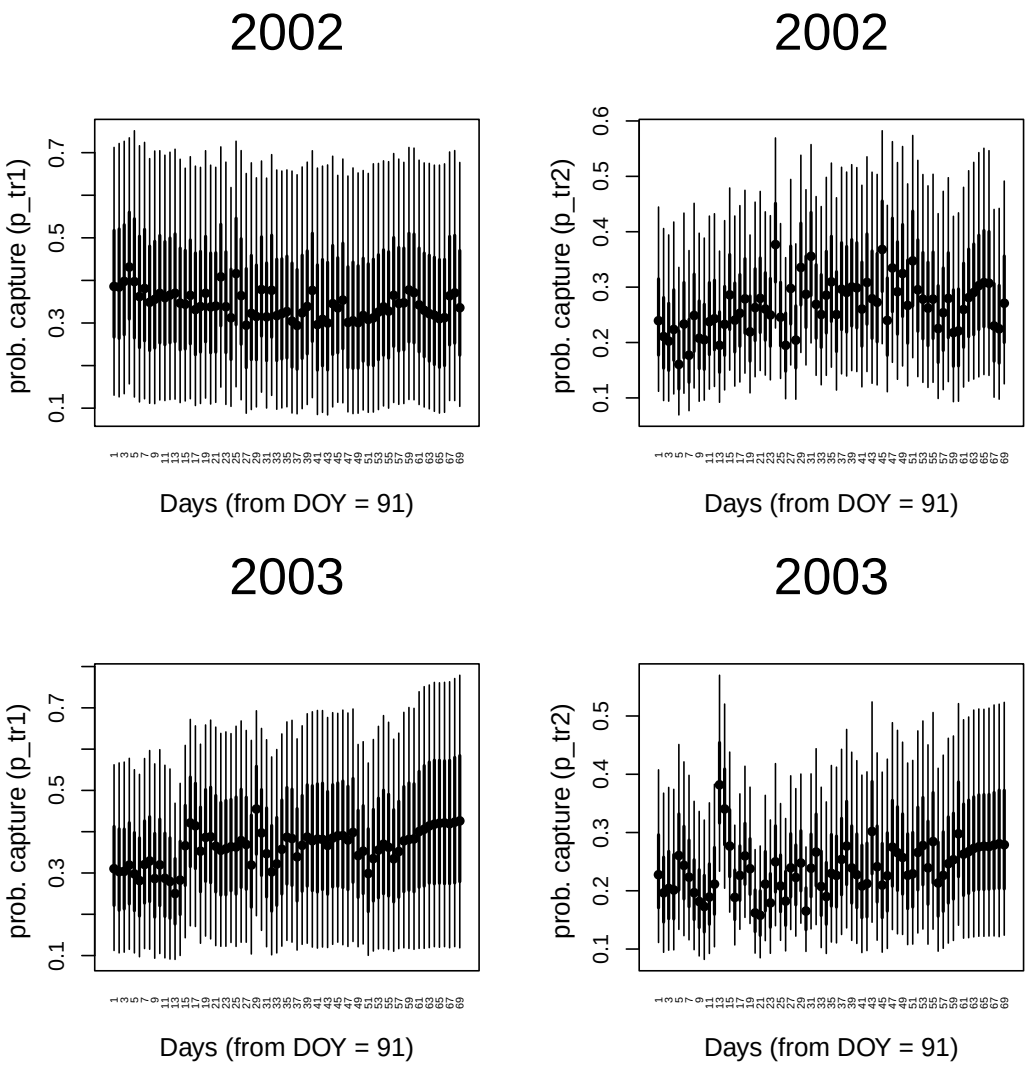
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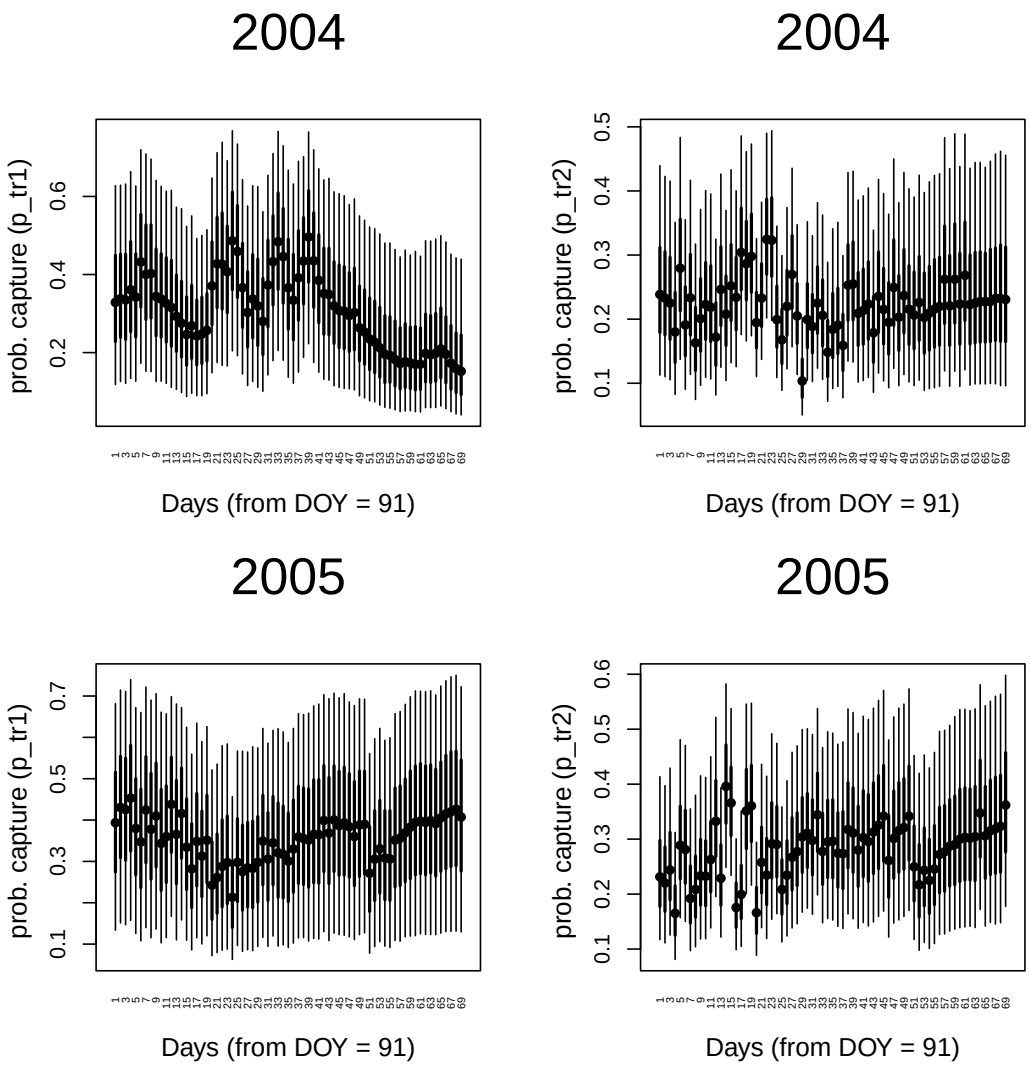
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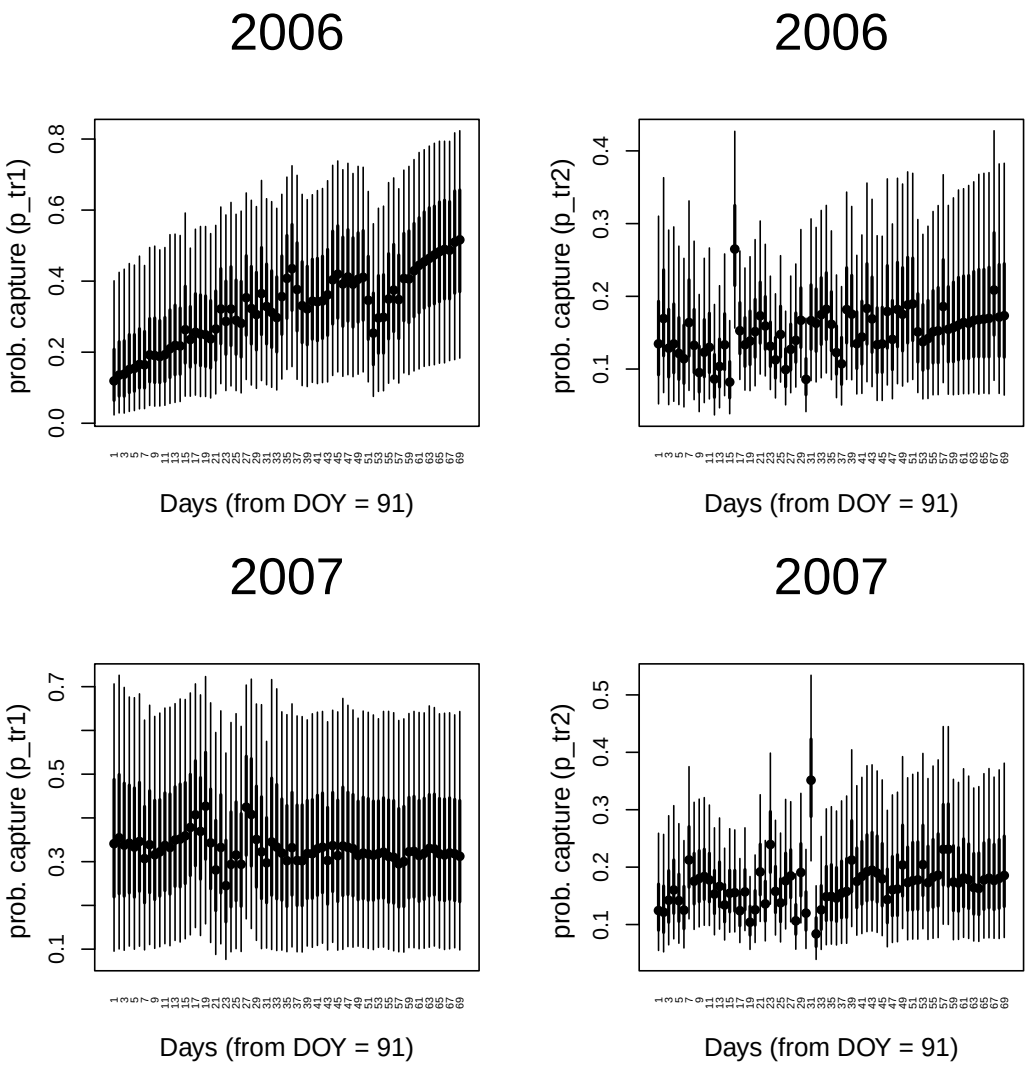
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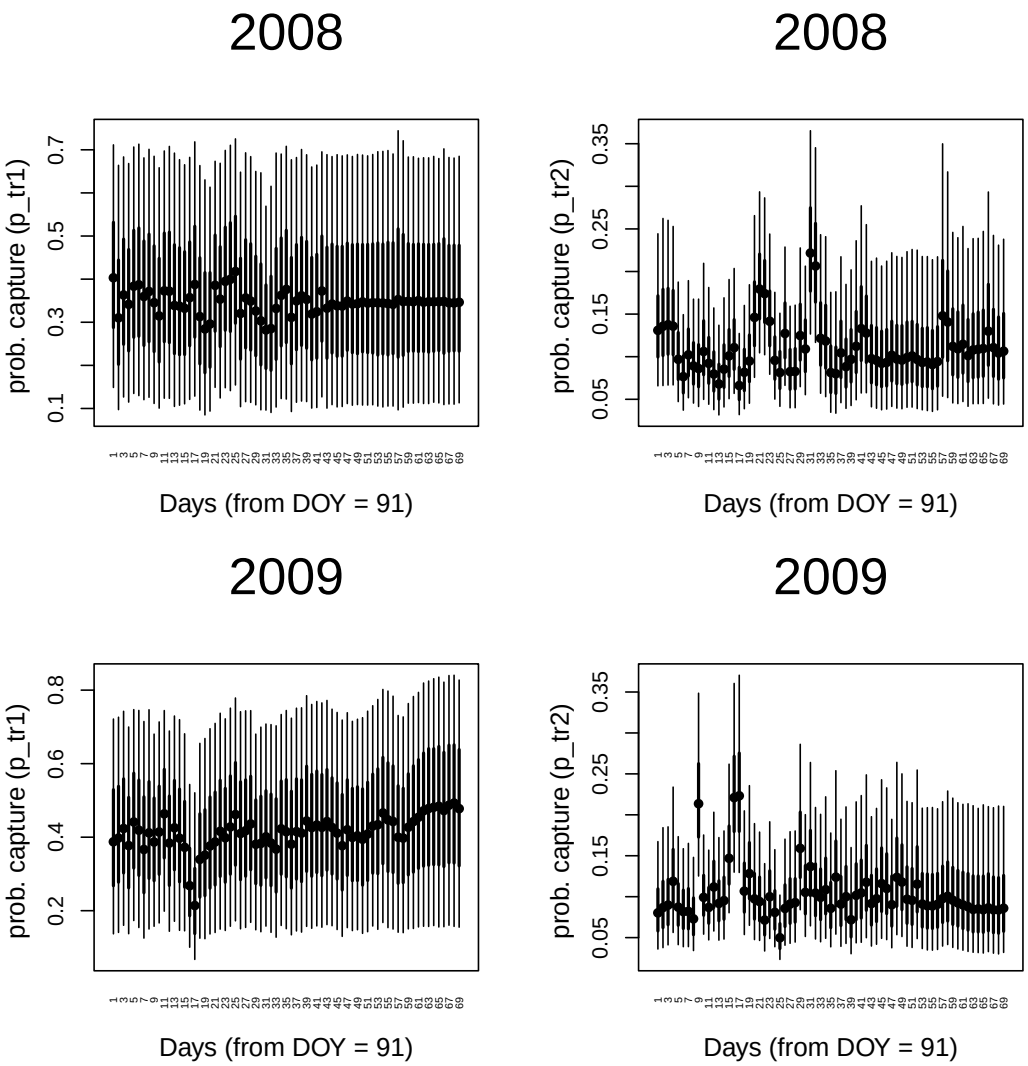
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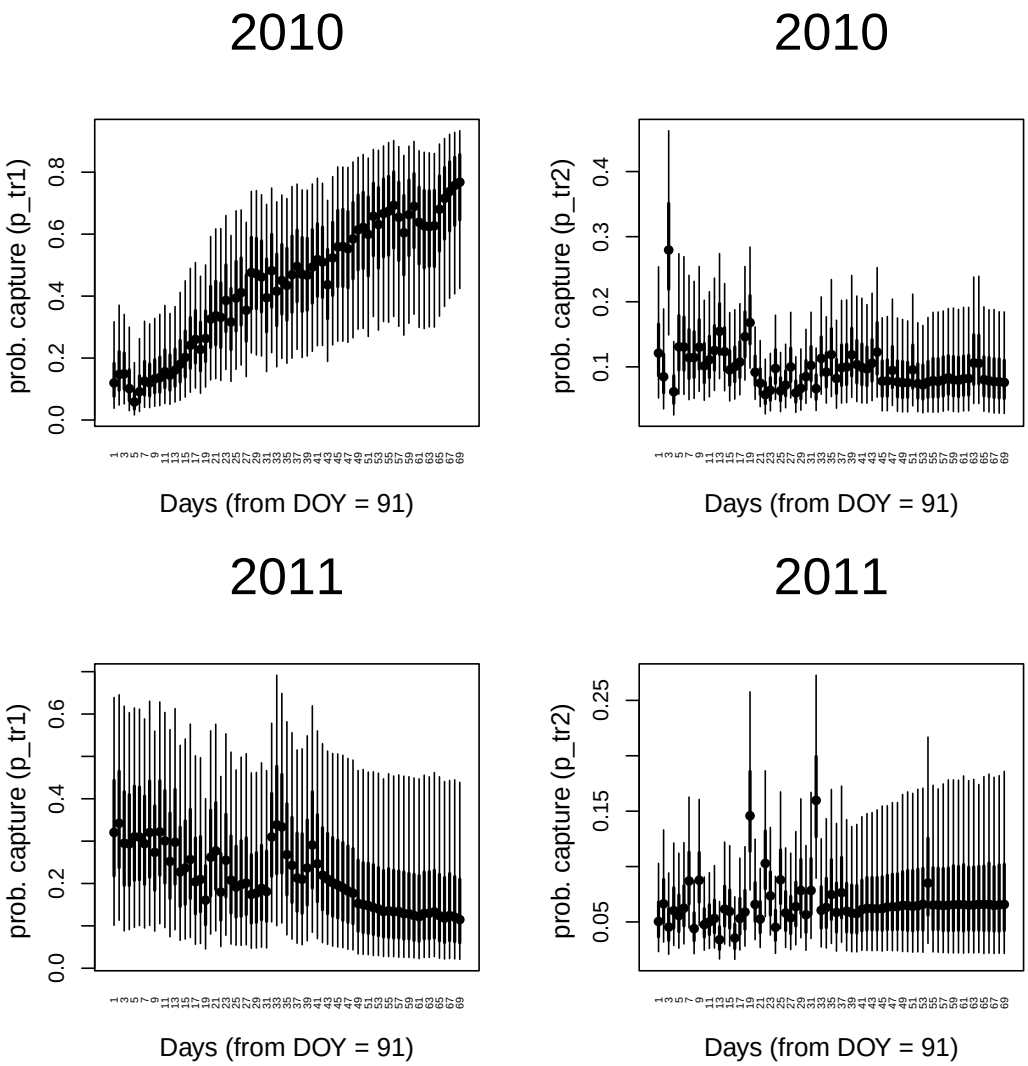
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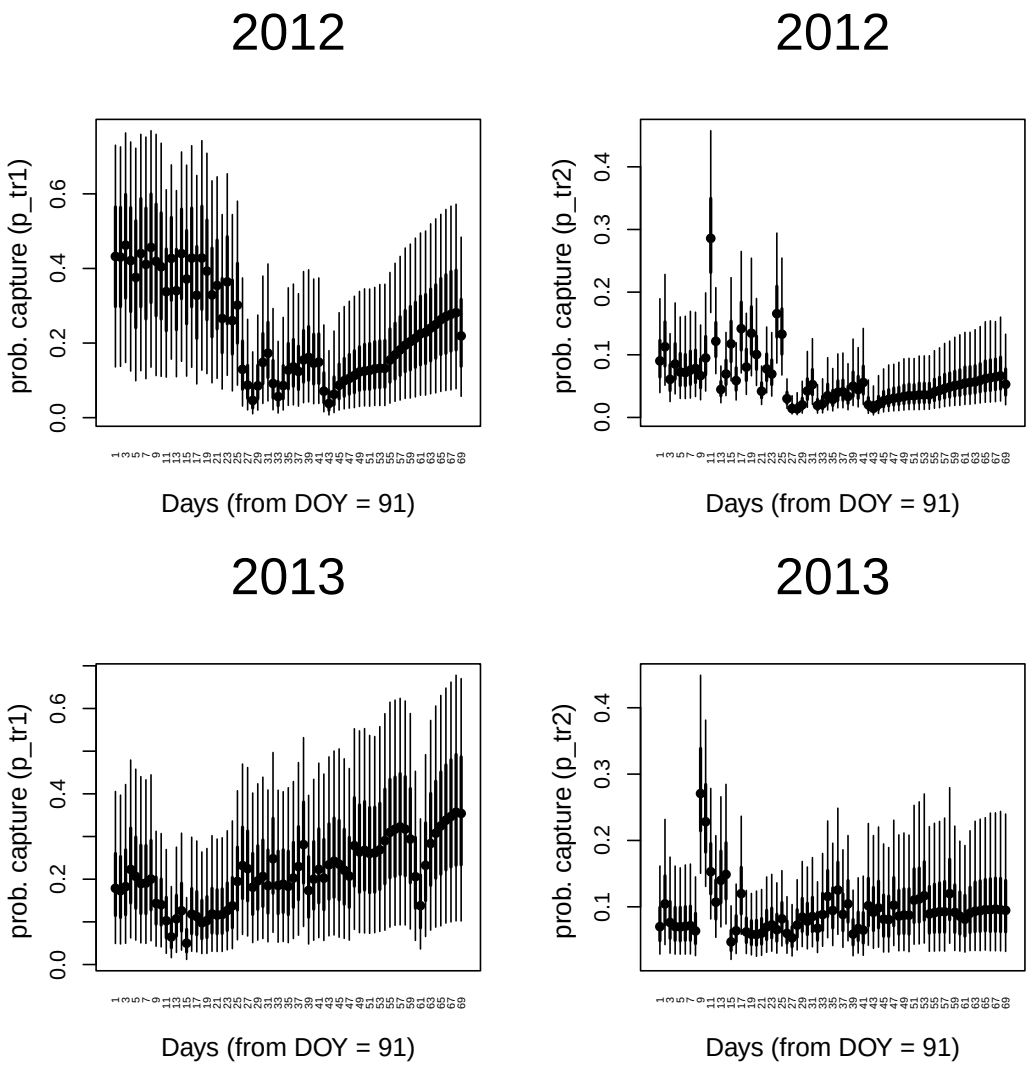
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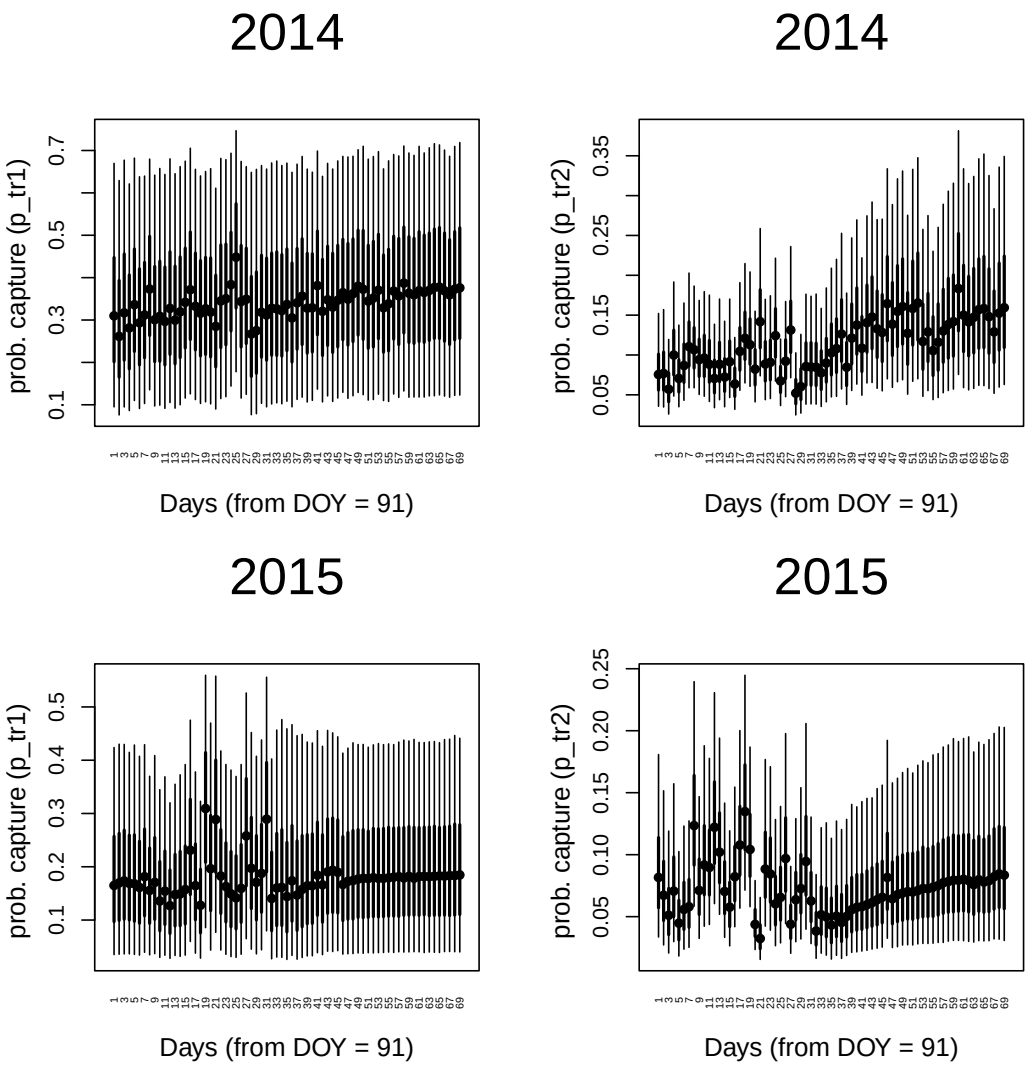
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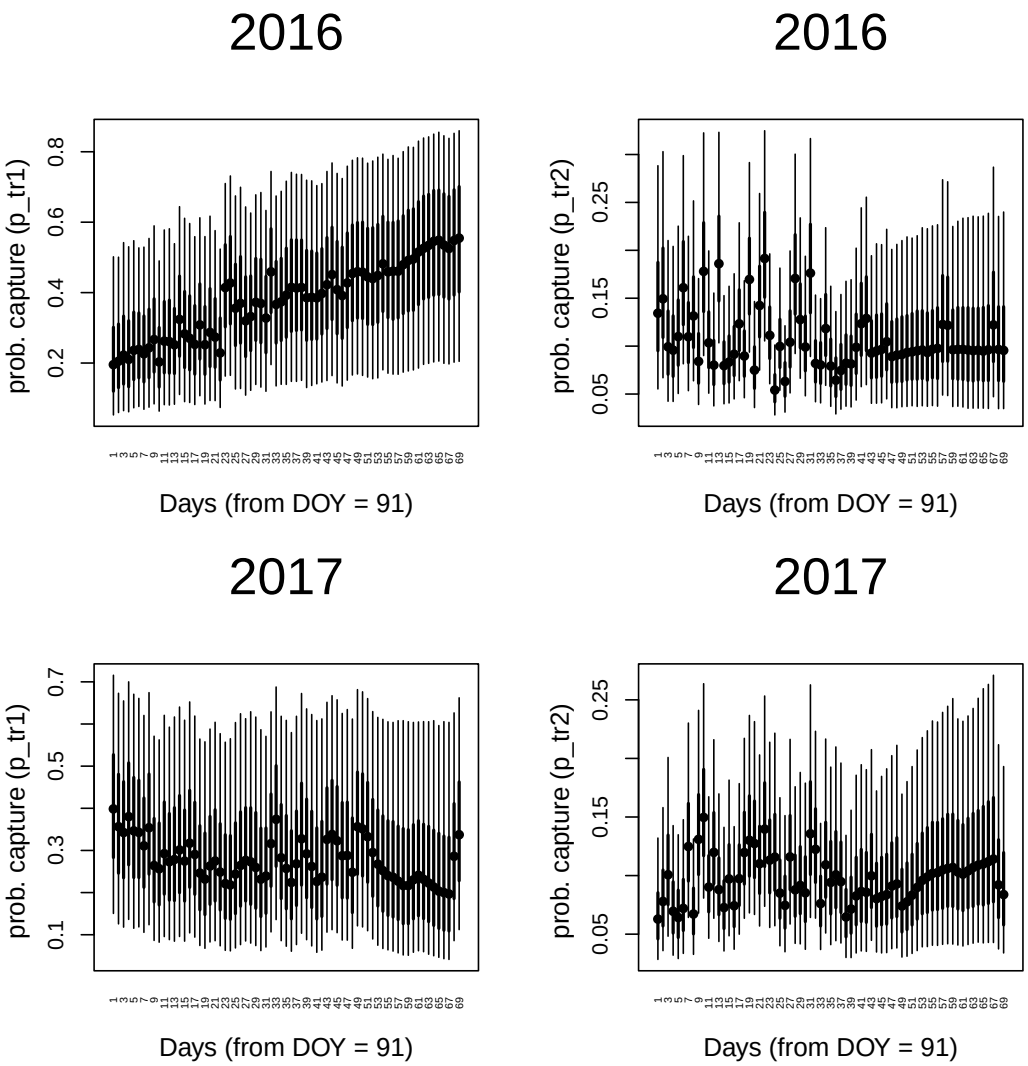
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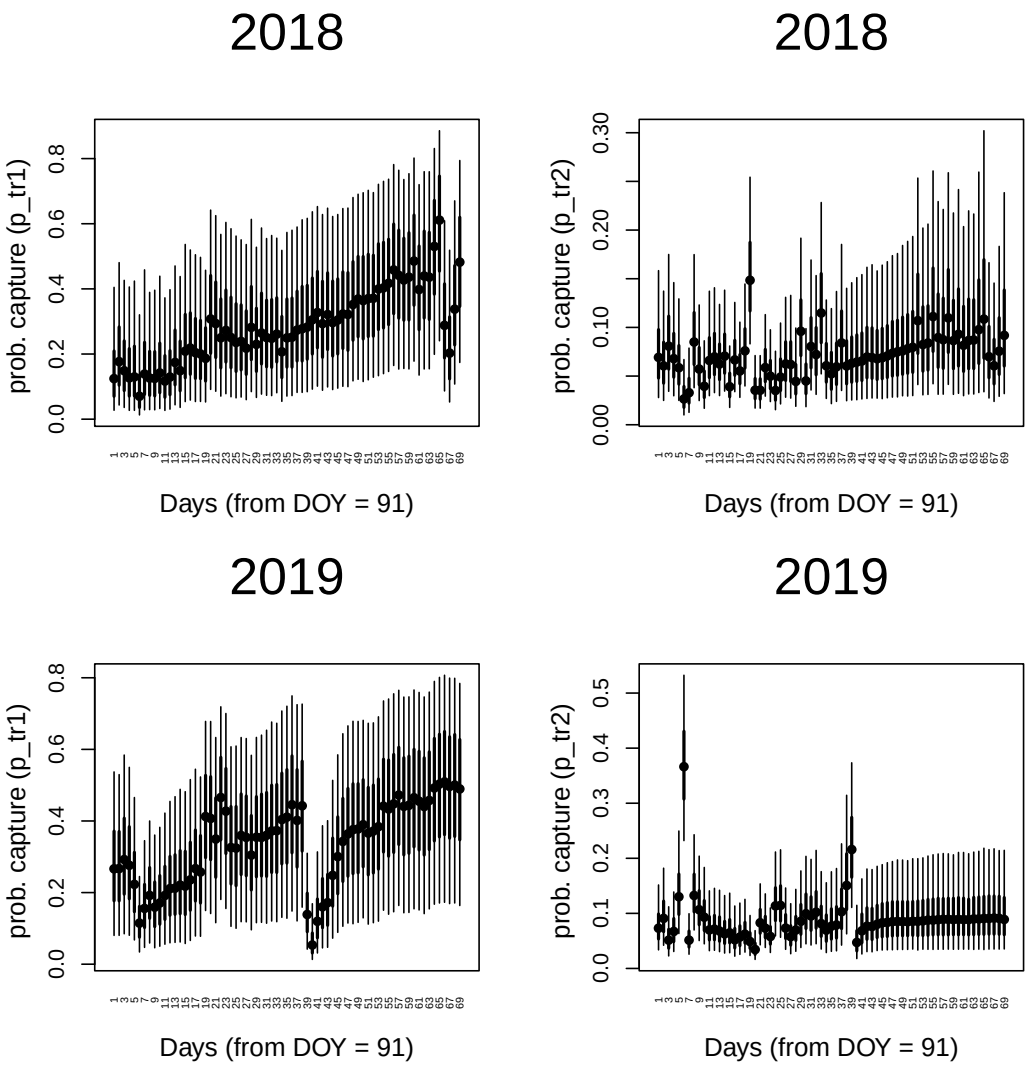
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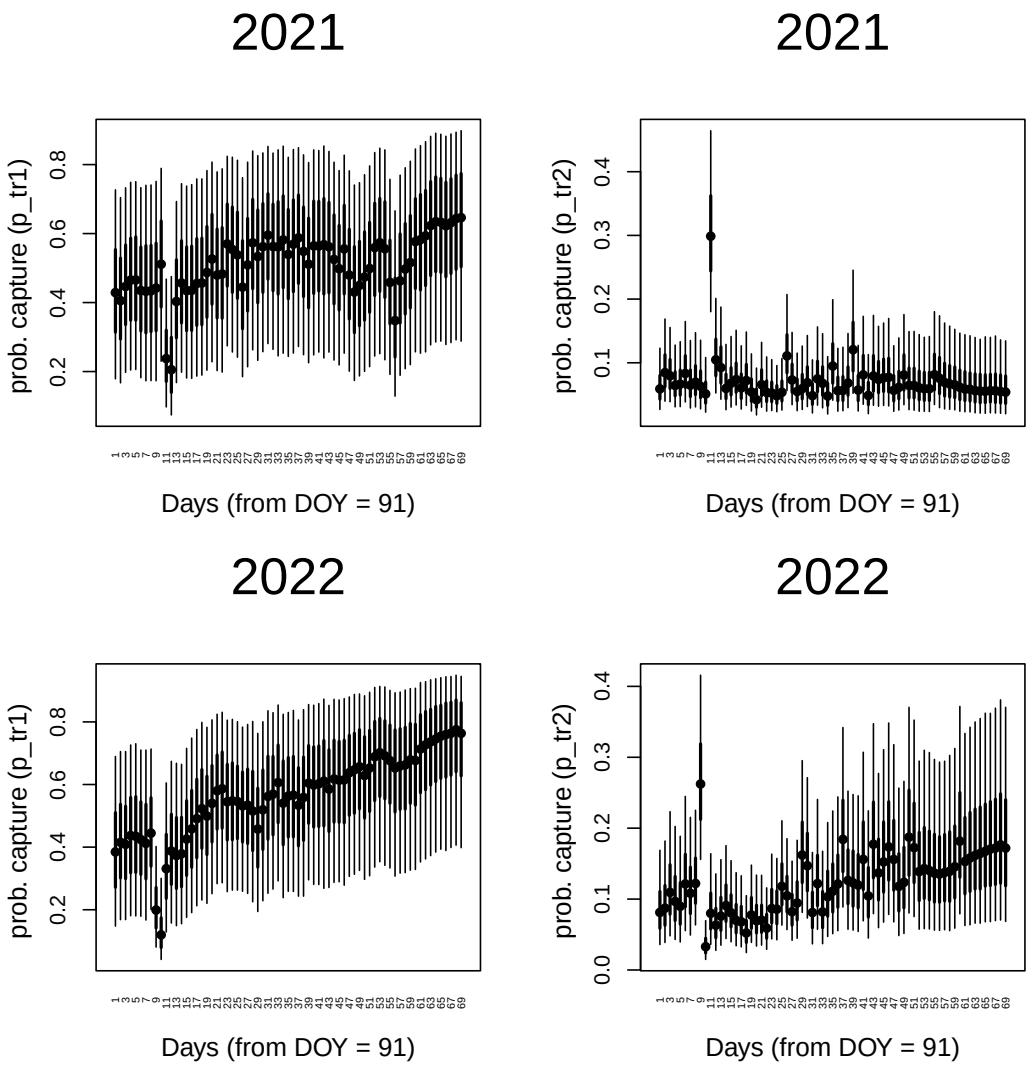
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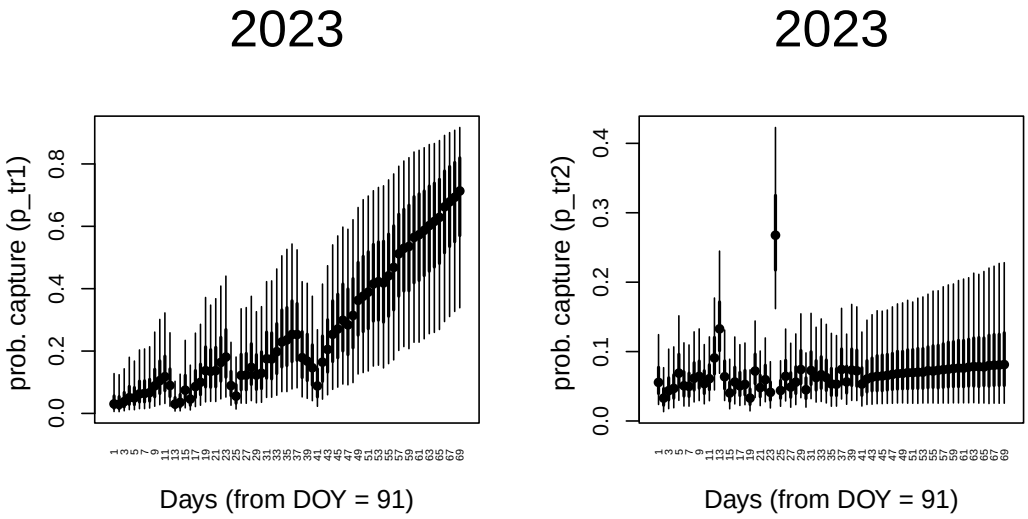
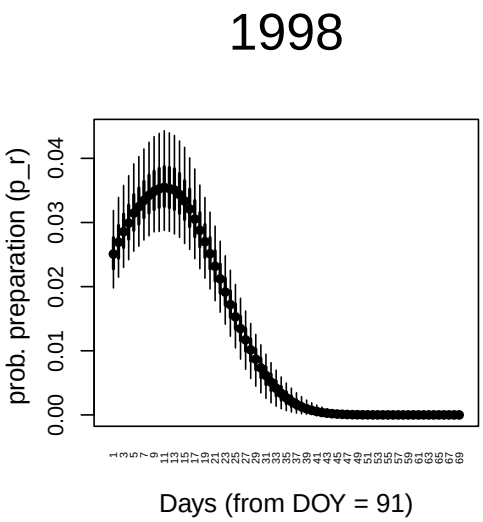


Figure 3.S1 – **Posterior distributions of the trapping efficiency (p_{tr1} and p_{tr2}) for each years.** The plain dot represents the median, the thick line the 50% interval and the thin line the 90% interval.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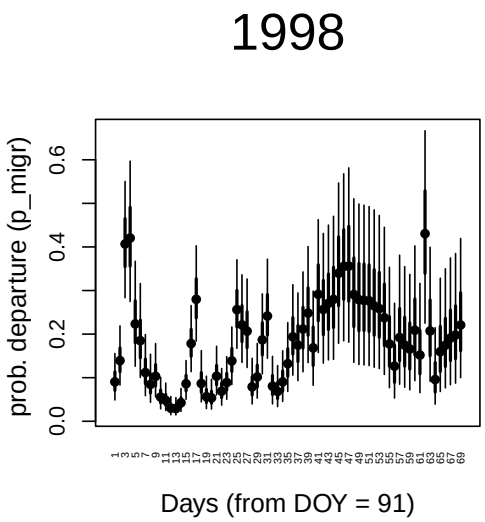
0.00
0.01
0.02
0.03
0.04
Days (from DOY = 91)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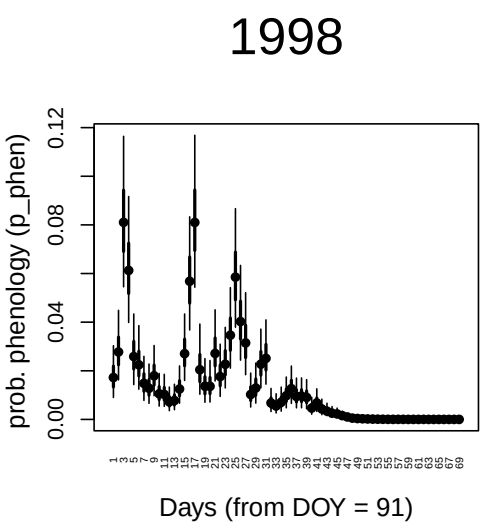
0.4
0.6
Days (from DOY = 91)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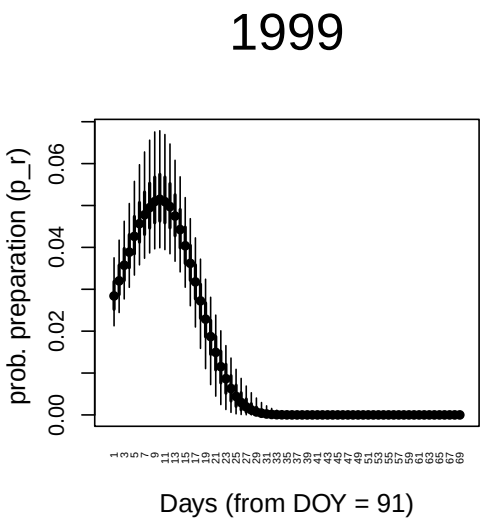
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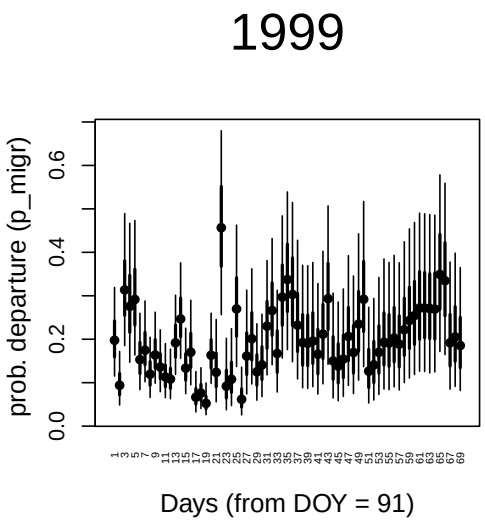
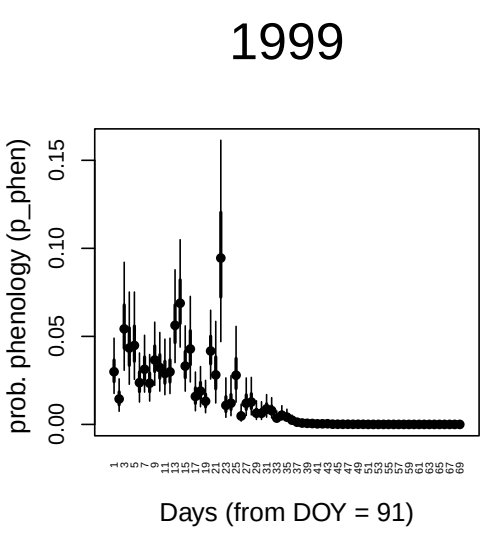
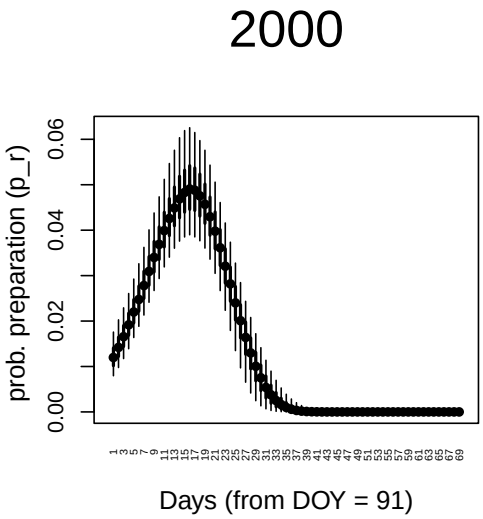
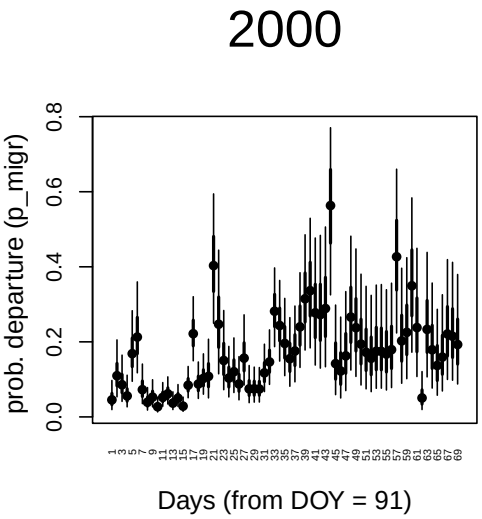
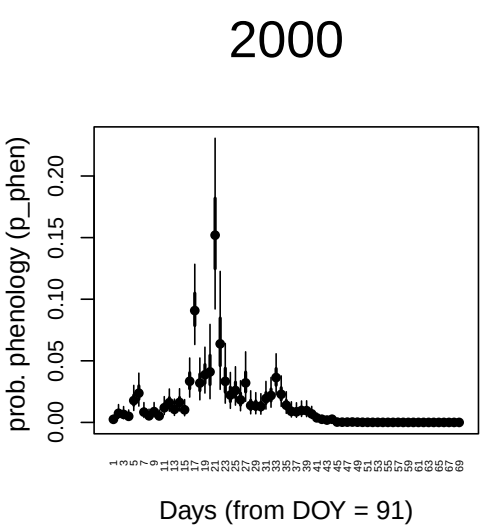
0.00
0.02
0.04
0.06
Days (from DOY = 91)

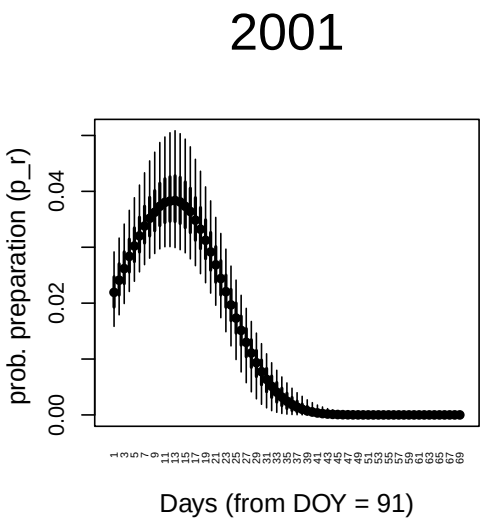

1999
prob. departure (p_migr)
0.0
0.2
0.4
0.6
Days (from DOY = 91)

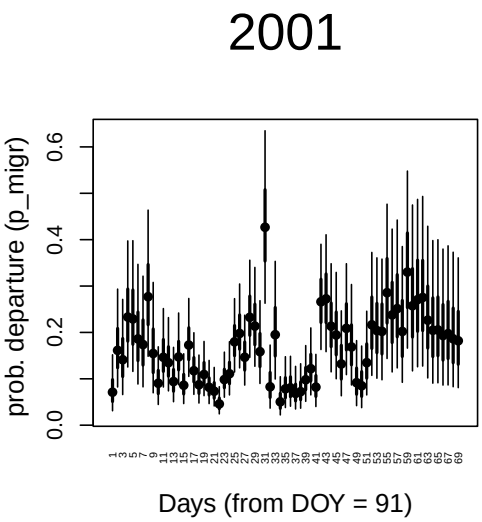

1999
prob. phenology (p_phen)
0.00
0.05
0.10
0.15
Days (from DOY = 91)

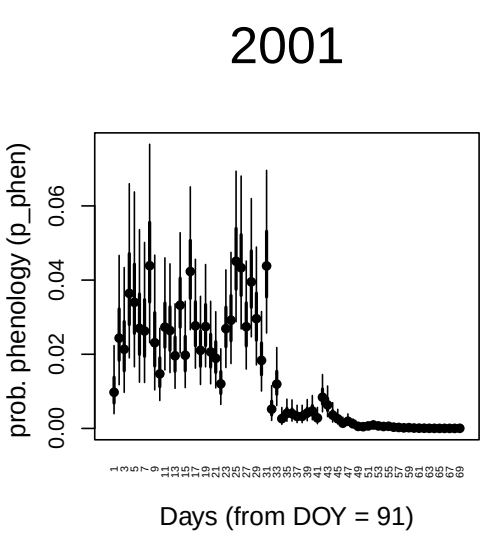

2000
prob. preparation (p_r)
0.00
0.02
0.04
0.06
Days (from DOY = 91)

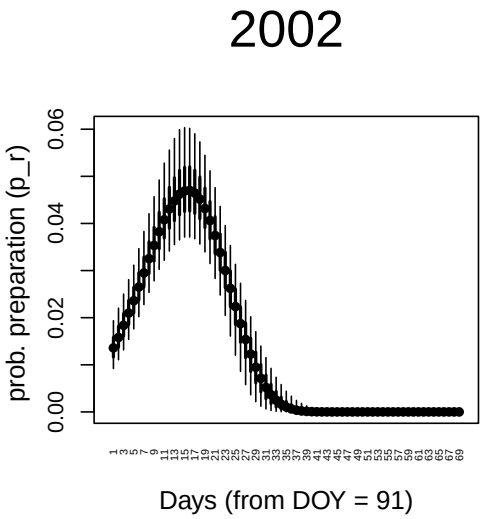

2000
prob. departure (p_migr)
0.0
0.2
0.4
0.6
0.8
Days (from DOY = 91)

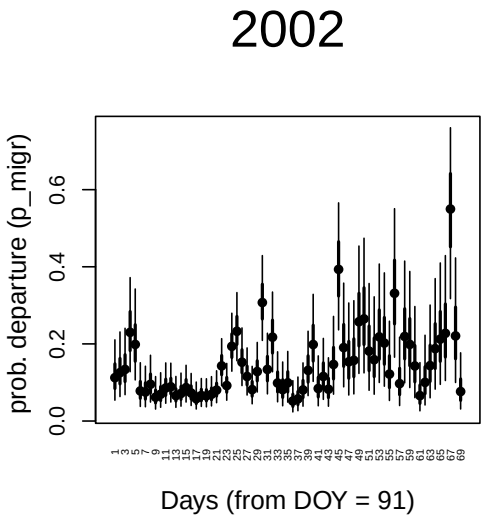

2000
prob. phenology (p_phen)
0.00
0.05
0.10
0.15
0.20
Days (from DOY = 91)

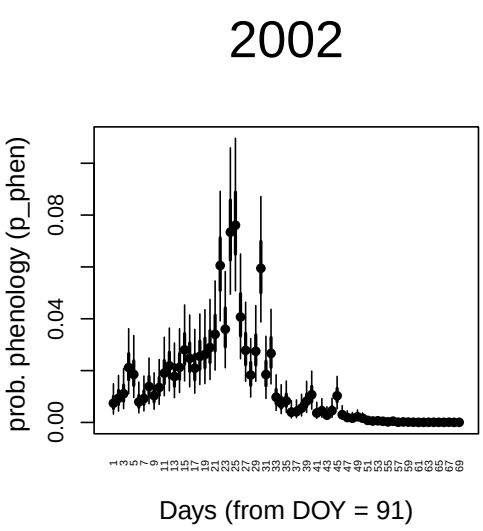

2001
prob. preparation (p_r)
0.00
0.02
0.04
Days (from DOY = 91)

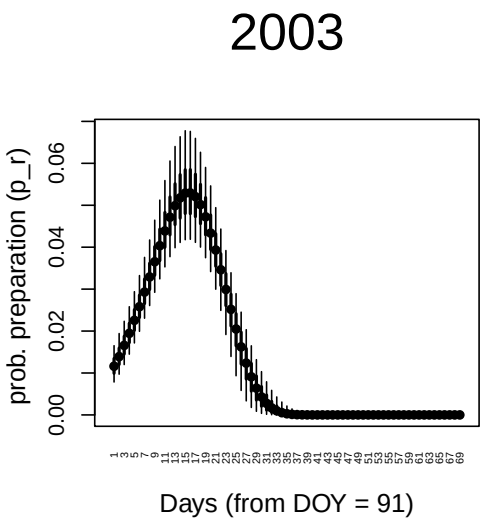

2001
prob. departure (p_migr)
0.0
0.2
0.4
0.6
Days (from DOY = 91)

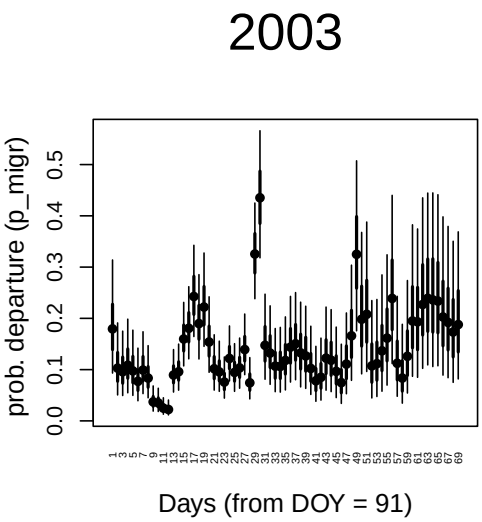

2001
prob. phenology (p_phen)
0.00
0.02
0.04
0.06
Days (from DOY = 91)

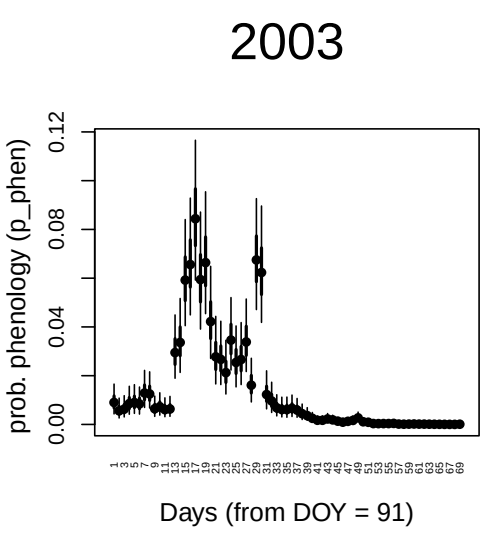

2002
prob. preparation (p_r)
0.00
0.02
0.04
0.06
Days (from DOY = 91)

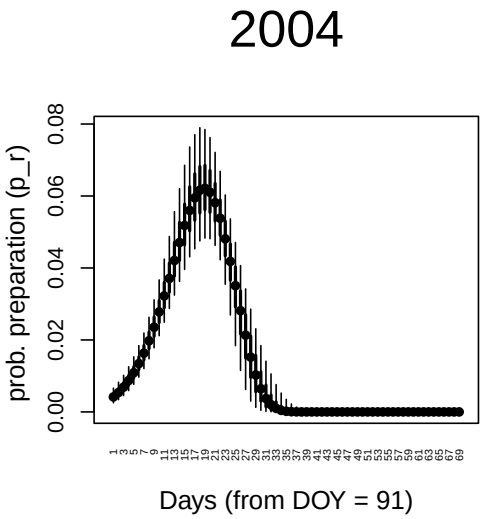

2002
prob. departure (p_migr)
0.0
0.2
0.4
0.6
Days (from DOY = 91)

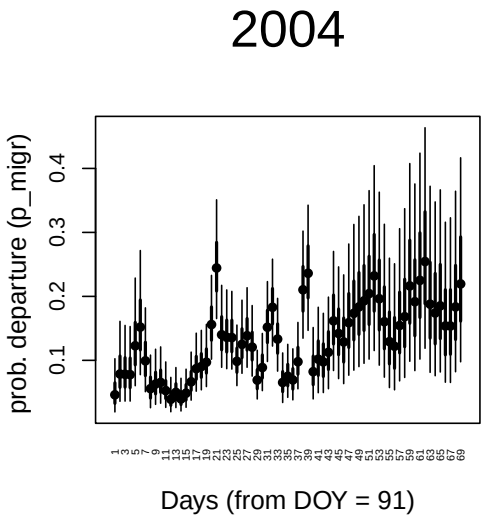

2002
prob. phenology (p_phen)
0.00
0.04
0.08
Days (from DOY = 91)

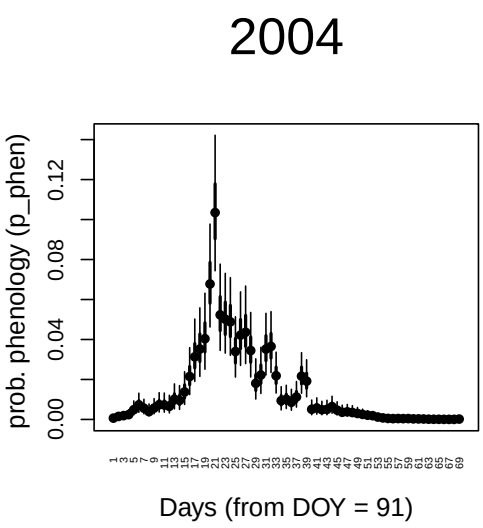

2003
prob. preparation (p_r)
0.00
0.02
0.04
0.06
Days (from DOY = 91)

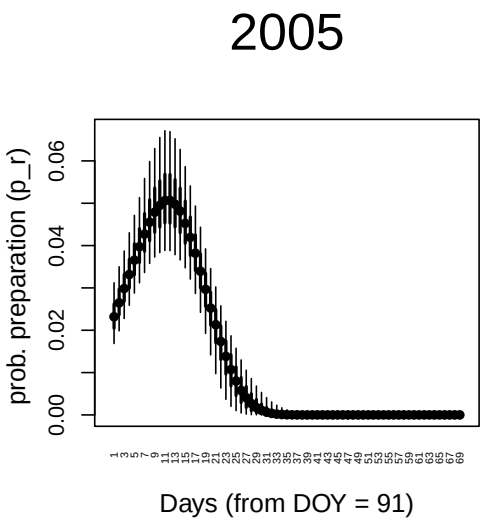

2003
prob. departure (p_migr)
0.0
0.1
0.2
0.3
0.4
0.5
Days (from DOY = 91)

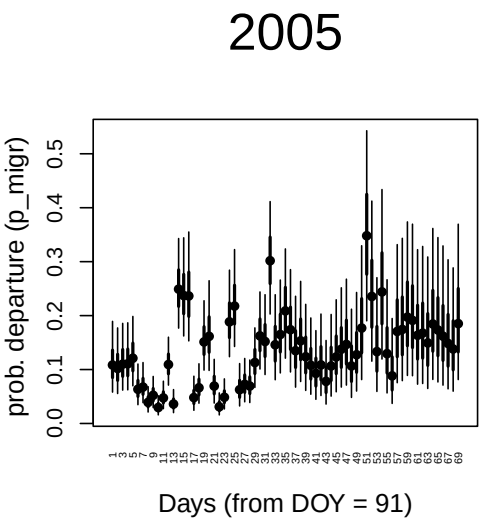

2003
prob. phenology (p_phen)
0.00
0.04
0.08
0.12
Days (from DOY = 91)

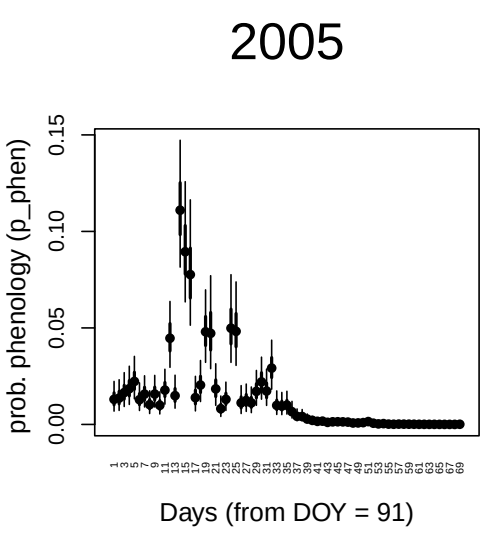

2004
prob. preparation (p_r)
0.00
0.02
0.04
0.06
0.08
Days (from DOY = 91)

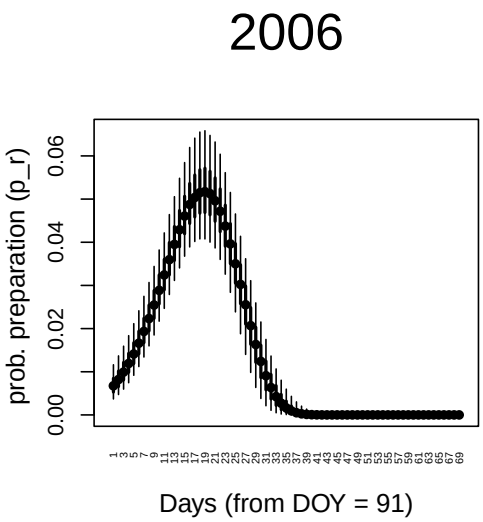

2004
prob. departure (p_migr)
0.1
0.2
0.3
0.4
Days (from DOY = 91)

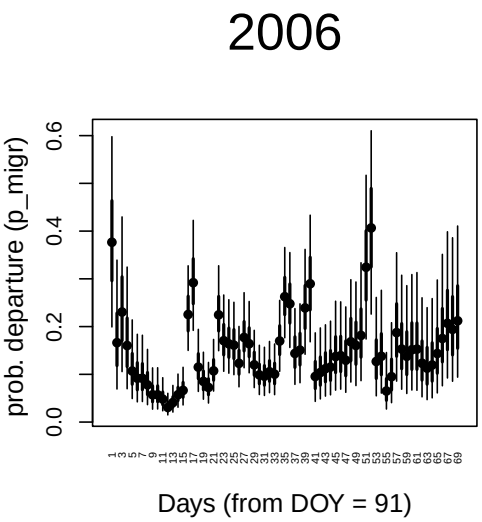

2004
prob. phenology (p_phen)
0.00
0.04
0.08
0.12
Days (from DOY = 91)

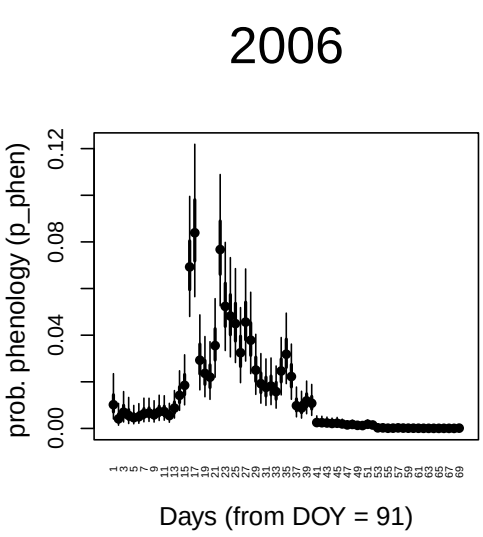

2005
prob. preparation (p_r)
0.00
0.02
0.04
0.06
Days (from DOY = 91)

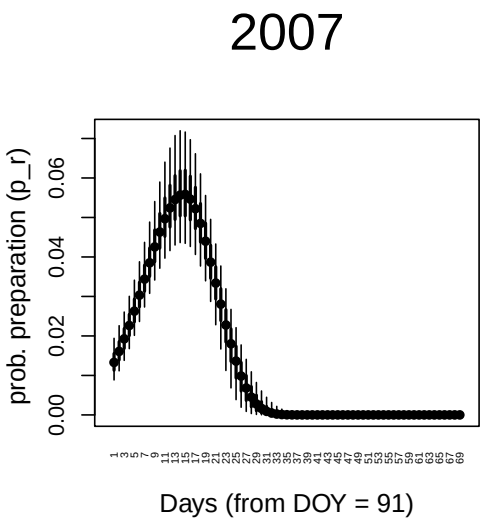

2005
prob. departure (p_migr)
0.0
0.1
0.2
0.3
0.4
0.5
Days (from DOY = 91)

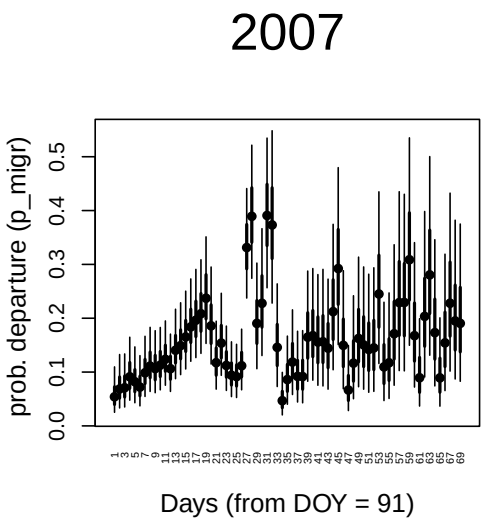

2005
prob. phenology (p_phen)
0.00
0.05
0.10
0.15
Days (from DOY = 91)

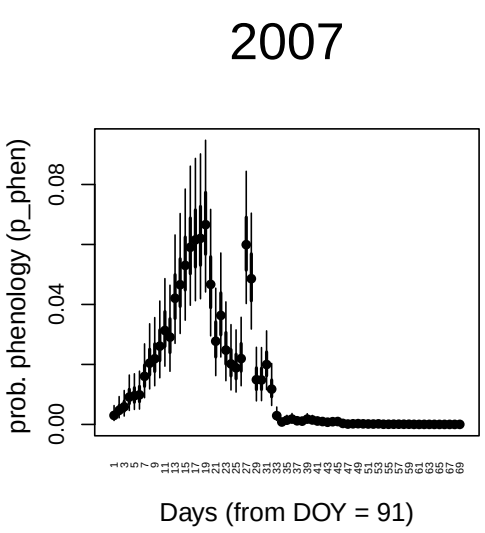

2006
prob. preparation (p_r)
0.00
0.02
0.04
0.06
Days (from DOY = 91)

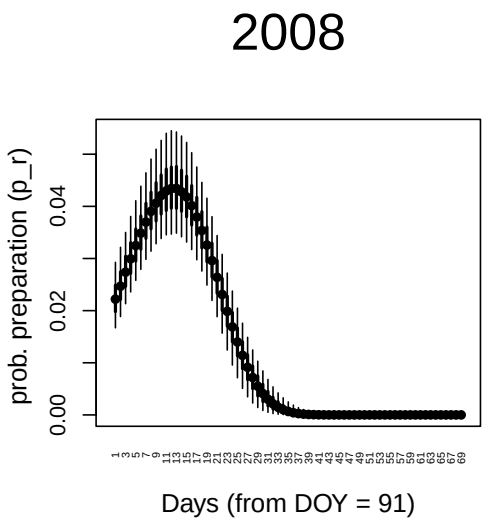

2006
prob. departure (p_migr)
0.0
0.2
0.4
0.6
Days (from DOY = 91)

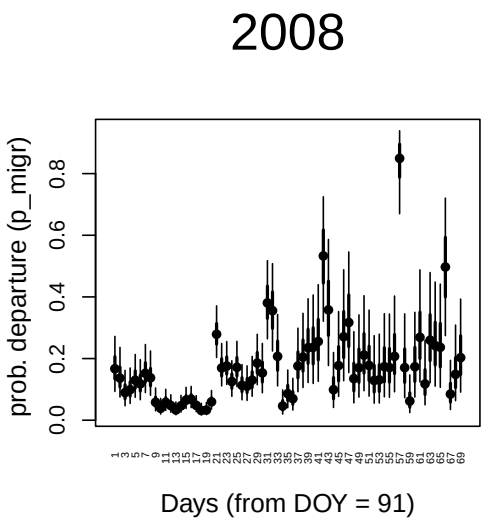

2006
prob. phenology (p_phen)
0.00
0.04
0.08
0.12
Days (from DOY = 91)

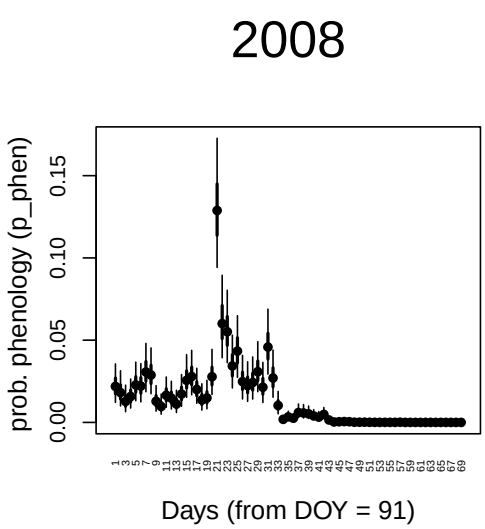

2007
prob. preparation (p_r)
0.00
0.02
0.04
0.06
Days (from DOY = 91)

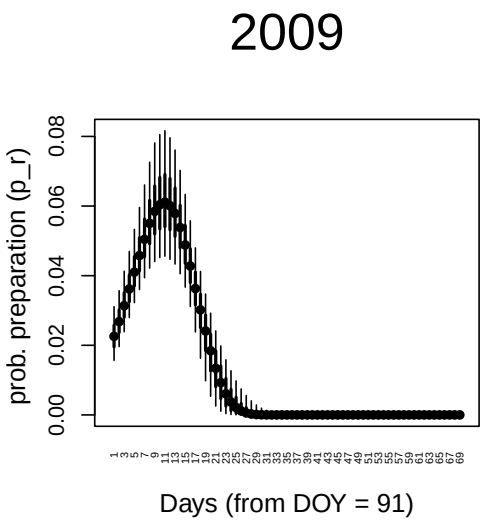

2007
prob. departure (p_migr)
0.0
0.1
0.2
0.3
0.4
0.5
Days (from DOY = 91)

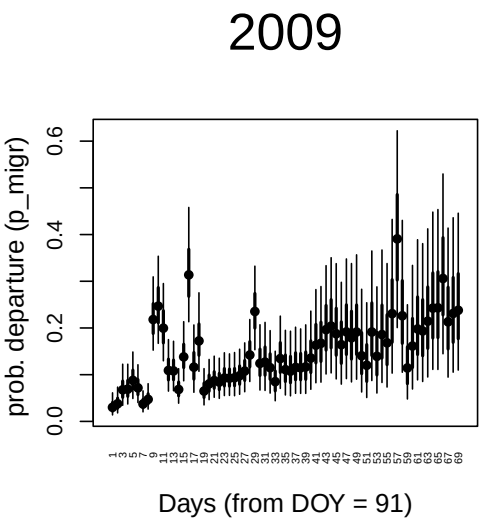

2007
prob. phenology (p_phen)
0.00
0.04
0.08
Days (from DOY = 91)

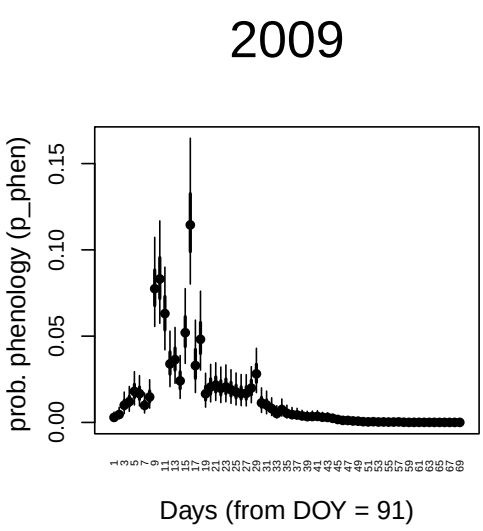

2008
prob. preparation (p_r)
0.00
0.02
0.04
Days (from DOY = 91)


2008
prob. departure (p_migr)
0.0
0.2
0.4
0.6
0.8
Days (from DOY = 91)


2008
prob. phenology (p_phen)
0.00
0.05
0.10
0.15
Days (from DOY = 91)


2009
prob. preparation (p_r)
0.00
0.02
0.04
0.06
0.08
Days (from DOY = 91)


2009
prob. departure (p_migr)
0.0
0.2
0.4
0.6
Days (from DOY = 91)


2009
prob. phenology (p_phen)
0.00
0.05
0.10
0.15
Days (from DOY = 91)

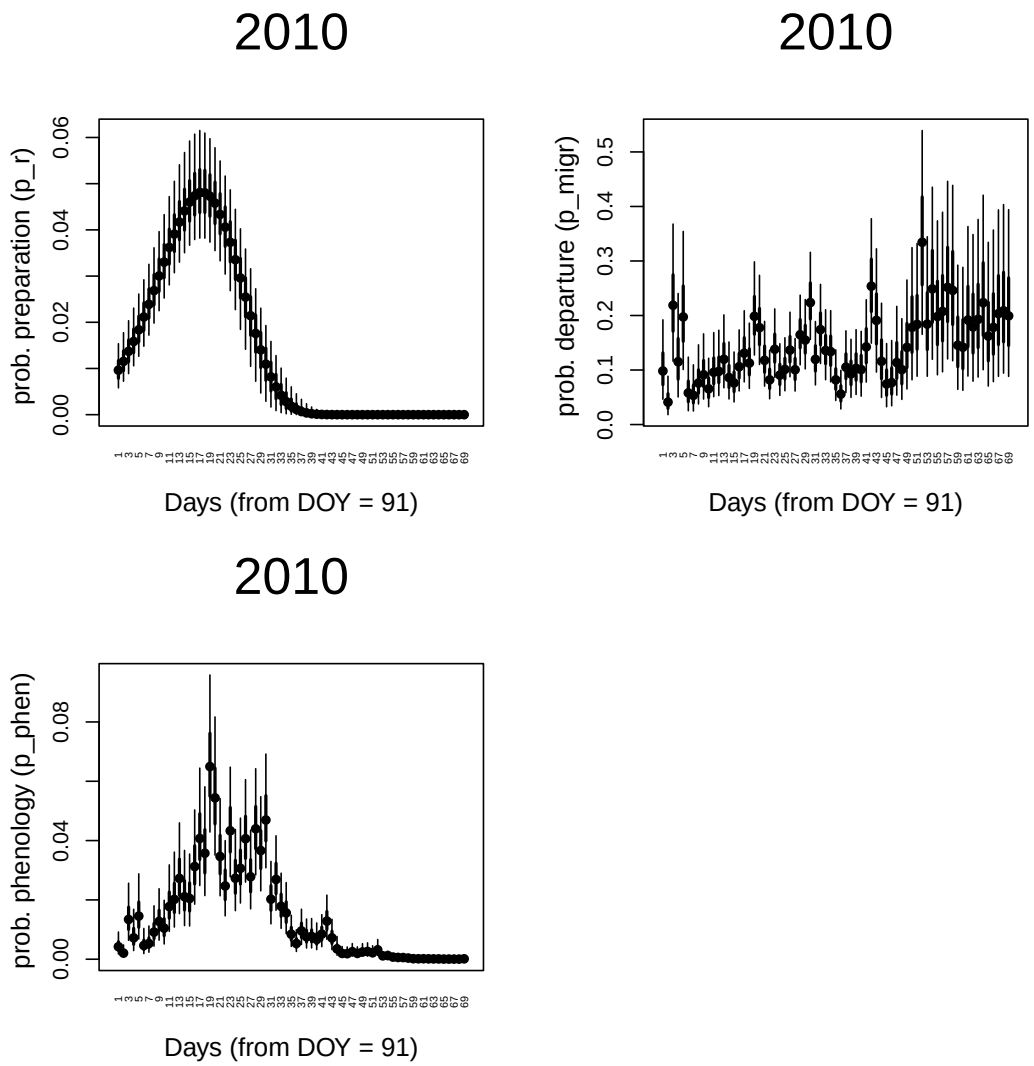
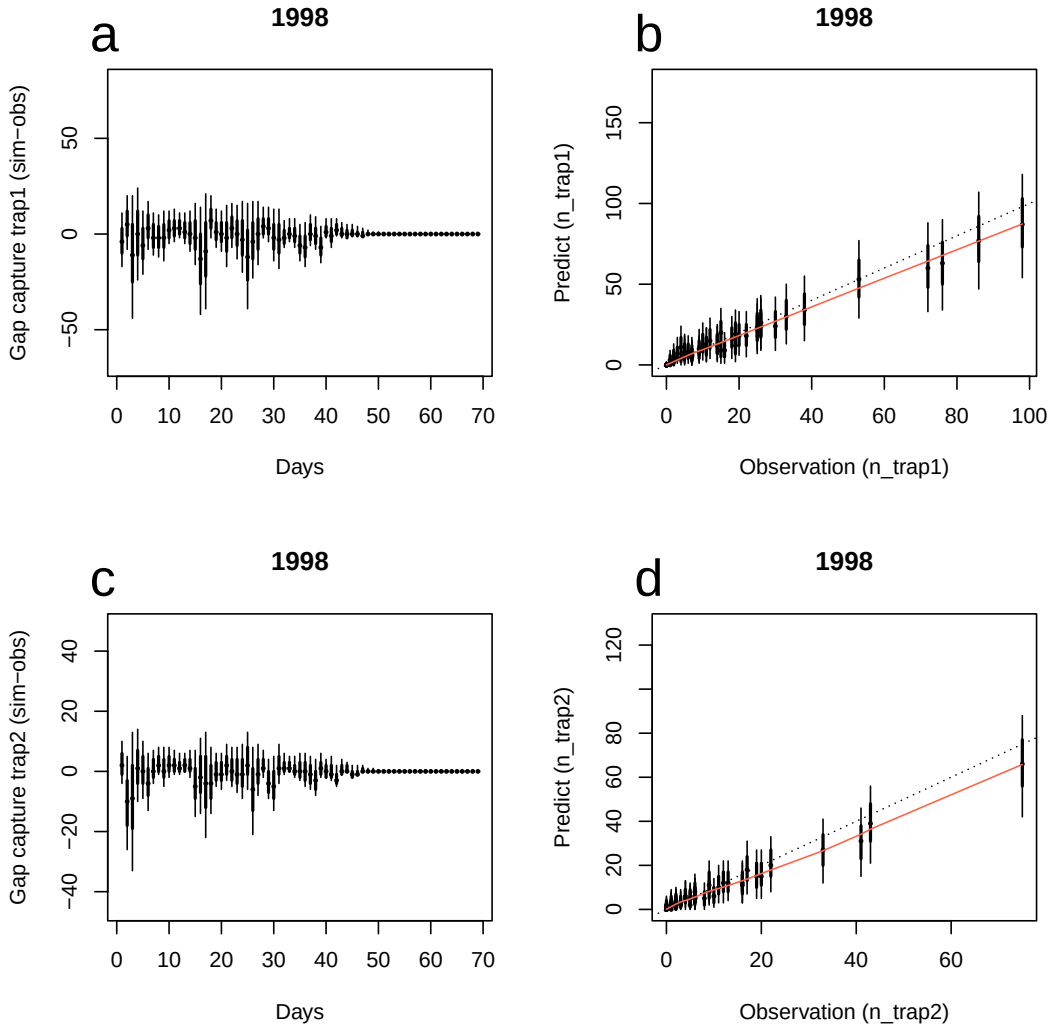
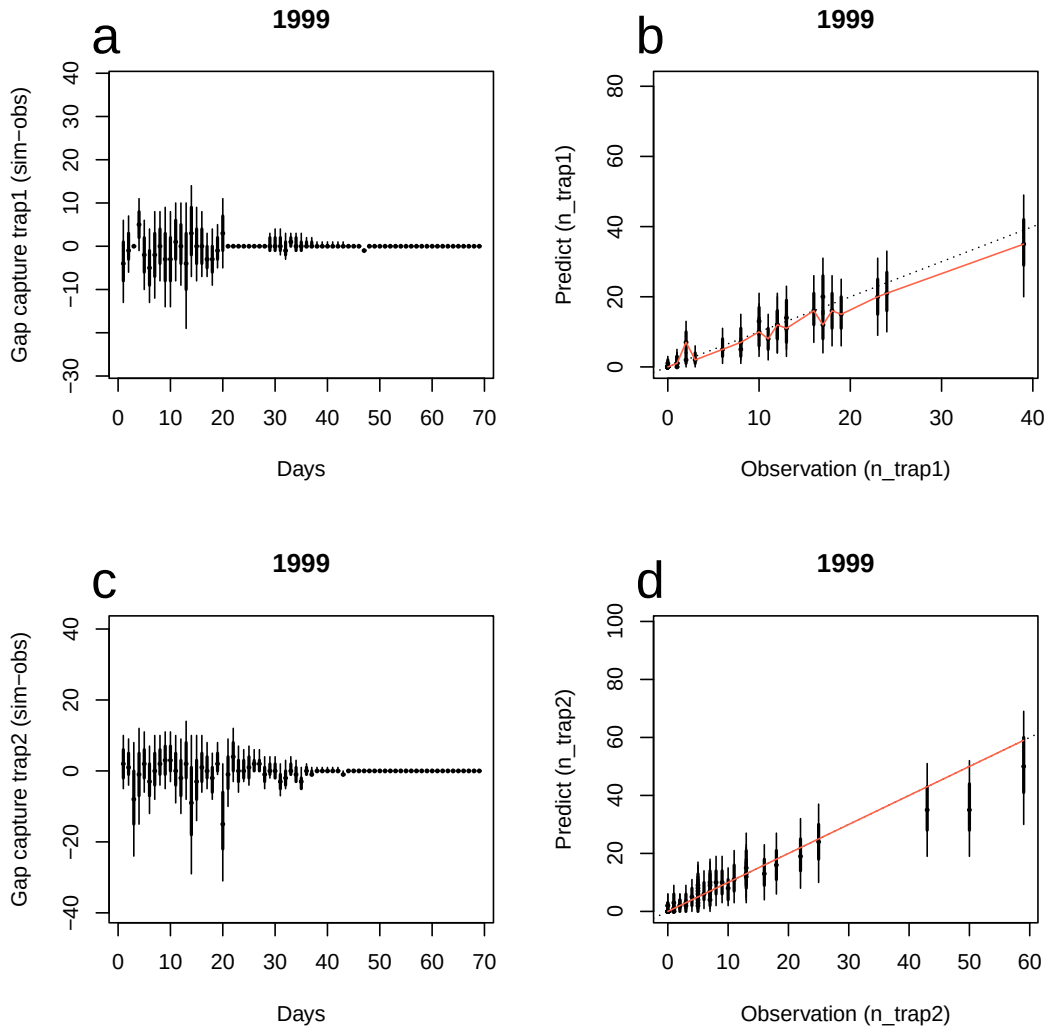
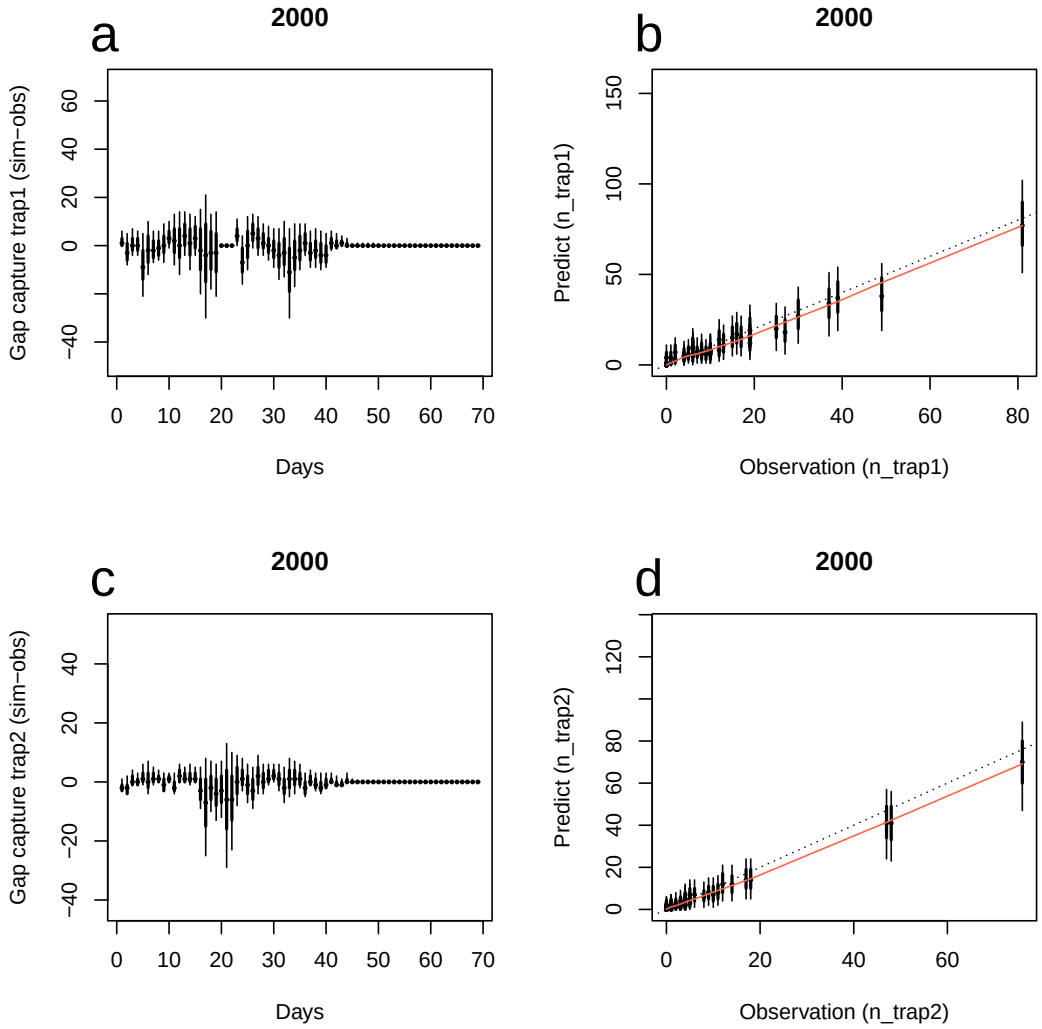
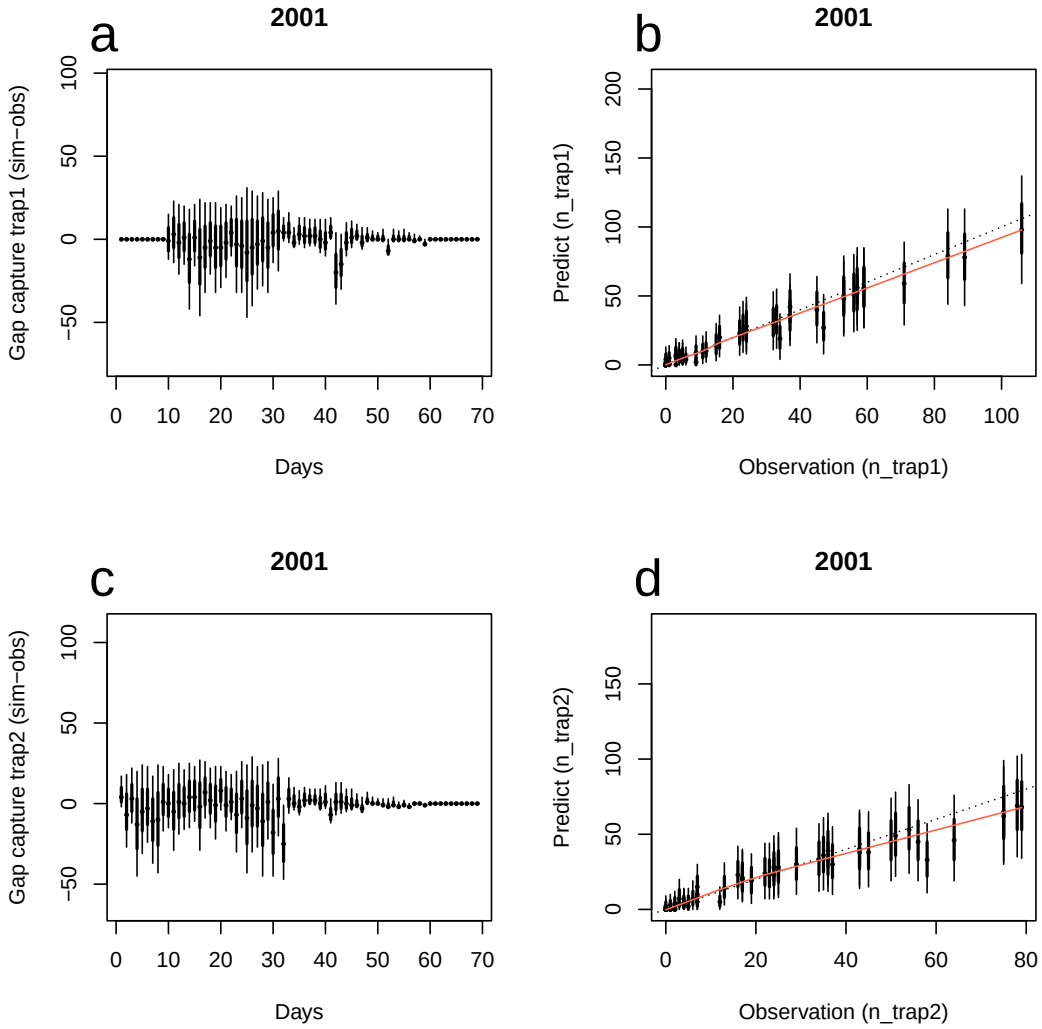


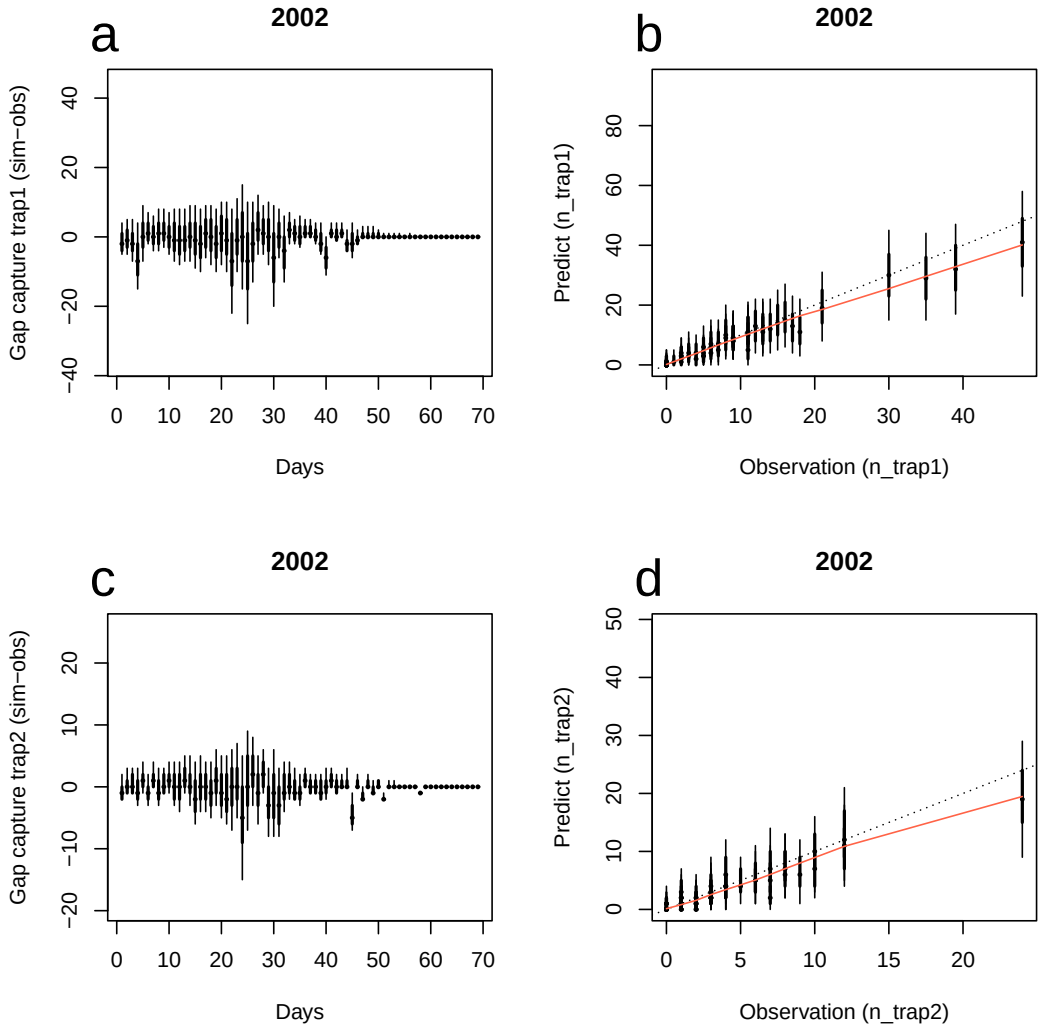
Figure 3.S2 – Posterior distributions of the preparation, migration, and phenological process (p_r, p_{migr} and p_{phen}) for each years. The plain dot represents the median, the thick line the 50% interval and the thin line the 90% interval.

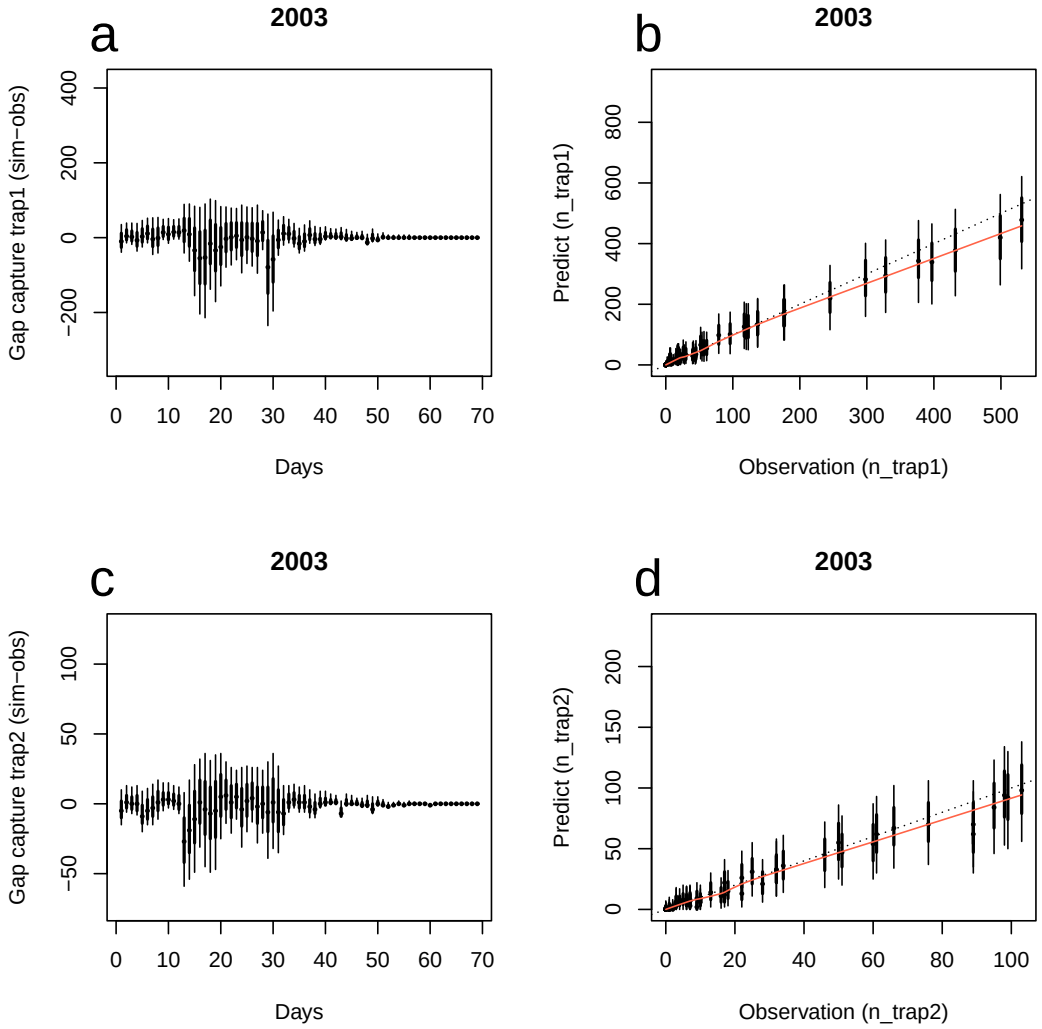

a
1998
Gap capture trap1 (sim−obs)
−50
0
50
0
10
20
30
40
50
60
70
Days
b
1998
Predict (n_trap1)
0
50
100
150
0
20
40
60
80
100
Observation (n_trap1)
c
1998
Gap capture trap2 (sim−obs)
−40
−20
0
20
40
0
10
20
30
40
50
60
70
Days
d
1998
Predict (n_trap2)
0
20
40
60
80
120
0
20
40
60
Observation (n_trap2)

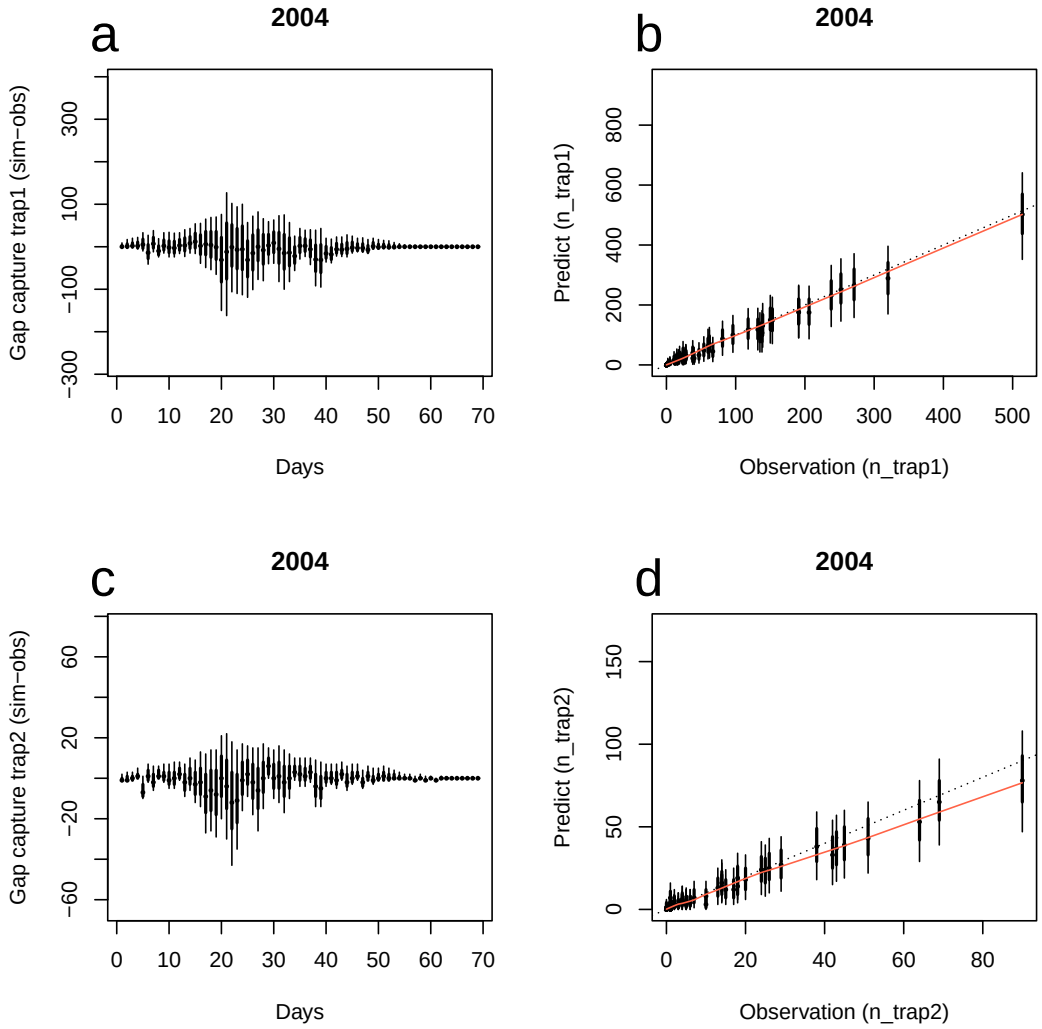

a
1999
Gap capture trap1 (sim−obs)
−30
−10
0
10
20
30
40
0
10
20
30
40
50
60
70
Days
b
1999
Predict (n_trap1)
0
20
40
60
80
0
10
20
30
40
Observation (n_trap1)
c
1999
Gap capture trap2 (sim−obs)
−40
−20
0
20
40
0
10
20
30
40
50
60
70
Days
d
1999
Predict (n_trap2)
0
20
40
60
80
100
0
10
20
30
40
50
60
Observation (n_trap2)

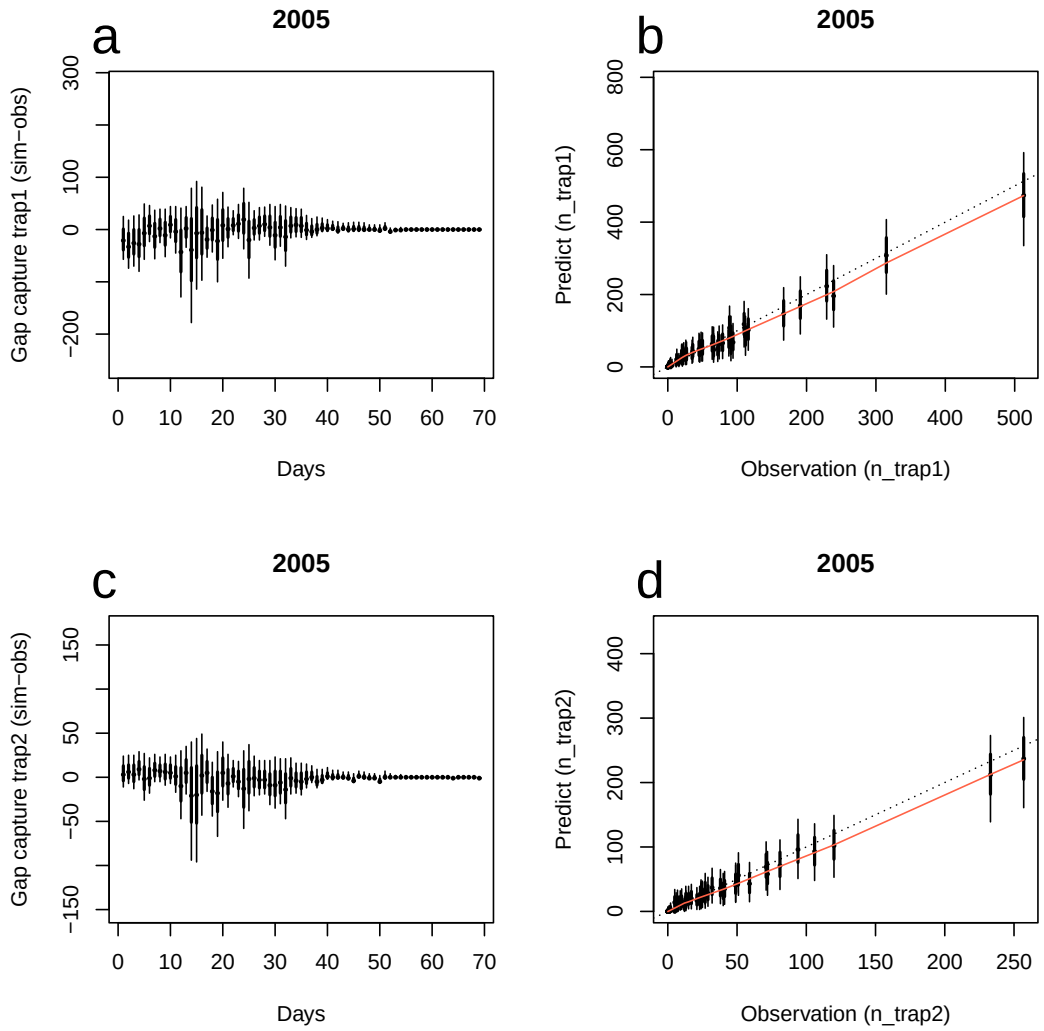

a
2000
Gap capture trap1 (sim−obs)
−40
0
20
40
60
0
10
20
30
40
50
60
70
Days
b
2000
Predict (n_trap1)
0
50
100
150
0
20
40
60
80
Observation (n_trap1)
c
2000
Gap capture trap2 (sim−obs)
−40
−20
0
20
40
0
10
20
30
40
50
60
70
Days
d
2000
Predict (n_trap2)
0
20
40
60
80
120
0
20
40
60
Observation (n_trap2)


a
2001
Gap capture trap1 (sim−obs)
100
50
0
−50
0
10
20
30
40
50
60
70
Days
b
2001
Predict (n_trap1)
200
150
100
50
0
0
20
40
60
80
100
Observation (n_trap1)
c
2001
Gap capture trap2 (sim−obs)
100
50
0
−50
0
10
20
30
40
50
60
70
Days
d
2001
Predict (n_trap2)
150
100
50
0
0
20
40
60
80
Observation (n_trap2)


a
2002
Gap capture trap1 (sim−obs)
−40
−20
0
20
40
0
10
20
30
40
50
60
70
Days
b
2002
Predict (n_trap1)
0
20
40
60
80
0
10
20
30
40
Observation (n_trap1)
c
2002
Gap capture trap2 (sim−obs)
−20
−10
0
10
20
0
10
20
30
40
50
60
70
Days
d
2002
Predict (n_trap2)
0
10
20
30
40
50
0
5
10
15
20
Observation (n_trap2)


a
2003
Gap capture trap1 (sim−obs)
−200
0
200
400
0
10
20
30
40
50
60
70
Days
b
2003
Predict (n_trap1)
0
200
400
600
800
0
100
200
300
400
500
Observation (n_trap1)
c
2003
Gap capture trap2 (sim−obs)
−50
0
50
100
0
10
20
30
40
50
60
70
Days
d
2003
Predict (n_trap2)
0
50
100
150
200
0
20
40
60
80
100
Observation (n_trap2)


a
2004
Gap capture trap1 (sim−obs)
−300
−100
100
300
0
10
20
30
40
50
60
70
Days
b
2004
Predict (n_trap1)
0
200
400
600
800
0
100
200
300
400
500
Observation (n_trap1)
c
2004
Gap capture trap2 (sim−obs)
−60
−20
20
60
0
10
20
30
40
50
60
70
Days
d
2004
Predict (n_trap2)
0
50
100
150
0
20
40
60
80
Observation (n_trap2)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2005
Gap capture trap1 (sim−obs)
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100
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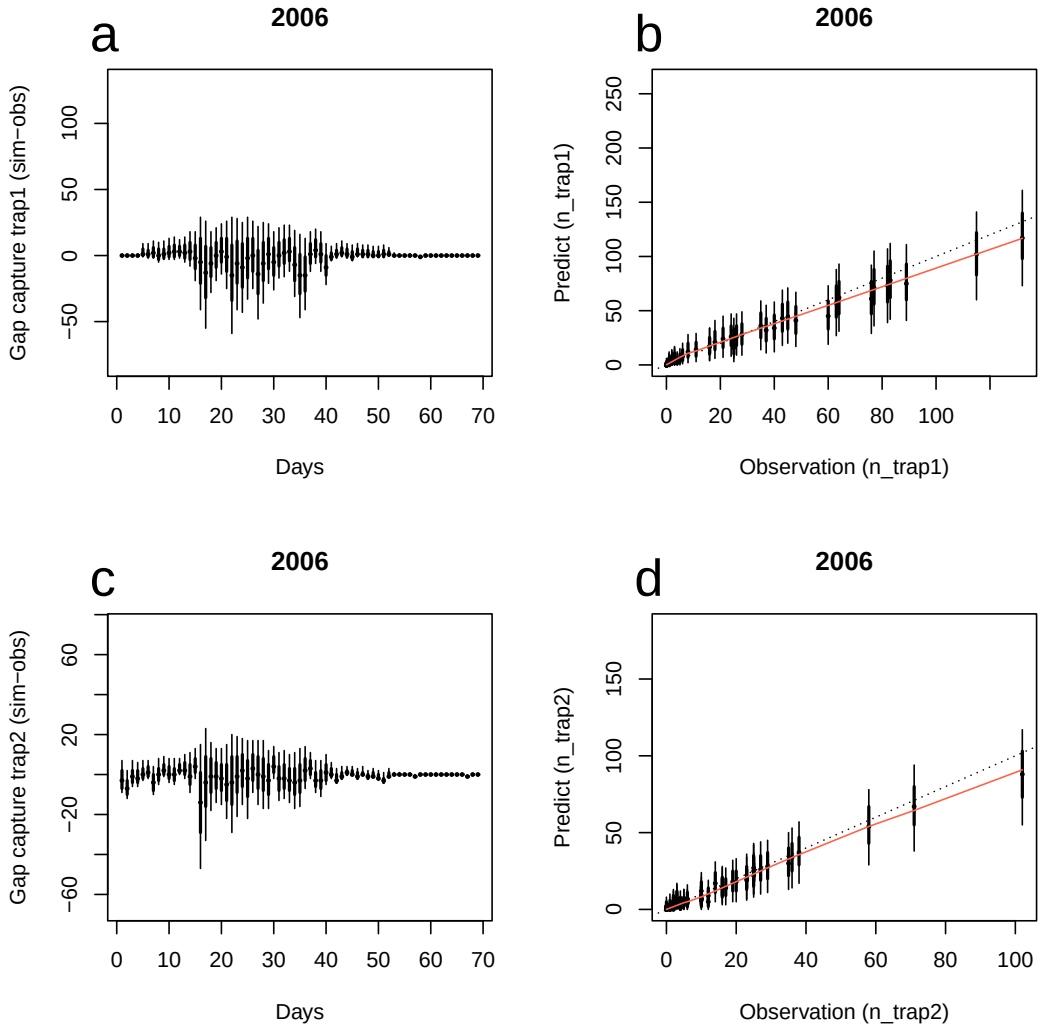
−200
0
10
20
30
40
50
60
70
Days
b
2005
Predict (n_trap1)
800
600
400
200
0
0
100
200
300
400
500
Observation (n_trap1)
c
2005
Gap capture trap2 (sim−obs)
150
50
0
−50
−150
0
10
20
30
40
50
60
70
Days
d
2005
Predict (n_trap2)
400
300
200
100
0
0
50
100
150
200
250
Observation (n_trap2)


a
2006
Gap capture trap1 (sim−obs)
−50
0
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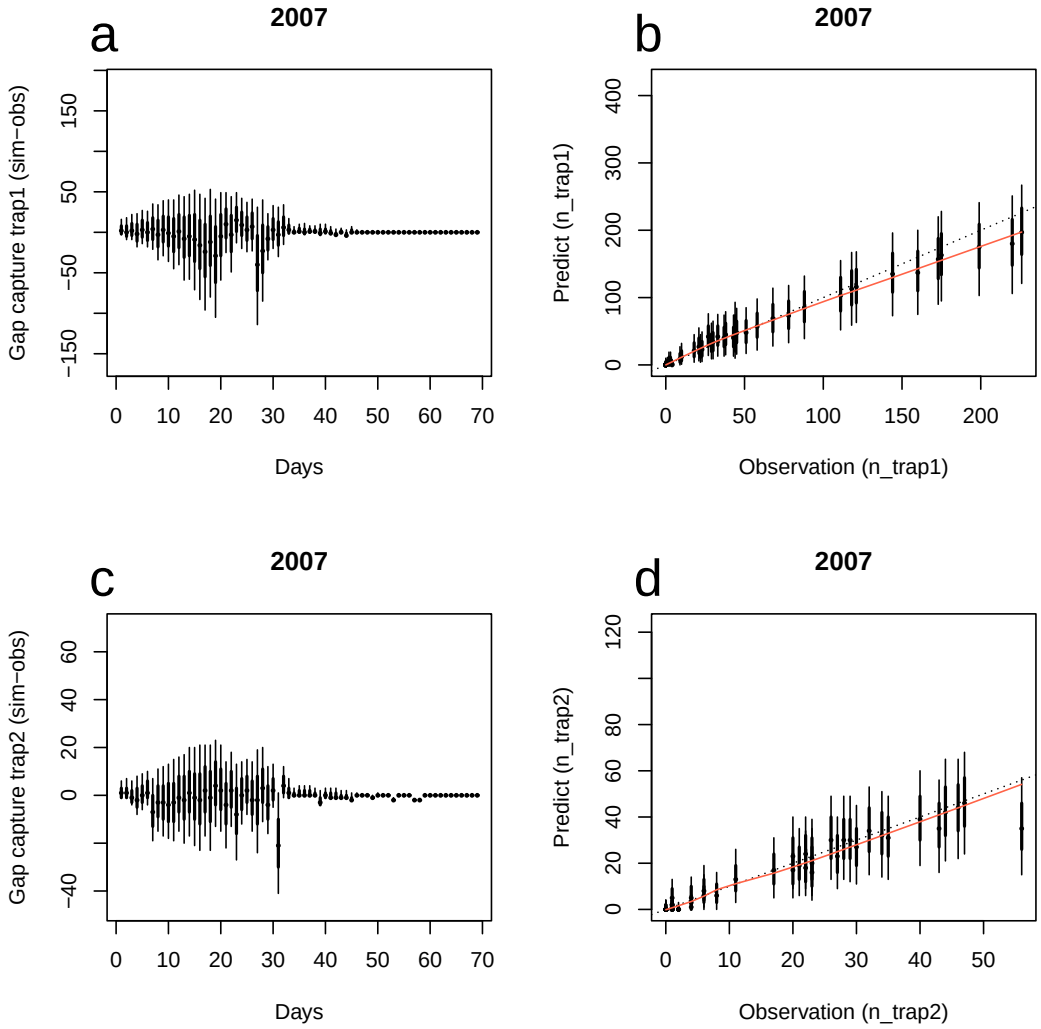
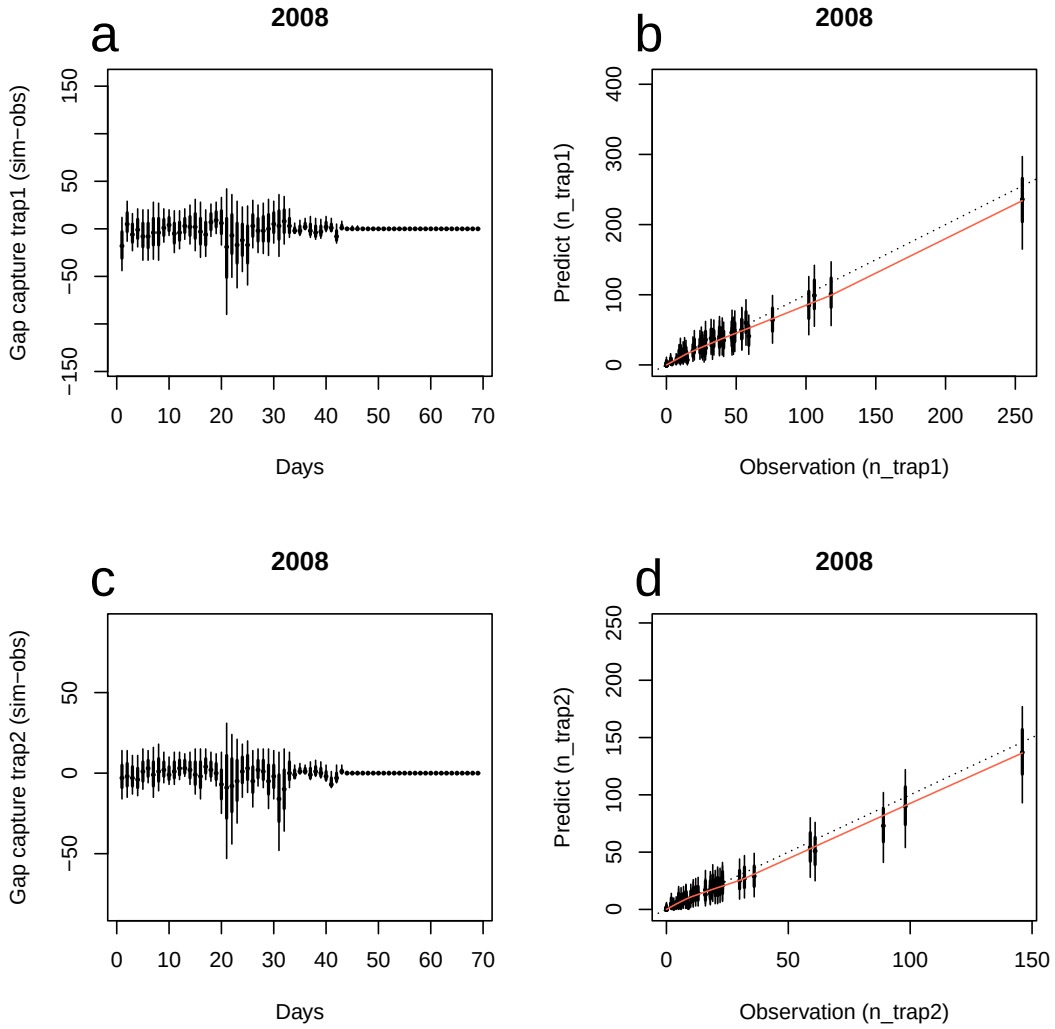
100
0
10
20
30
40
50
60
70
Days
b
2006
Predict (n_trap1)
0
50
100
150
200
250
0
20
40
60
80
100
Observation (n_trap1)
c
2006
Gap capture trap2 (sim−obs)
−60
−20
20
60
0
10
20
30
40
50
60
70
Days
d
2006
Predict (n_trap2)
0
50
100
150
0
20
40
60
80
100
Observation (n_trap2)


a
2007
Gap capture trap1 (sim−obs)
−150
−50
50
150
0
10
20
30
40
50
60
70
Days
b
2007
Predict (n_trap1)
0
100
200
300
400
0
50
100
150
200
Observation (n_trap1)
c
2007
Gap capture trap2 (sim−obs)
−40
0
20
40
60
0
10
20
30
40
50
60
70
Days
d
2007
Predict (n_trap2)
0
20
40
60
80
120
0
10
20
30
40
50
Observation (n_trap2)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2008
Gap capture trap1 (sim−obs)
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−50
−150
0
10
20
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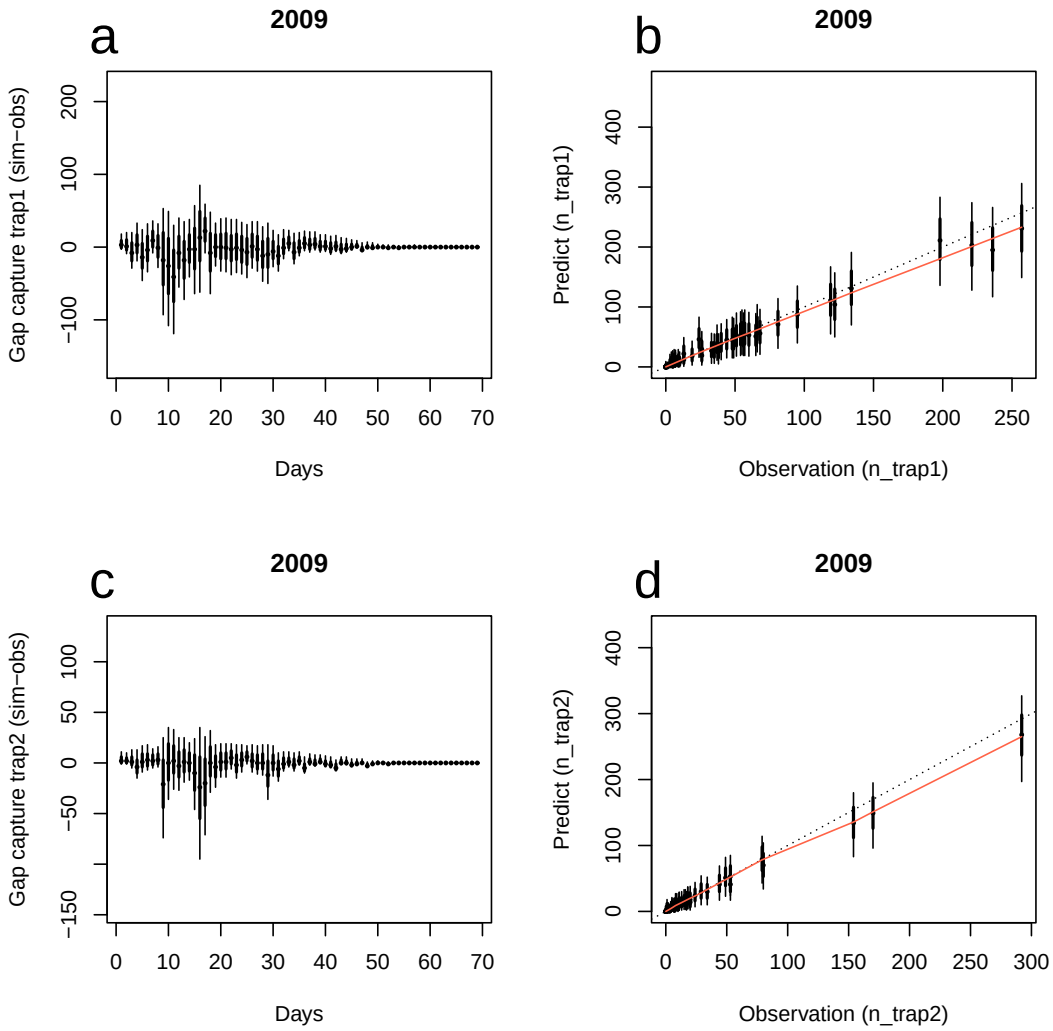
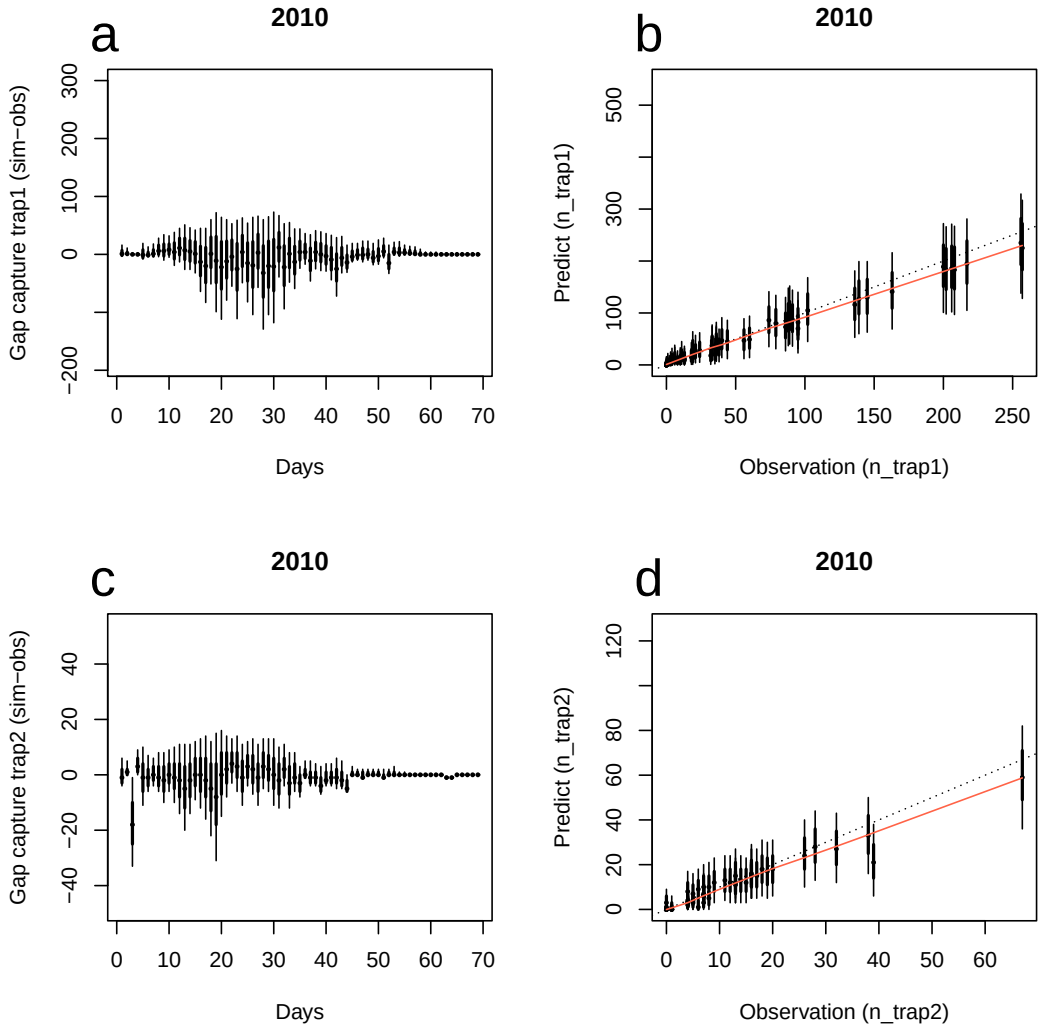
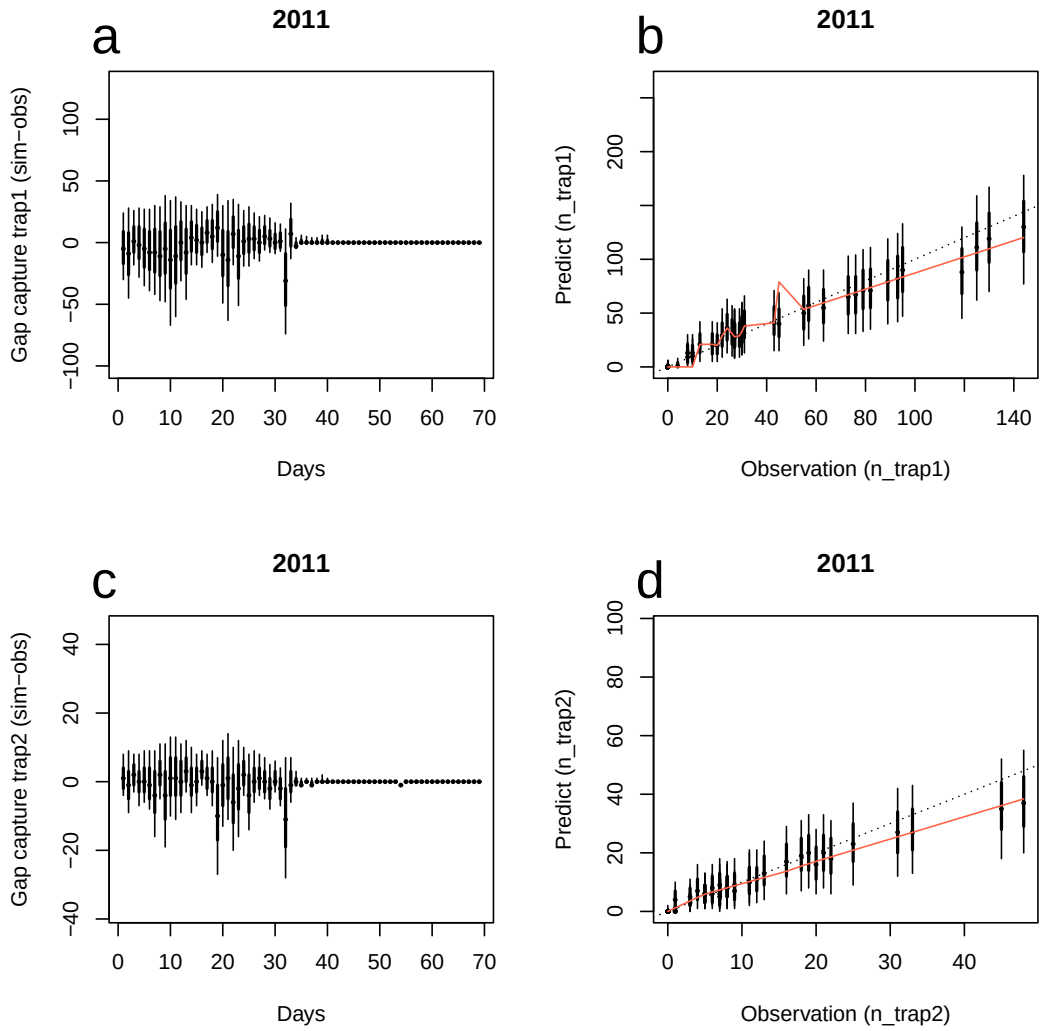
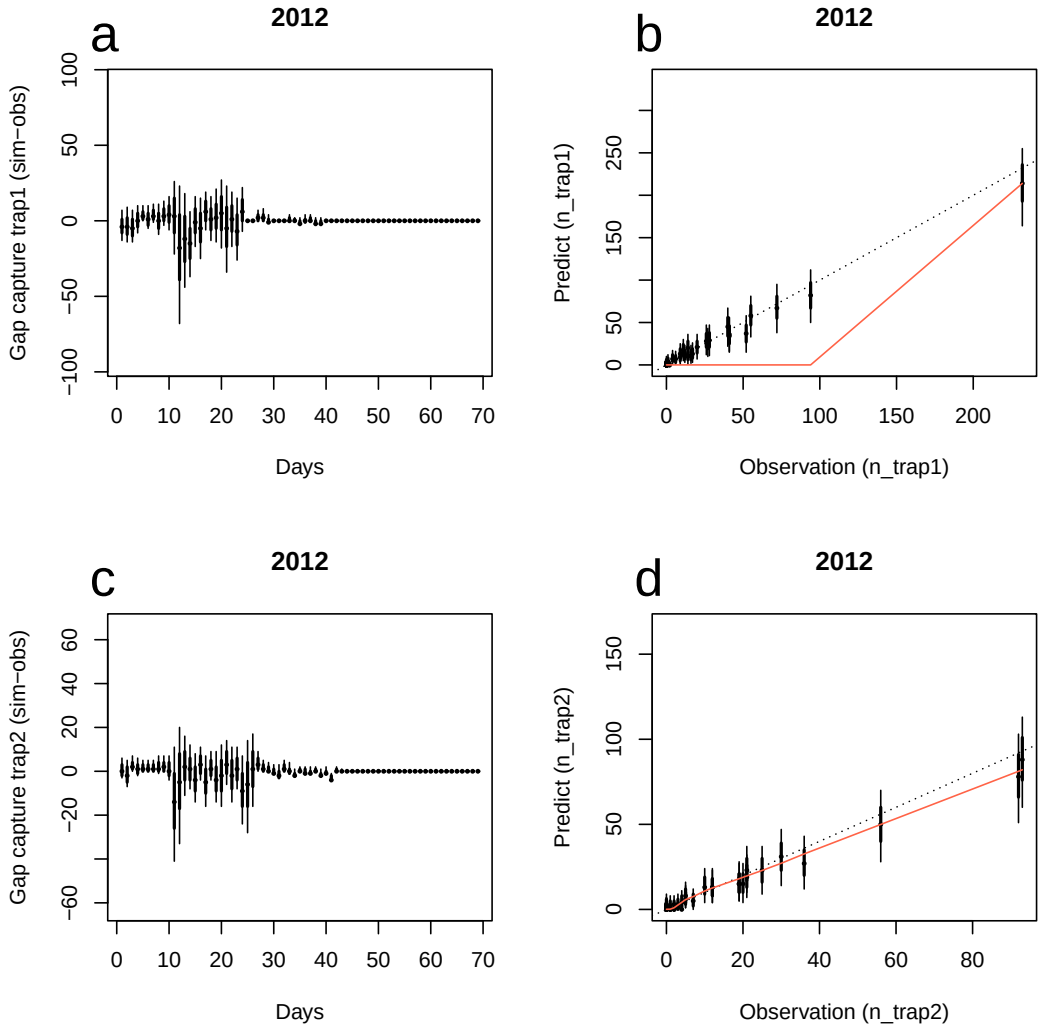
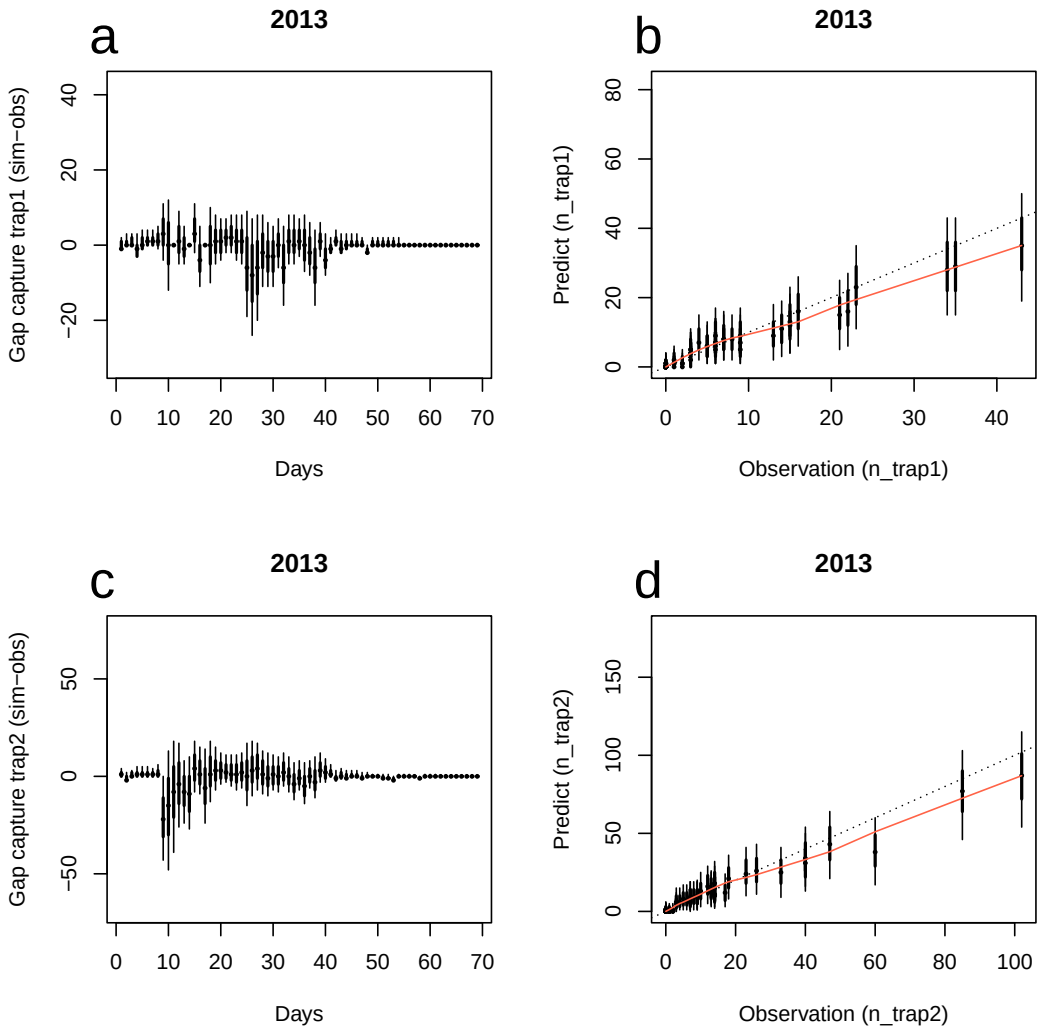
40
50
60
70
Days
b
2008
Predict (n_trap1)
400
300
200
100
0
0
50
100
150
200
250
Observation (n_trap1)
c
2008
Gap capture trap2 (sim−obs)
50
0
−50
0
10
20
30
40
50
60
70
Days
d
2008
Predict (n_trap2)
250
200
150
100
50
0
0
50
100
150
Observation (n_trap2)

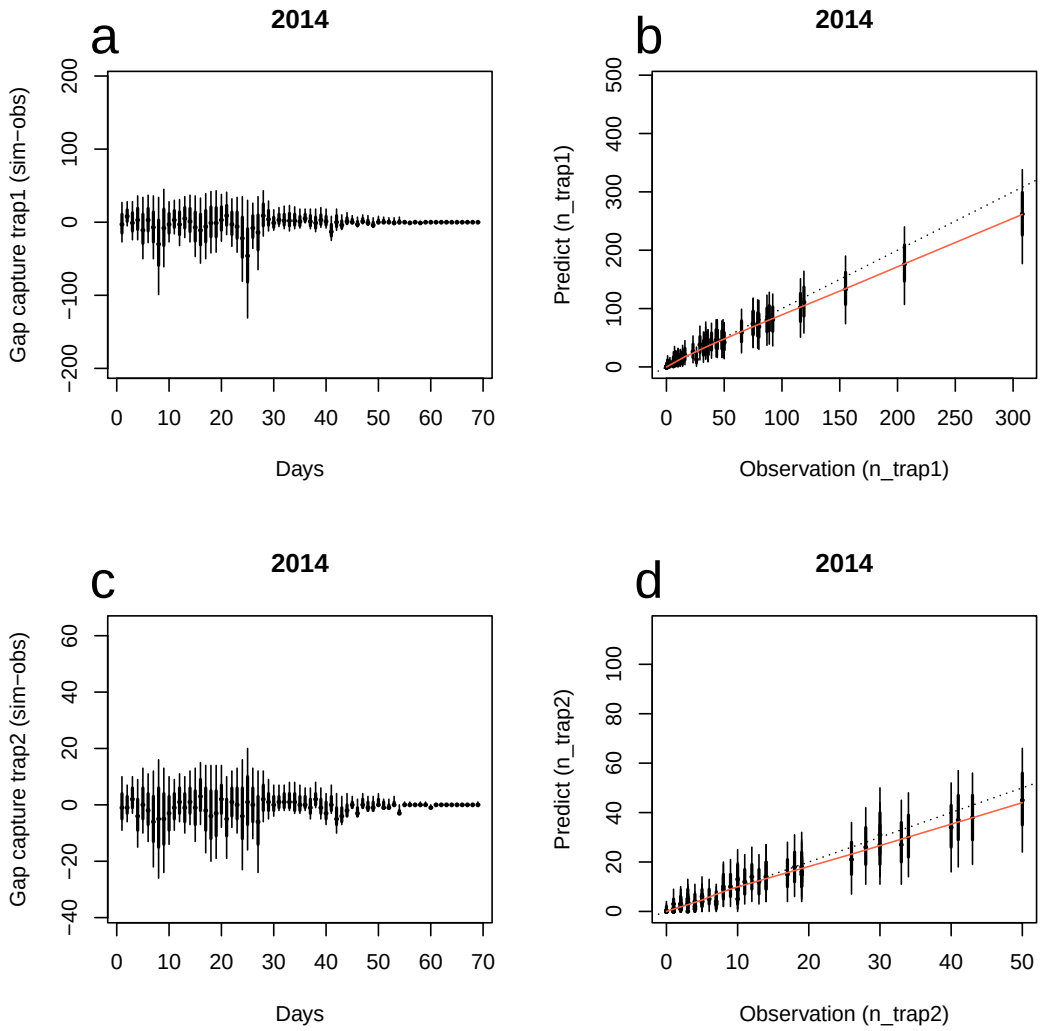

a
2009
Gap capture trap1 (sim−obs)
−100
0
100
200
0
10
20
30
40
50
60
70
Days
b
2009
Predict (n_trap1)
0
100
200
300
400
0
50
100
150
200
250
Observation (n_trap1)
c
2009
Gap capture trap2 (sim−obs)
−150
−50
0
50
100
0
10
20
30
40
50
60
70
Days
d
2009
Predict (n_trap2)
0
100
200
300
400
0
50
100
150
200
250
300
Observation (n_trap2)

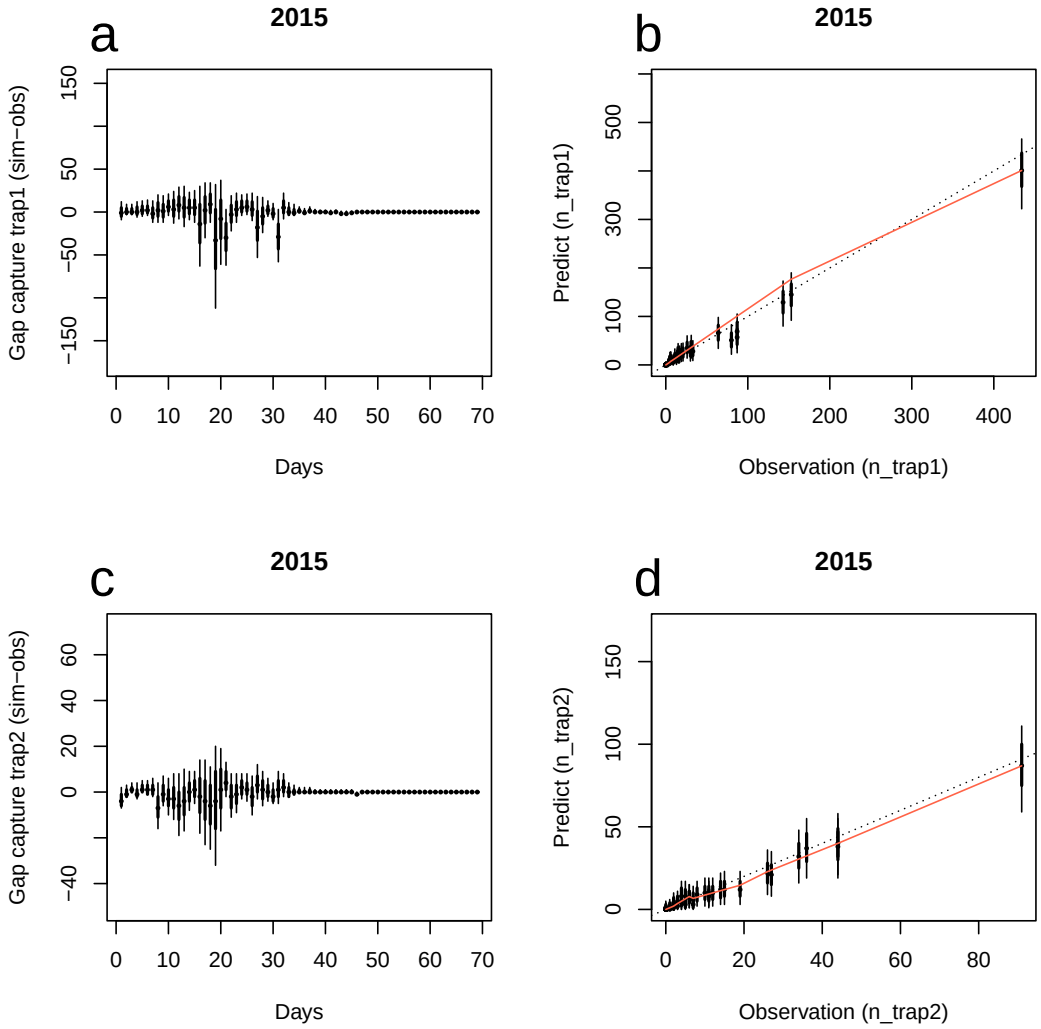

a
2010
Gap capture trap1 (sim−obs)
−200
0
100
200
300
0
10
20
30
40
50
60
70
Days
b
2010
Predict (n_trap1)
0
100
300
500
0
50
100
150
200
250
Observation (n_trap1)
c
2010
Gap capture trap2 (sim−obs)
−40
−20
0
20
40
0
10
20
30
40
50
60
70
Days
d
2010
Predict (n_trap2)
0
20
40
60
80
120
0
10
20
30
40
50
60
Observation (n_trap2)

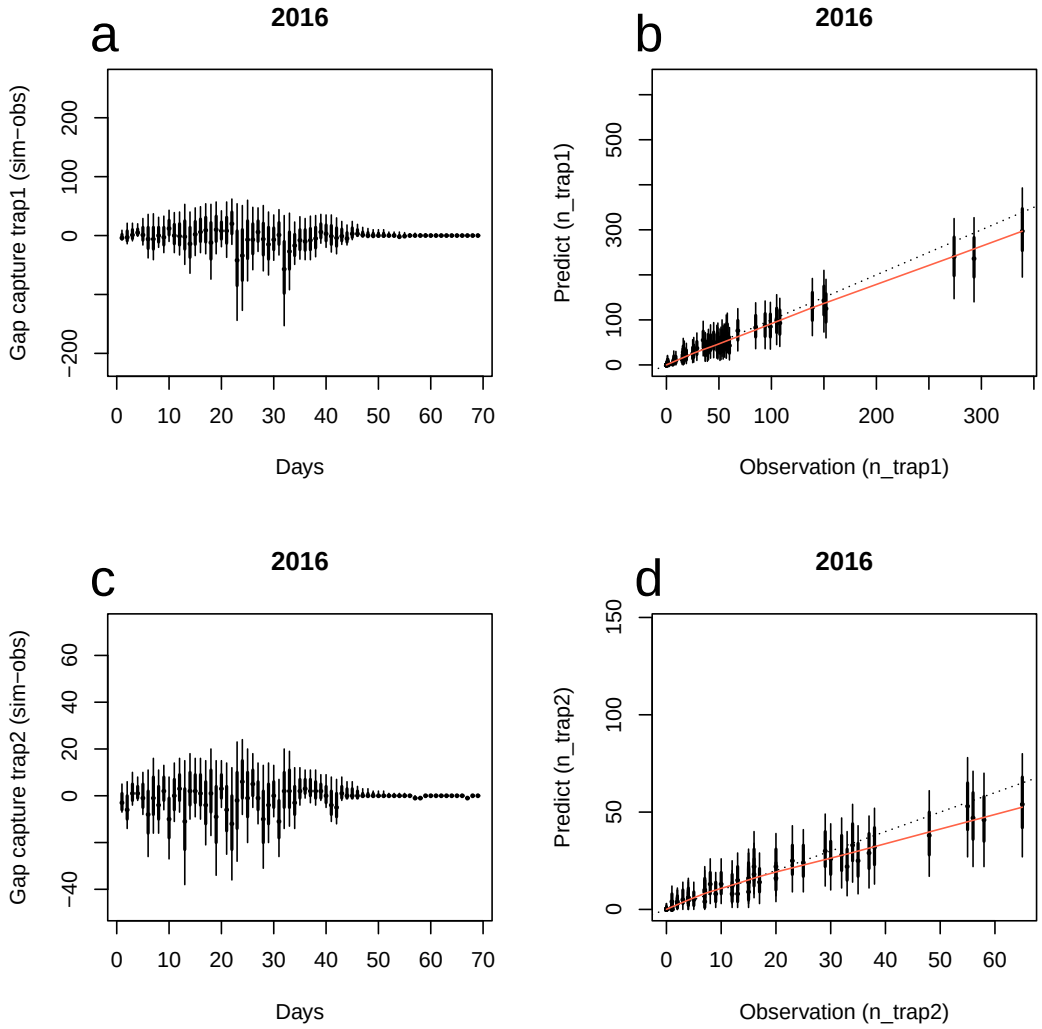

a
2011
Gap capture trap1 (sim−obs)
−100
−50
0
50
100
0
10
20
30
40
50
60
70
Days
b
2011
Predict (n_trap1)
0
50
100
200
0
20
40
60
80
100
140
Observation (n_trap1)
c
2011
Gap capture trap2 (sim−obs)
−40
−20
0
20
40
0
10
20
30
40
50
60
70
Days
d
2011
Predict (n_trap2)
0
20
40
60
80
100
0
10
20
30
40
Observation (n_trap2)

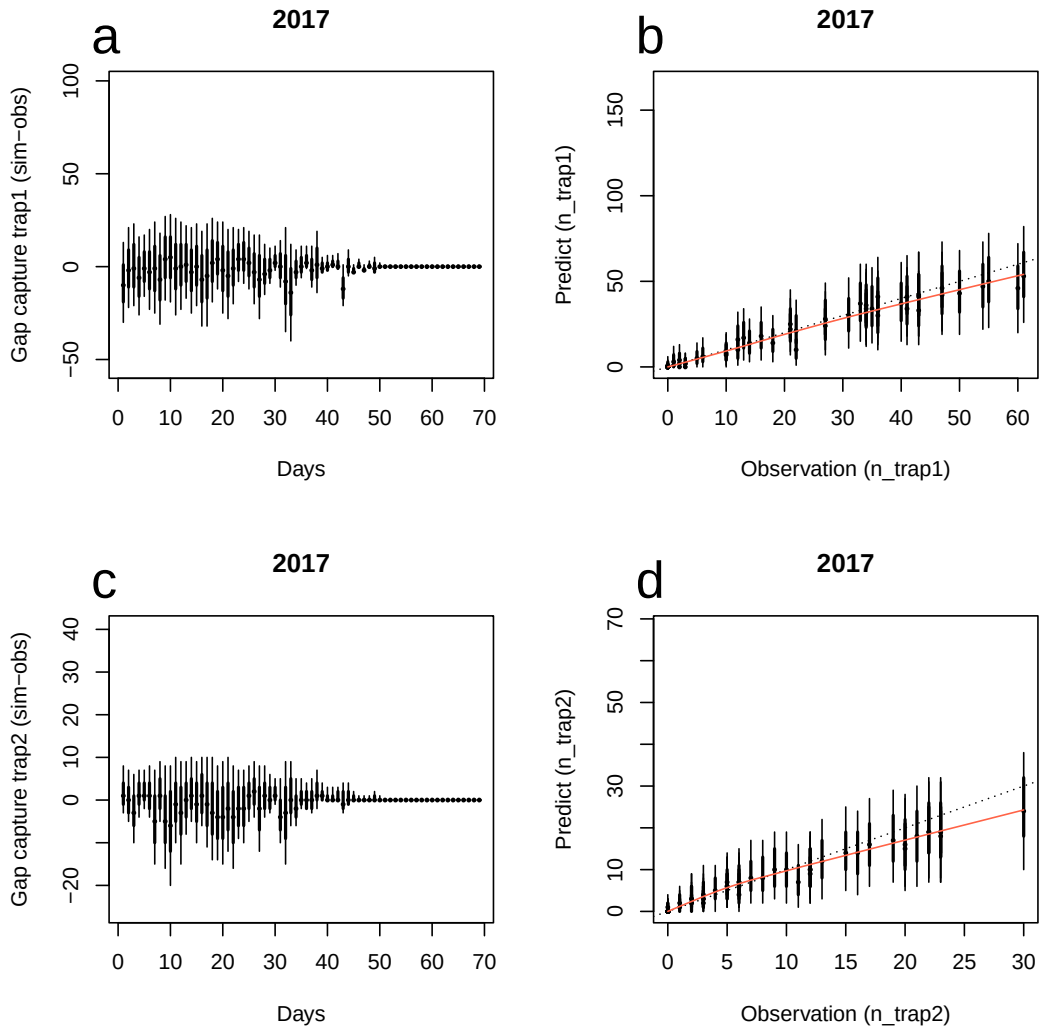

a
2012
Gap capture trap1 (sim−obs)
100
50
0
−50
−100
0
10
20
30
40
50
60
70
Days
b
2012
Predict (n_trap1)
250
150
50
0
0
50
100
150
200
Observation (n_trap1)
c
2012
Gap capture trap2 (sim−obs)
60
40
20
0
−20
−60
0
10
20
30
40
50
60
70
Days
d
2012
Predict (n_trap2)
150
100
50
0
0
20
40
60
80
Observation (n_trap2)

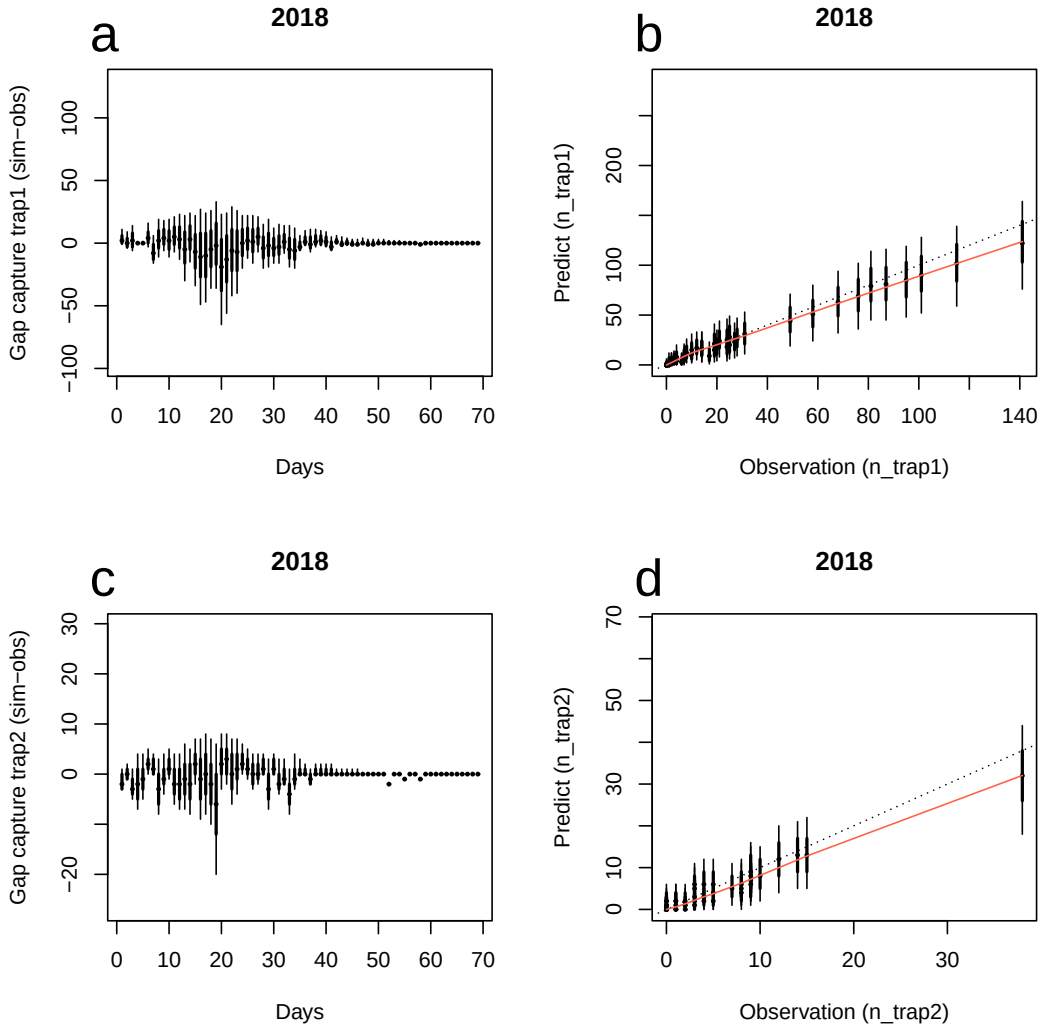

a
2013
Gap capture trap1 (sim−obs)
−20
0
20
40
0
10
20
30
40
50
60
70
Days
b
2013
Predict (n_trap1)
0
20
40
60
80
0
10
20
30
40
Observation (n_trap1)
c
2013
Gap capture trap2 (sim−obs)
−50
0
50
0
10
20
30
40
50
60
70
Days
d
2013
Predict (n_trap2)
0
50
100
150
0
20
40
60
80
100
Observation (n_trap2)

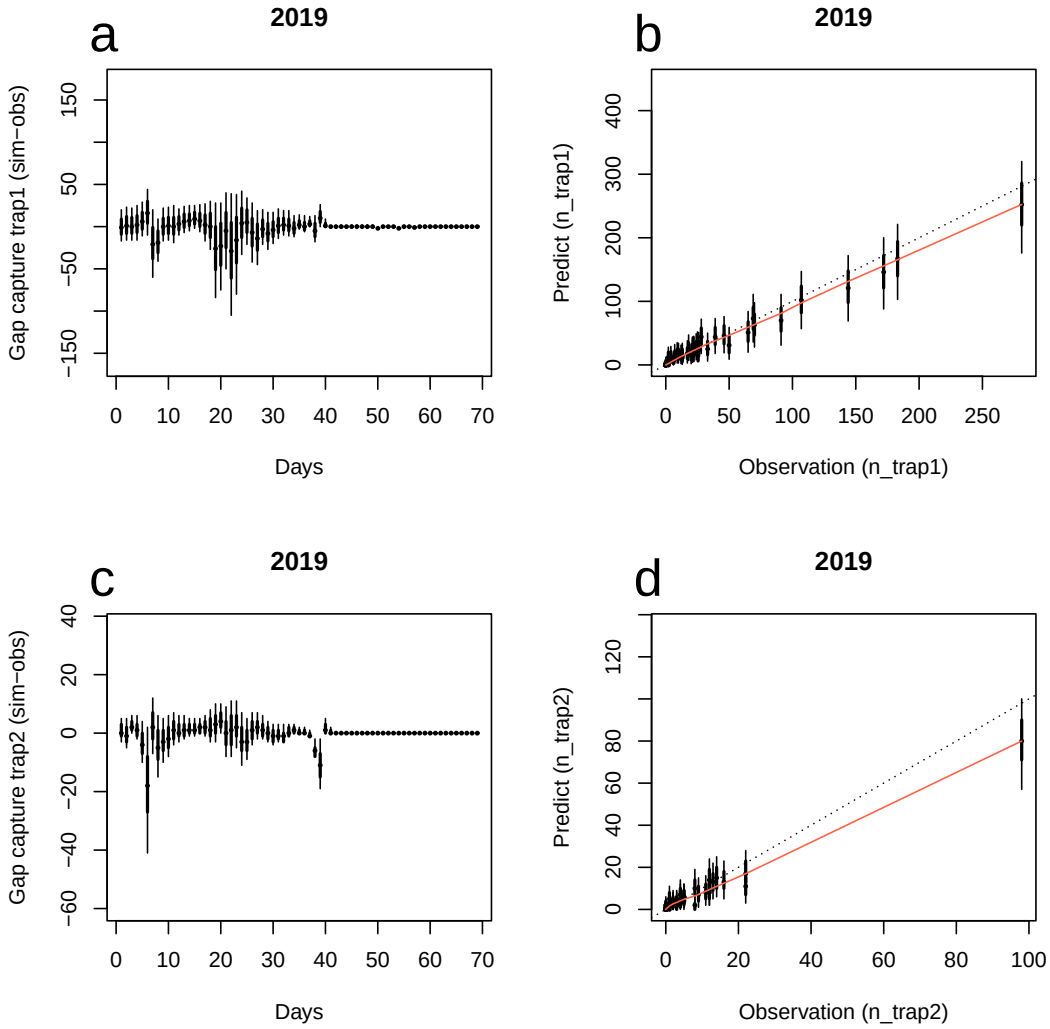

a
2014
Gap capture trap1 (sim−obs)
−200
−100
0
100
200
0
10
20
30
40
50
60
70
Days
b
2014
Predict (n_trap1)
0
100
200
300
400
500
0
50
100
150
200
250
300
Observation (n_trap1)
c
2014
Gap capture trap2 (sim−obs)
−40
−20
0
20
40
60
0
10
20
30
40
50
60
70
Days
d
2014
Predict (n_trap2)
0
20
40
60
80
100
0
10
20
30
40
50
Observation (n_trap2)

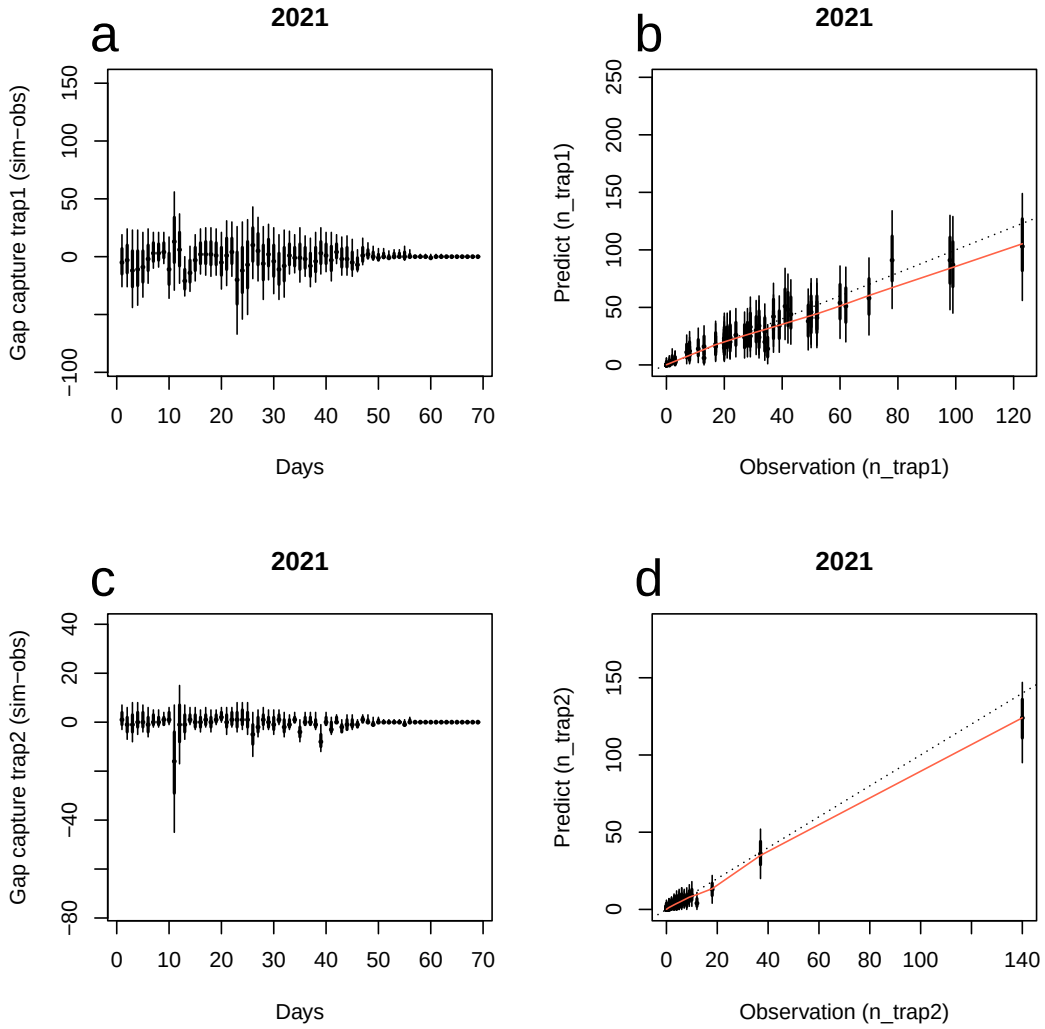

a
2015
Gap capture trap1 (sim−obs)
150
50
0
−50
−150
0
10
20
30
40
50
60
70
Days
b
2015
Predict (n_trap1)
500
300
100
0
0
100
200
300
400
Observation (n_trap1)
c
2015
Gap capture trap2 (sim−obs)
60
40
20
0
−40
0
10
20
30
40
50
60
70
Days
d
2015
Predict (n_trap2)
150
100
50
0
0
20
40
60
80
Observation (n_trap2)


a
2016
Gap capture trap1 (sim−obs)
−200
0
100
200
0
10
20
30
40
50
60
70
Days
b
2016
Predict (n_trap1)
0
100
300
500
0
50
100
200
300
Observation (n_trap1)
c
2016
Gap capture trap2 (sim−obs)
−40
0
20
40
60
0
10
20
30
40
50
60
70
Days
d
2016
Predict (n_trap2)
0
50
100
150
0
10
20
30
40
50
60
Observation (n_trap2)


a
2017
Gap capture trap1 (sim−obs)
100
50
0
−50
0
10
20
30
40
50
60
70
Days
b
2017
Predict (n_trap1)
150
100
50
0
0
10
20
30
40
50
60
Observation (n_trap1)
c
2017
Gap capture trap2 (sim−obs)
40
30
20
10
0
−20
0
10
20
30
40
50
60
70
Days
d
2017
Predict (n_trap2)
70
50
30
10
0
0
5
10
15
20
25
30
Observation (n_trap2)


a
2018
Gap capture trap1 (sim−obs)
−100
−50
0
50
100
0
10
20
30
40
50
60
70
Days
b
2018
Predict (n_trap1)
0
50
100
200
0
20
40
60
80
100
140
Observation (n_trap1)
c
2018
Gap capture trap2 (sim−obs)
−20
0
10
20
30
0
10
20
30
40
50
60
70
Days
d
2018
Predict (n_trap2)
0
10
30
50
70
0
10
20
30
Observation (n_trap2)


a
2019
Gap capture trap1 (sim−obs)
150
50
−50
−150
0
10
20
30
40
50
60
70
Days
b
2019
Predict (n_trap1)
400
300
200
100
0
0
50
100
150
200
250
Observation (n_trap1)
c
2019
Gap capture trap2 (sim−obs)
40
20
0
−20
−40
−60
0
10
20
30
40
50
60
70
Days
d
2019
Predict (n_trap2)
120
80
60
40
20
0
0
20
40
60
80
100
Observation (n_trap2)


a
2021
Gap capture trap1 (sim−obs)
−100
0
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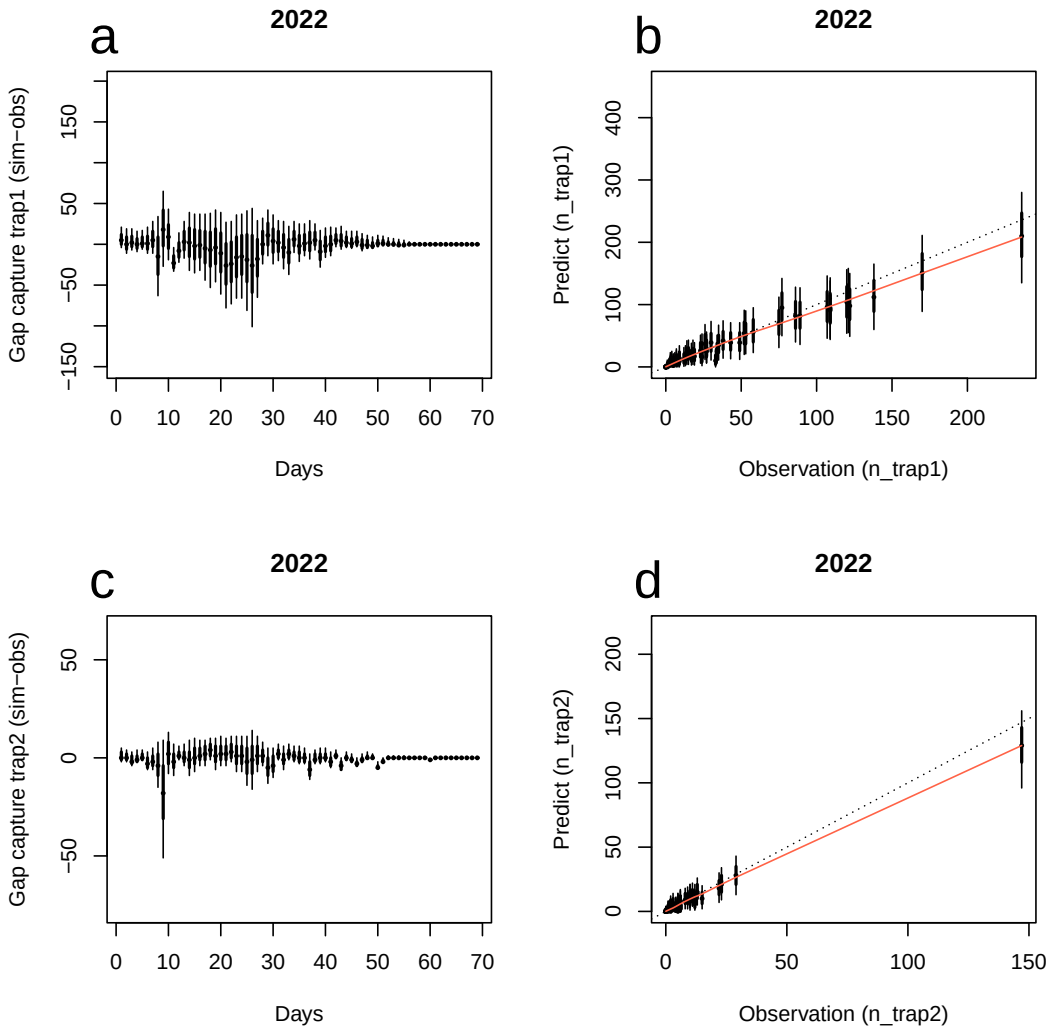
100
150
0
10
20
30
40
50
60
70
Days
b
2021
Predict (n_trap1)
0
50
100
150
200
250
0
20
40
60
80
100
120
Observation (n_trap1)
c
2021
Gap capture trap2 (sim−obs)
−80
−40
0
20
40
0
10
20
30
40
50
60
70
Days
d
2021
Predict (n_trap2)
0
50
100
150
0
20
40
60
80
100
140
Observation (n_trap2)


a
2022
Gap capture trap1 (sim−obs)
150
50
−50
−150
0
10
20
30
40
50
60
70
Days
b
2022
Predict (n_trap1)
400
300
200
100
0
0
50
100
150
200
Observation (n_trap1)
c
2022
Gap capture trap2 (sim−obs)
50
0
−50
0
10
20
30
40
50
60
70
Days
d
2022
Predict (n_trap2)
200
150
100
50
0
0
50
100
150
Observation (n_trap2)

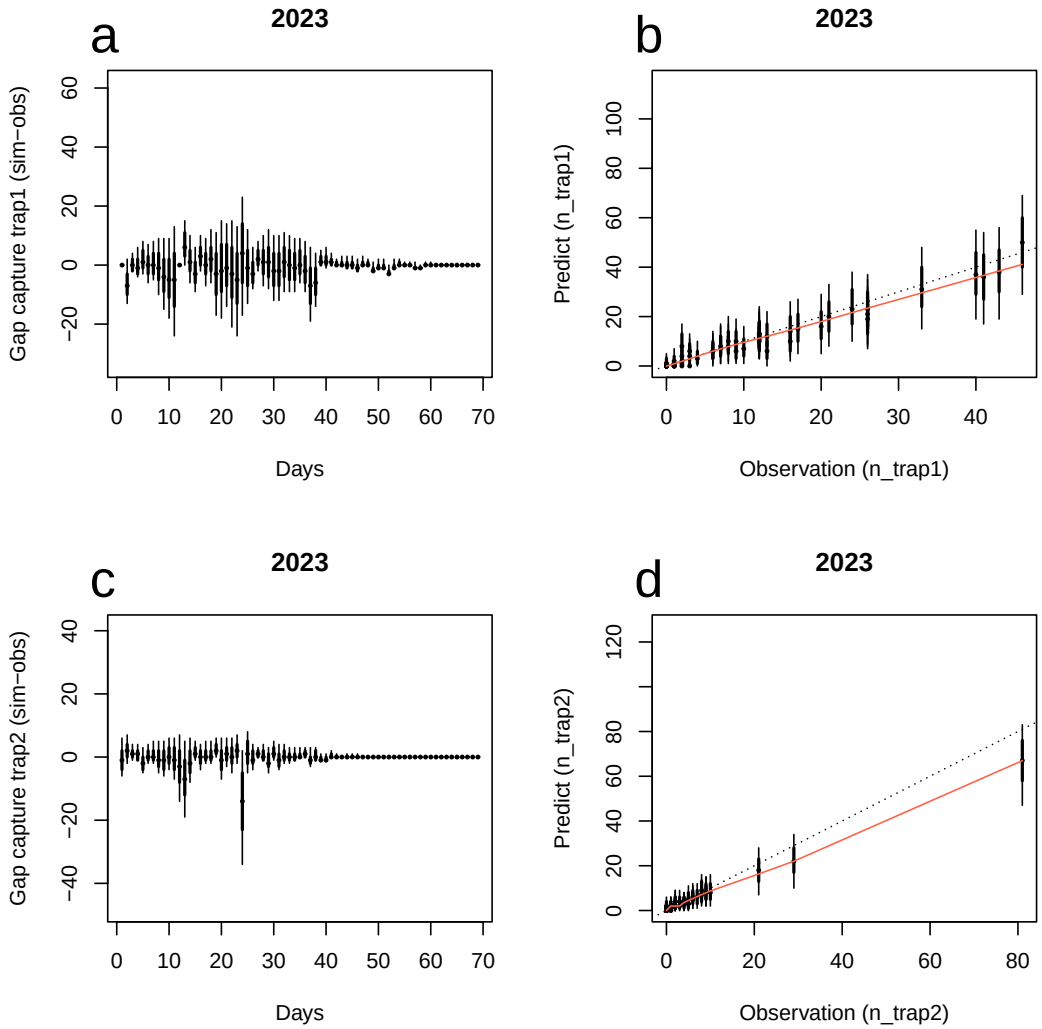
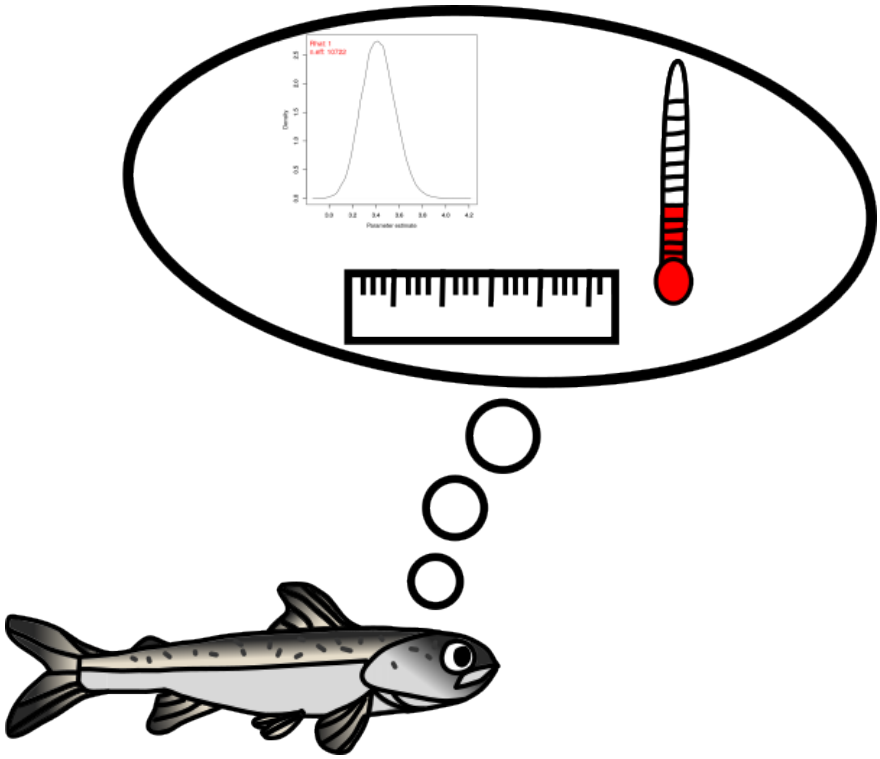


Figure 3.S3 – **Posterior prediction of trap 1 and trap 2 captures for each year.** The plain dot represents the median, the thick line the 50% interval and the thin line the 90% interval. The orange line is the "loess" line. a. Difference between predicted captures values and data from trap 1. b. Predicted captures vs observation in trap 1. c. Difference between predicted captures values and data from trap 2. d. Predicted captures vs observation in trap 2.

Chapter 4

Discussion

In the following section, the aim is to explore and discuss the results in order to develop avenues of reflection for the future. This is why, for the parameters of interest, I will use the median of their marginal *a posteriori* distributions.



4.1 The importance of modelling both the capture process and the phenological process

4.1.1 Exploratory analyses

We have carefully modelled the capture process and the phenological process. Variations in the efficiency of the trap, as well as the quantity of migrants, can cause variationS in the number of captures. The aim was to disentangle the role of the observation process from the biological process.

In this section, I want to see the effect of including the capture process in our view of phenology. To do this, I compared the phenology estimated by the model with the capture we obtain in the trap. I focused on the first trap, as this is where the phenology is estimated.

Figure 4.1 shows, for 1999, 2013, 2015 and 2017, the cumulative distribution of p_{phen} (CDF) as a function of the cumulative trap 1 catch frequency (CF). I present this four years because they show the different patterns we found. In 1999, the CDF was lower than the CF, as the CF was much faster than the CDF. In 2013, the trend is the opposite. 2015 presents a S-shape, with CF slower at the beginning of the period and the opposite at the end. Finally, 2017 presents also a S-shape but CDF and CF are closer together. 1999 corresponds to a year with early catch peaks. In 2013 the catches are very noisy, going from many catches to very few, in 2015 the captureS were low at the beginning of the period contrary to the end of the period, and in 2017, the p_{phen} seems to follow the frequency of captures fairly well (Fig 4.2). This shows that p_{phen} can be very different from the raw data in some years.

Figure 4.3 compares the 25%, 50%, 75% and 90% quantiles for p_{phen} and the captures for each 25 years. I have not looked at the 10% quantile because the start of the process is fairly uncertain, unlike the end of the process, since for each year the migration period seems to have ended at the end of the period studied. The 75% and the 90% quantiles and the median of the captures are more dispersed than the one from of p_{phen}. This could be explained by the fact that the observation process is overdipersed: the data are more dispersed than the underlying phenology.

Figures 4.4 a & b show evolution over time of the difference between the 25% and 50% quantiles of p_{phen} and the 25% and 50% quantiles of the raw data. I present these quantiles, as the others do not show any particular temporal trends. The most obvious temporal trend concerns the 25% quantile. Over the years, the difference between the estimated 25% quantile and the 25% quantile of the raw data decreases and becomes negative: the 25% quantile of p_{phen} is earlier than the 25% quantile of the raw data. The time trend for the 50% quantile is similar, but less marked. Figures 4.4 c & d and 4.4 e & f show the

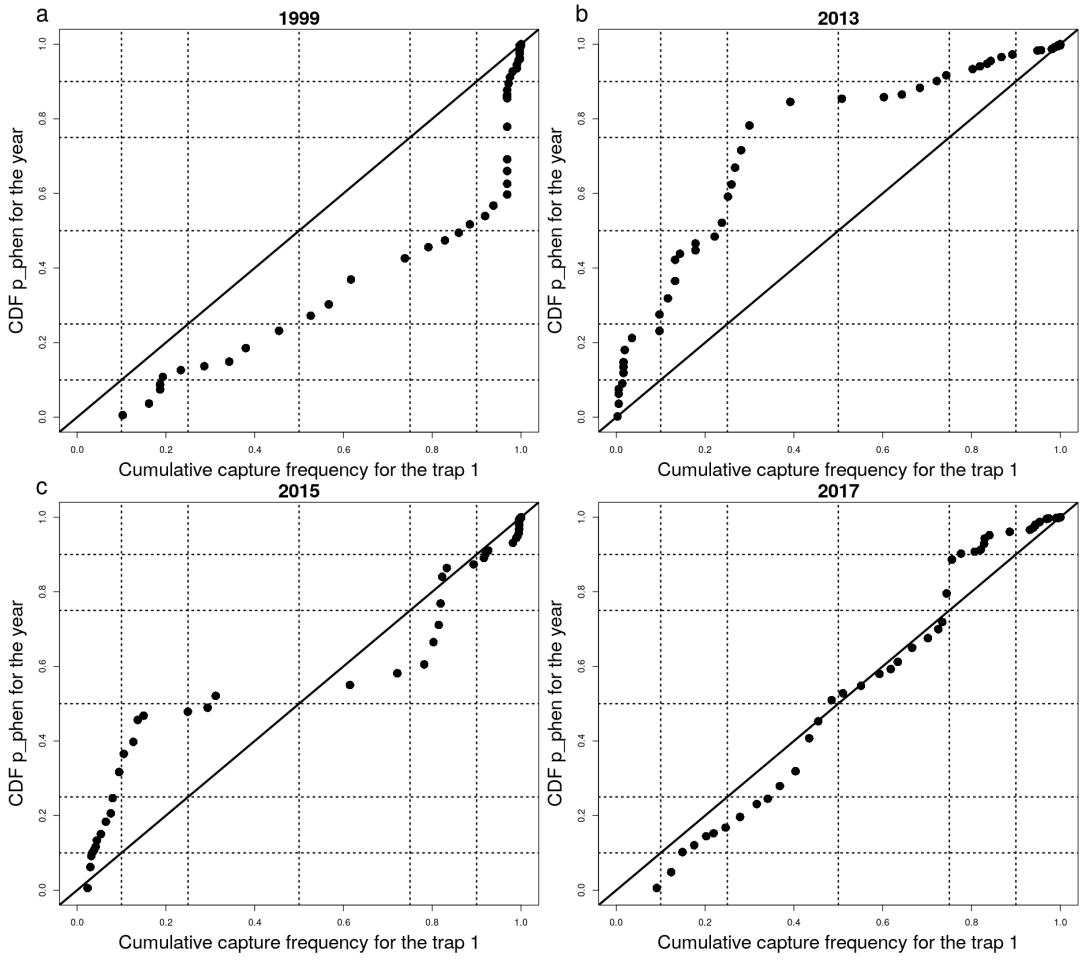


Figure 4.1 – **Cumulative distribution of p_{phen} as a function of the cumulative frequencies of trap 1 catches.** The vertical and horizontal dotted lines represent the 10%, 25%, 50%, 75% and 90% quantiles. The solid line represents the identity function. a. year 1998. b. year 2013. c. 2015. d. year 2017.

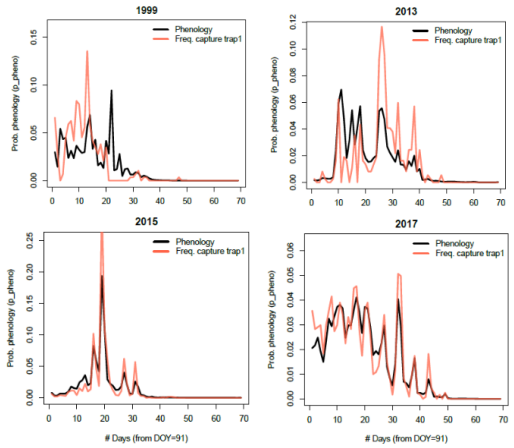


Figure 4.2 – p_{phen} and the capture frequency at trap 1 for 1999(a.), 2013(b.), 2015 (c.) and 2017(d.)

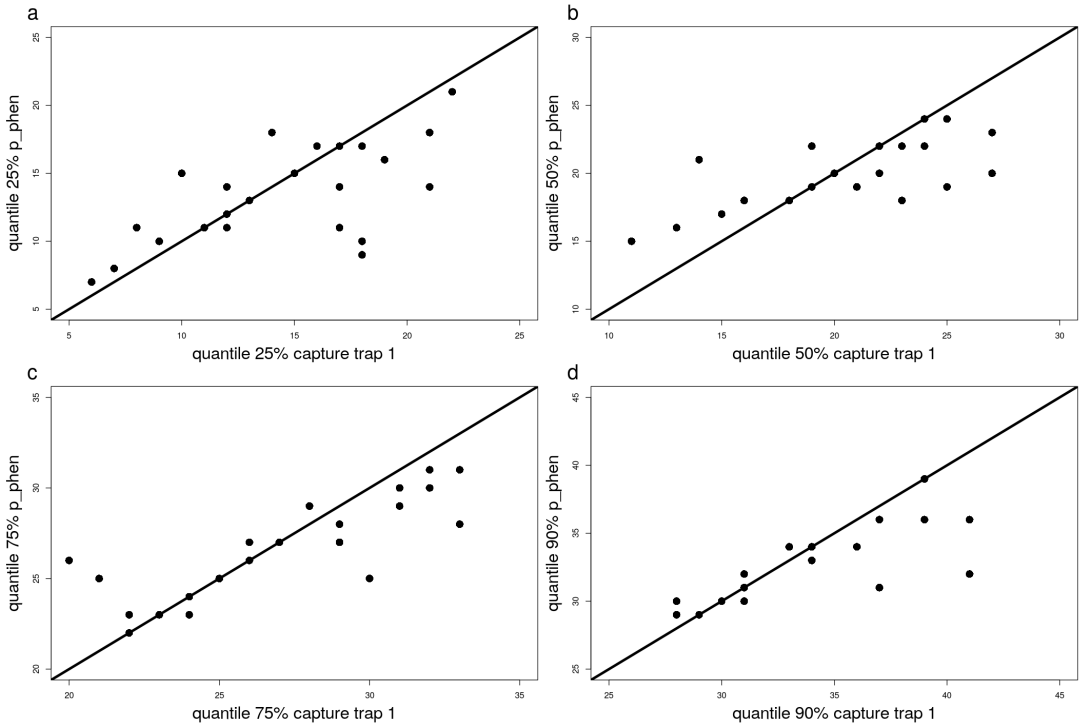


Figure 4.3 – **Quantile p_{phen} vs quantile of the capture at trap 1.** a. Quantile 25%. b. Quantile 50% c. Quantile 75%. d. Quantile 90%.

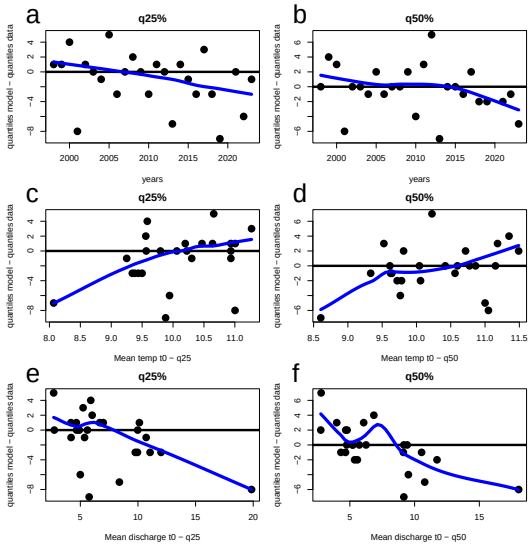


Figure 4.4 – **Difference between quantiles of p_{phen} and quantiles of data as a function of years, mean temperature or mean discharge between t_0 and the quantile of interest** The blue curves are the "loess" curves. a.Quantile 25%. b. Quantile 50% c. Quantile 25%. d. Quantile 50%. e. Quantile 25% f. Quantile 50%

difference between the quantiles 25% and 50% of p_{phen} and the quantiles of the raw data as a function of the mean temperature and the mean discharge respectively. For the temperature, the trends are very marked, and are strongly influenced by the year with the minimum temperature, 2013. But even if this year is removed, the trend is still visible for the quantile 25%. The higher the water temperature, the more positive the difference, i.e. the 25% quantile of p_{phen} is later than the 25% quantile of the raw data. For the discharge, the visible trends are strongly influenced by the year with the most extreme river discharge, 2002, but even if this year is removed, the higher the river discharge, the more negative the difference. Thus, the raw data seem to show trends due to the observation process.

4.1.2 Conclusion

These preliminary results suggest that, the raw data are biased by the observation process, over-dispersed and influenced by environmental factors. In a context of climate change that modifies these environmental factors, a systematic bias could set in and distort our view of phenology. Therefore, not explicitly modelling the observation process and the phenological process may make it more difficult to detect evolutionary patterns of the phenology.

4.2 Variations of the preparation process

We distinguished two processes in the phenological mechanism: p_r and p_{migr} (Chapter 3). Here, I will concentrate on p_r. As mentioned in chapter 3, p_r profiles are different from one year to the next: different widths, different peak dates, and different skewness.

To illustrate these variations, the figure 4.5 shows the 25%, 50%, 75% and 90% quantiles of p_r. These quantiles vary considerably from one year to the next. The 25% quantile even seems to show a temporal trend: it seems to increase at the beginning of the period and then fall again. This trend is also present for the 50% quantile, although a little less clearly. The two final quantiles do not present the same trend, although the 90% quantile shows a slight inverse trend to the first two quantiles presented. The shape parameter of the Weibull distribution k is shown on the figure 4.6: it also varies from year to year, and shows a slight temporal trend, increasing at the beginning and decreasing at the end of the period. These variations have major consequences for the p_r profile. Figure 4.6.b. shows these changes: it displays two Weibull distributions with the same scale, but different shapes: the smallest (in 1998) and the highest (in 2004) estimated by the model. This clearly shows very different distributions. The curve with the lowest shape is more symmetrical than the curve with the highest shape: skewness depends on the shape parameter (Versluis et al., 2015). Variations in shape therefore give rise to very different profiles from one year to the next and correspond to very different temporal dynamics of fish ready to migrate. Despite this, the medians differ little, even if the distribution with the lowest shape parameter has a slightly earlier median. The question arises as to the reasons for these variations of p_r.

Reminder

This process partly represents the 'preparation' of fish before they migrate, i.e. the moment when they become sensitive to the factors that trigger their migration. The preparation of the migration for the salmon is linked with the smoltification, i.e. all the modifications (including growth) that allows smolts to cope with marine conditions (McCormick et al., 1998).

We can put forward various hypotheses about the factors that can influence the earliness and the form of this process.

Firstly, the winter conditions that smolts undergo before the migration period could influence their growth and the smoltification, i.e. their preparation for migration. Indeed, winter temperature and discharge have been found to have an impact on the growth rate during winter (Simmons et al., 2020). Approaching the migration period, an increase in photoperiod promotes smoltification, but low temperatures can reduce the effect of photoperiod, i.e. delay

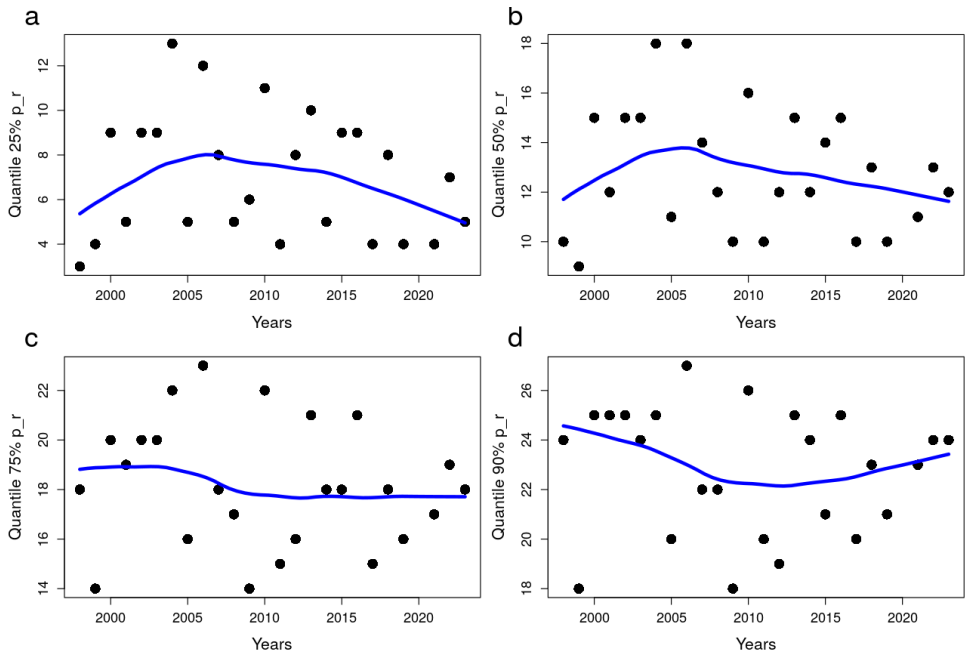


Figure 4.5 – **Quantiles of probability p_r as a function of years** : The blue curves are the "loess" curves. The y-axis corresponds to the dates in April. a. Quantile 25% b. Quantile 50% c. Quantile 75% d.Quantile 90%

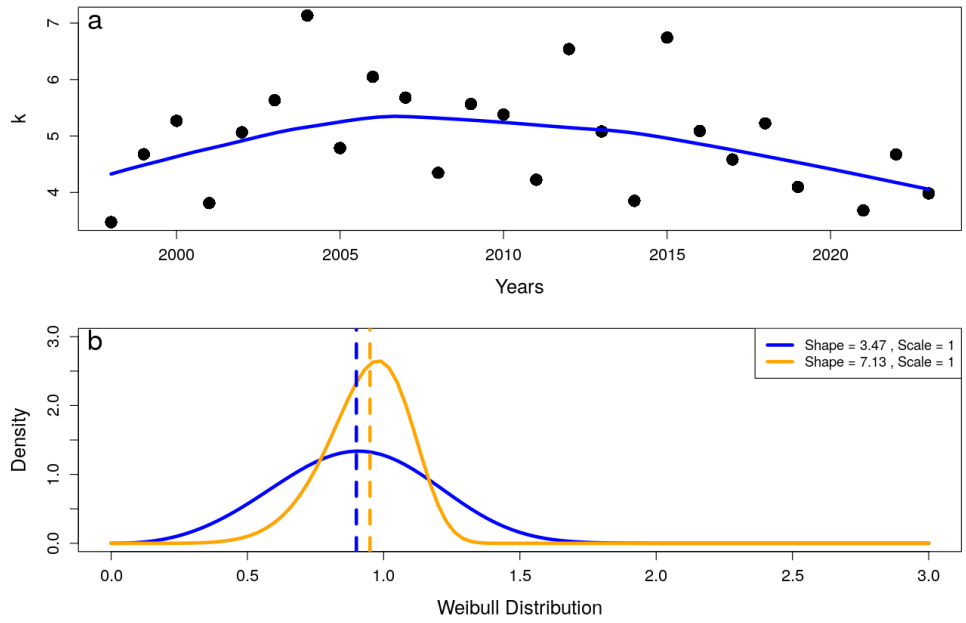


Figure 4.6 – **Shape k of probability p_r** : a. Shape of probability p_r as a function of years. The blue curves are the "loess" curves. b. Weibull distribution for the minimum and the maximum values of k and the same scale. The vertical doted line represents the median of each distribution.

smoltification (McCormick et al., 2000; Zydlewski et al., 2005) and reduce growth (Zydlewski et al., 2005). On the contrary, a higher temperature at this period speeds up the start and end of the migration period, which may indicate that it speeds up preparation (Kastl et al., 2022). We can therefore hypothesise that winter conditions, in particular temperature, and maybe discharge, could have an influence on the speed of smolt preparation, especially that warmer temperatures would be associated with earlier preparation.

The smolts in the Scorff population are mainly 1+ and 2+ years old. As the 2+ smolts have had more time to grow and prepare, it can be assumed that they would be ready before the 1+ smolts, so the process would be earlier in years when the 2+/1+ ratio is higher (Kennedy et al., 2010).

The last assumption concerns the size at the end of the summer. If winter conditions can have an impact on the migration size, growth during the first few months could also have an impact: if the smolts were behind in their growth during the summer preceding their migration, compared with other more favourable years, the time it takes them to catch up could delay the moment when they are ready. To test these hypotheses, I ran a linear model.

Methods and variables

The response variables I use here are the 25%, 50%, 75% and 90% quantiles of p_r (q_r25, q_r50, q_r75 and q_r90 resp.) and the shape parameter of the Weibull distribution k. The quantiles are good indicators of the precocity of the process, and the shape parameter k, as shown by the figure 4.6, encapsulates a lot of information on p_r. All models used the logarithm of the response variable, which ameliorates the residuals aspect.

I tried different explanatory variables. Note that, for simplicity, I have not tested interaction between variables. To test the effect of the age, I used the logarithm of the ratio of 2+ smolt on 1+ smolt per year. These data come from the same monitoring program as the rest of the data used in chapter 2 and 3, i.e. they are part of the Observatoire de recherche sur les poissons diadromes des fleuves côtiers (ORE DiaPFC; Azam et al., 2020) program. Electric fishing are carried out in September, targeting parrs. The captured parrs are measured, so I calculated the logarithm of the mean size of the 0+ parr (S_{0+}). Thus, for a migrating year y, I have an estimate of the mean size of the 0+ parrs the year $y-1$, at the end of summer. I assume this is representative of the size of the uncaught parrs.

For the environmental factors, I looked at the conditions from January to March, the end of winter when the fish are supposed to start growing again (Jonsson et al., 2016). I used the mean discharge from January to the end of March (Q). For the temperature, I used the mean temperature during each month, i.e. January, February and March (T_J, T_F, T_M resp.). I do not have

the temperature for January and/or February for the years 1999, 2000, 2003 and 2010, so these years are not used in the rest of this section.

The statistical analysis was carried out using R. To select the best model, I used the setpAIC procedure from the package MASS. Among the models chosen by this procedure, I selected the one that presents the best fitting and where the more factors were significant. I checked the normality of the residuals by graphical visualisation, especially by a quantiles-quantiles plot.

Results and discussion

The models presented here are the one that were selected by the procedure explained above. The values of the coefficients associated with the explanatory variables of interest are presented in the table 4.2. No model with significant effects was selected for the 90% quantile.

Table 4.1 – Model selected for each response variables f the preparation process (lines) and the coefficient associated to the explanatory variables (columns). The stars indicate significance with $p-value < 0.01 : `***' p-value < 0.05 : `**', p-value < 0.1 : `*'$

Symbol	T_M	Q	R^2
$log(k)$	-0.14 **	-0.01 *	0.40
$log(q_r25\%)$	-0.31 ***		0.39
$log(q_r50\%)$	-0.13 ***		0.30
$log(q_r75\%)$	-0.07 *		0.18

In the best model, the shape k depends on the temperature in March. The value of the coefficient of the temperature is negative: the warmer is the water in March, the lowest is k. Lowest k is associated with earlier preparation. The mean temperature in March is significant with a negative effect for all other response variables (except q_r90). Thus, the warmer are the water temperature in March, the faster is the preparation process.

The effect of temperature in March on q_r25, q_r50 and q_r75 and the shape k are consistent with each other and with the literature: a warmer temperature before the migration period, i.e. while the photoperiod is increasing, accelerates growth and smoltification (Matte et al., 2024; McCormick et al., 2000; Simmons et al., 2020; Zydlewski et al., 2005). The effect of March temperature diminished as the migration progressed. This could suggest a greater plasticity on the start date than on the end date, which could explain why no model is selected for the 90% quantile. It could also be that it is the temperatures in April that determine the end date.

The temperature during January and February has never been selected. These months might be too far from the migration period, i.e. with too short photoperiod, and with too low temperature, so the preparation has not begin yet.

Discharge has a significant and negative effect on the shape k. The effect is negative for the shape k. High water velocity (associated with high discharge) does not seem to be a limiting factor for parr growth (Fabris et al., 2017), and long period of high flow can favour growth (Simmons et al., 2020). Thus, this result seems to be consistent with the literature.

The effect of the average parr size is not significant, which can be surprising assuming that salmons have to reach a minimum size before migrating (ØKland et al., 1993): they have to catch up their "delay". This can be explained by the fact that parrs are capable of what is known as 'compensatory growth', i.e. accelerated growth during the autumn and winter if conditions allow, and especially during the period before migration. Indeed, pre-smolt exhibit a strong growth at this period (Jonsson et al., 2016; Sigourney et al., 2013; Simmons et al., 2020), which can be sufficient to catch up the minimum size before the migration period. Although more 2+ are observed at the beginning of the smolt outmigration, the effect of the smolt 2+/1+ ratio were not significant for any of the response variables. These preliminary studies may not be sufficient to detect the effect of this ratio.

Conclusion

These exploratory, and still preliminary, analyses suggest that the most important factor for preparation speed is temperature during the pre-migration period, probably for its link with growth and smoltification. These results highlight the role of conditions during the preparation phase (temperature and discharge), which seems more preponderant than past life history traits (size of 0+ at the end of the first growth period, ratio of 2+/1+ smolts) on salmon phenology determination. Further analyses are needed to better disentangle and confirm (or not) these effects.

Perspective 1

Informing the preparation process more precisely in our model by introducing explanatory variables such as discharge and March temperature could improve our model and help identify the factors involved in phenological determination.

Captured parrs are tagged in September and may be recaptured during the smolts outmigration in the spring, so we have some individual data. These could be used in an individual based model to better understand the impact of life-history traits on phenology, i.e. the impact of growth trajectories and age on the departure decision.

4.3 Phenological trend

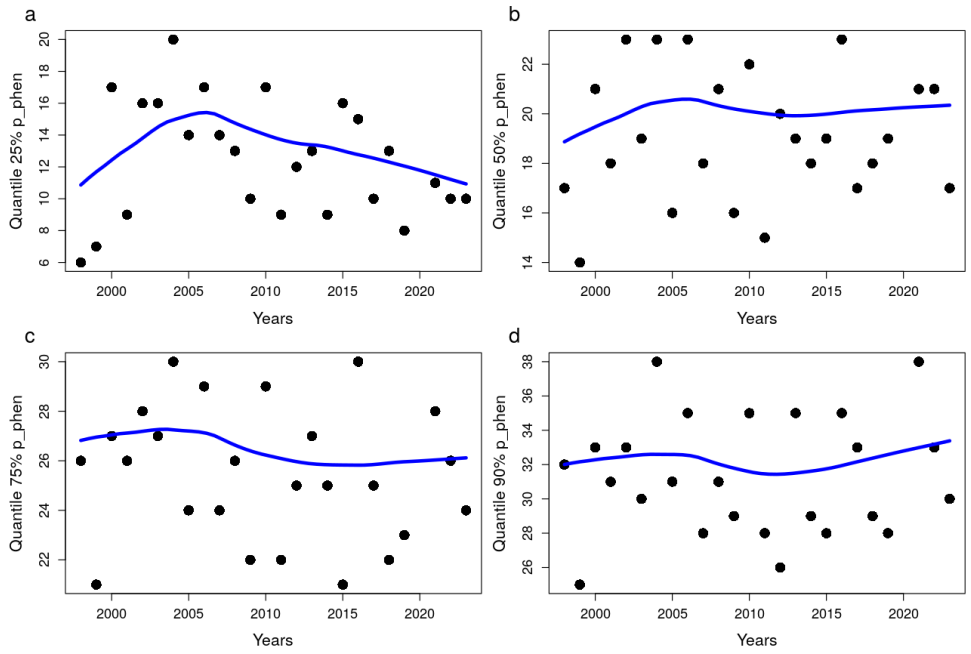


Figure 4.7 – **Quantiles of probability p_{phen} as a function of years** : The blue curves are the "loess" curves. The y-axis corresponds to the dates in April. a. Quantile 25% b. Quantile 50% c. Quantile 75% d.Quantile 90%

The profile of p_{phen} (3.6), derived from p_r and p_{migr}, is very different from one year to the next. Figure 4.7, which displays the 25% quantiles of p_{phen}, $q_{phen}25$, i.e. the date when the cumulated p_{phen} reaches 25% for each year, shows the same time trend as the 25% quantile of p_r (4.5). It even seems that this trend is more pronounced. However, the date at which p_{phen} reaches 50%, $q_{phen}50$ shows a slight upward trend from 1998 to 2005, less visible than for p_r, and seems to stabilise from 2005 to 2023.

Figure 4.8 shows the differences between the quantiles at 50% and 25% of p_{phen}. There is a downward trend between 1998 and 2005. Then, from 2005 onwards, this trend increases markedly.

Otero et al., 2013 studied the phenology of Atlantic salmon migration in North America and Europe over the period 1961-2010. They found that salmon migration was increasingly earlier over this period. Consequently, the fact that the phenology of salmon in the Scorff is later and later at the beginning of our period may seem contradictory, but this seems to come mainly from the first 3 years, which were quite early. In their studies, they worked on a large regional

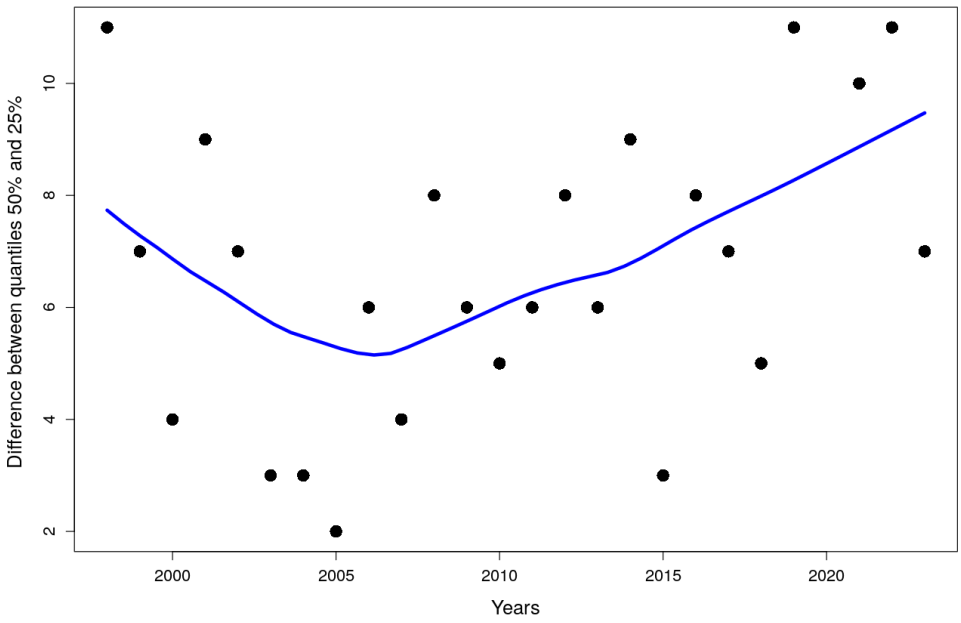


Figure 4.8 – Differences between the quantiles 50% and 25% of p_{phen} as a function of years

scale, i.e. the main range of distribution of A. salmon. This could simply be because local conditions have not followed the general conditions on a regional scale. The rest of the period is in line with Otero et al., 2013 and Kovach et al., 2013, which found that salmon migration is getting earlier and earlier. In Otero et al., 2013, they found that the difference between the date on which they capture 50% of the effective total and the date on which they capture 25% increases. Our results are consistent with theirs, since this difference decreases as the quantile 25% becomes later and increases as the quantile 25% becomes earlier.

$q_{phen}25$ is the only quantity to clearly show a temporal trend. How can we understand these differences?

The role of the preparation

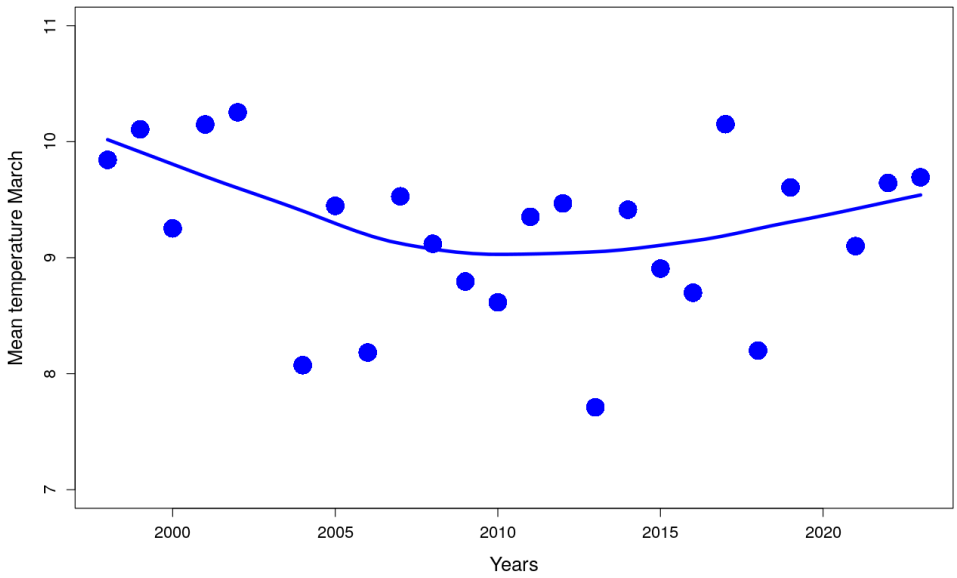


Figure 4.9 – Mean temperature March as function of years. The curves are the "loess" curves

The evolution of $q_{phen}25$ may be due to the preparation process, as q_r25 observe the same tendencies. In fact, at the start of the migration period, few fish are ready, so that the migration dynamic is highly dependent on the accumulation of fish. This dependence may decrease as more fish accumulate. Thus, the temperature evolution in March could explain these evolution. Indeed, the average temperature March slightly fell during the first few years, followed by a slight increase (4.9).

The role of the migration conditions

We saw in the third chapter that the temperature, the discharge and the variation of discharge have an impact on the decisions to migrate. Thus, variation of these factors during the migration period can influence the final phenology.

To find out whether warmer years, or years with higher discharge, were the years with earlier phenology, I ran linear models on the logarithm of the quantile of p_{phen}. The explanatory variables I tested are : the averaged temperature between t_0 and the quantile of interest, the averaged discharge between t_0 and the quantile of interest, and the standard deviation of the discharge between t_0 and the quantile of interest. For example, for the $q_{phen}25$, I averaged the temperature between t_0 and $q_{phen}25$, and for $q_{phen}50$, I averaged the temperature between t_0 and $q_{phen}50$. Then I used the same procedure to choose the more relevant model as for the p_r quantiles. I tested the interaction between the explanatory variables. These selected models are presented in the table 4.3.

Table 4.2 – Model selected for each response variables of the phenology (lines) and the coefficient associated to the explanatory variables (columns). The stars indicate significance with $p-value < 0.01 : `***' p-value < 0.05 : `**', p-value < 0.1 : `*'$. Note that the explanatory variables are not the same for each response variable because they are averaged between t_0 and the quantile of interest.

Symbol	T	Q	σ_Q	R^2
$log(q_{phen}25\%)$	-0.14 *			0.26
$log(q_{phen}50\%)$	-0.09 ***			0.30
$log(q_{phen}75\%)$	-0.07 **	-0.14 **	0.05 *	0.32
$log(q_{phen}90\%)$	-0.08 **			0.20

No interaction was selected. The only explanatory variable that is selected for all four quantiles is the temperature. The two others are selected only for $q_{phen}75$.

As expected, the effect of temperature was negative for all quantiles: the higher the water temperature, the earlier the phenology. This is consistent with our hypotheses and with the literature, which associate warmer water temperature with earlier migration (Kovach et al., 2013; Munsch et al., 2019; Otero et al., 2013).

The discharge also has a negative effect on $q_{phen}75$. As the smolt takes advantage of the increased flows to migrate, we can expect that when the current is on average strong, the stock of migrants will be depleted more quickly.

The effect of the standard deviation of the discharge on $q_{phen}75$ is positive. The years in which the standard deviation of flows is higher are years in which the differences in flow between two time steps are more often negative. In other words, the flow tends to fall from one day to the next, whereas we have seen that the decision to migrate is partly triggered by increases in flow. This explains the positive effect of the standard deviation on $q_{phen}75$.

The mean river discharge, and the standard deviation of the discharge, are only selected for the quantile $q_{phen}75$, while the temperature is selected for all quantiles. On the one hand, this shows the importance of temperature in salmon phenology, both in terms of its importance in preparation and in triggering migration (Chapter 3). On the other hand, these results in no way detract from the importance of river discharge on salmon phenology. Firstly, because the mean and standard deviation can hide very different flow profiles, hence very contrasted p_{phen} profiles. Secondly, because the effect of flow seems to be concentrated on the migration decision, less on preparation. Its effect seems to be more punctual, and therefore explains less of the major trends that emerge from the complete phenology analysis.

The temporal trends in mean temperature between t_0 and the quantiles $q_{phen}25$ and $q_{phen}50$ show patterns taht are consistent with the evolution of the p_{phen} quantiles (Fig. 4.10), i.e. a decrease at the beginning of the period and a slight increase at the end. These trends are less marked between the quantiles $q_{phen}75$ and $q_{phen}90$, which may also explain the absence of clear trends at the end of the migration period.

Conclusion

These results show that the Scorff salmon population, in the fifteen last years, seems to be following the same trend as elsewhere, i.e. an earlier migration, particularly at the start of the migration. The temporal evolution of the first part of the migration is strongly linked with the temporal evolution of the temperature, which seems to act both on the preparation process before the decision to migrate, and on the triggering of the migration. The second part of the migration period is slightly less variable and does not seem to follow a temporal trend. This may be due to the fact that this part depends on a greater number of variables, which can make the signal noisier. It may also be due to the fact that the mean temperature follows no clear trend for this part of the migration.

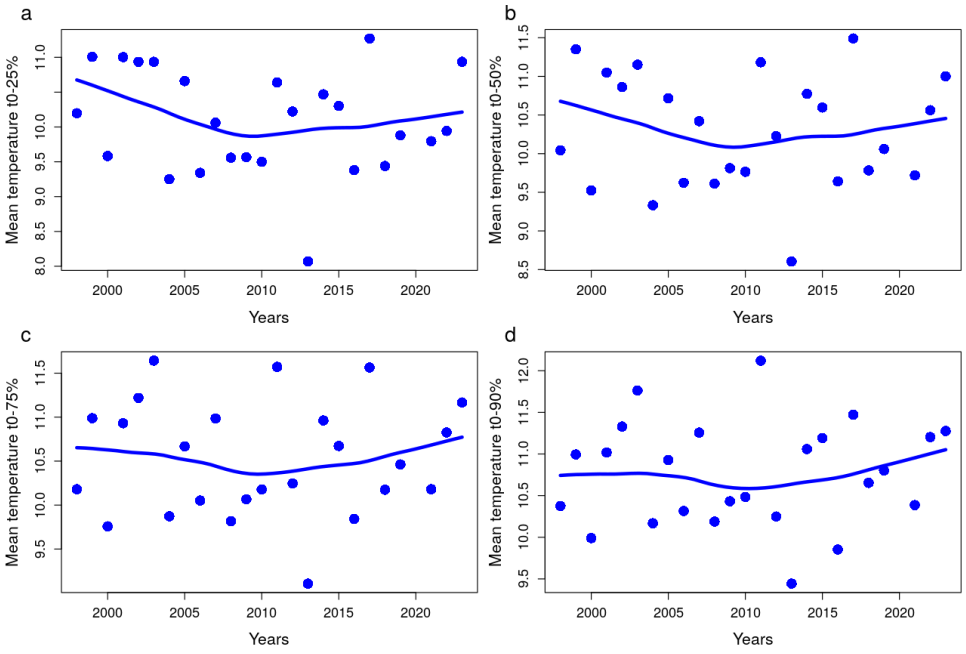


Figure 4.10 – **Mean temperature between t_0 and the quantile of p_{phen} as a fonction of the years.** The curves are the "loess" curves. Mean temperature between between t_0 and a. $q_{phen}25$, b. $q_{phen}50$, c. $q_{phen}75$, d. $q_{phen}90$.

4.4 Projection of the smolt migration phenology and its possible consequences

Temperature and discharge in the Scorff

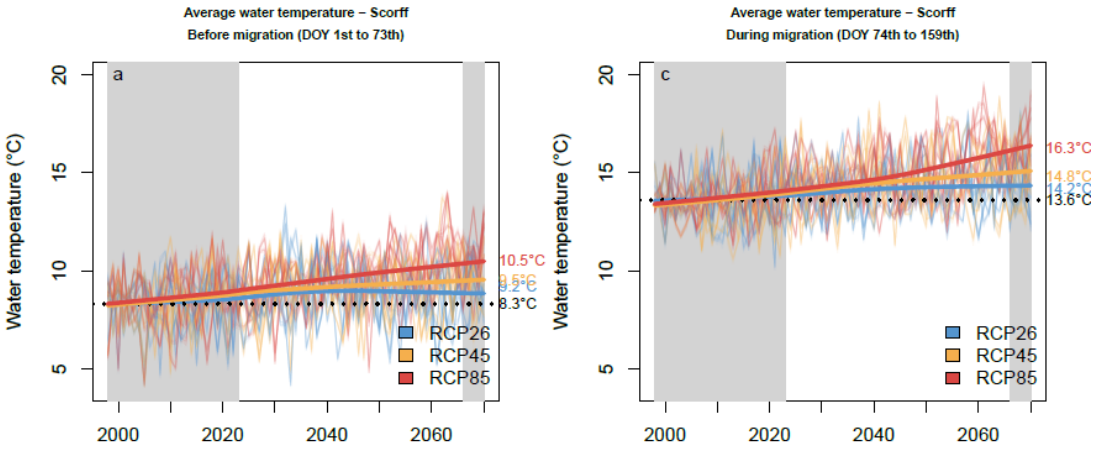


Figure 4.11 – **Projection of the mean water temperature in the Scorff per year under different scenarios** a. Forecast average water temperature from January to mid-March. b. Forecast average water temperature from mid-March to the beginning of June.

Figures 4.11 and 4.12 show projection for the Scorff water temperature and discharge respectively, before and during the migration period. These projections are derived from a hydrological model (https://hydrogr.github.io/airGR/; source of data and analysis: Guillaume Thirel, INRAE HYCAR), which uses SAFRAN analysis from Météo-France to simulate flows in the Scorff under three different IPCC climate scenarios: RCP2.6, RCP4.5, RCP8.5. Based on daily air temperatures and flows, daily water temperatures are reconstructed as in chapter 3 (see 3.5.1).

These projections show that, whatever the scenario, the temperature of the water in the Scorff is likely to rise, both before and during the migration period. These temperature are still in the temperature requirements of the A. salmon for both survival and growth (Elliott et al., 2010).

Thus, given the importance of temperature in the preparation process and in the decision to migrate, we can imagine that this would lead to earlier migration. This increase in temperature could also affect the smoltification, as rapid increases in temperature are likely to reduce the ability of smolts to cope with

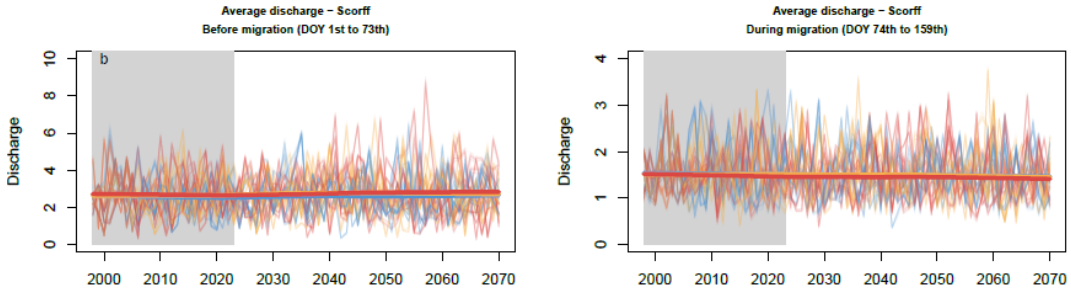


Figure 4.12 – **Projection of the mean Scorff discharge in logarithmic scale per year under different scenarios** a. Forecast average discharge from January to mid-March. b. Forecast average discharge from mid-March to the beginning of June.

the salinity of the water (Bernard et al., 2019), but it is not known whether this effect can delay the migration. However, this rise in temperature could be mitigated to some extent by the behaviour of smolts. These projections only concern the average temperature of the Scorff and may therefore mask spatial heterogeneity. For example, riparian forests can attenuate temperature (Malcolm et al., 2004). Salmon could then reduce their exposure to high temperatures by choosing colder environments, which could mitigate the effect of climate change to a certain extent.

The Scorff is a rain-fed river, so a change in rainfall patterns can alter its discharge patterns. The projections do not predict a change in the amount of rain but rather in the distribution of precipitation over the year. This does not seem to affect the period before and during migration. However, the river discharge depends not only on climatic effects, but also on the way in which humans directly impact that river. There is water collection point in the Scorff (Ganivet et al., 2024), so the future discharge will also depend on the socio-political choices that are made about how water is used. Land-use planning choices, such as soil artificialization or agricultural use, can also have an impact on the river (Ganivet, 2023).

Perspective 2

As river discharge, via precipitation, and water temperature can both be affected by climate change, we can assume that the temporal trend we observe in phenology may continue to get earlier in the future. It would be interesting to make projections with the phenological model, under different climate change scenarios, in order to better understand how climate change may affect salmon phenology.

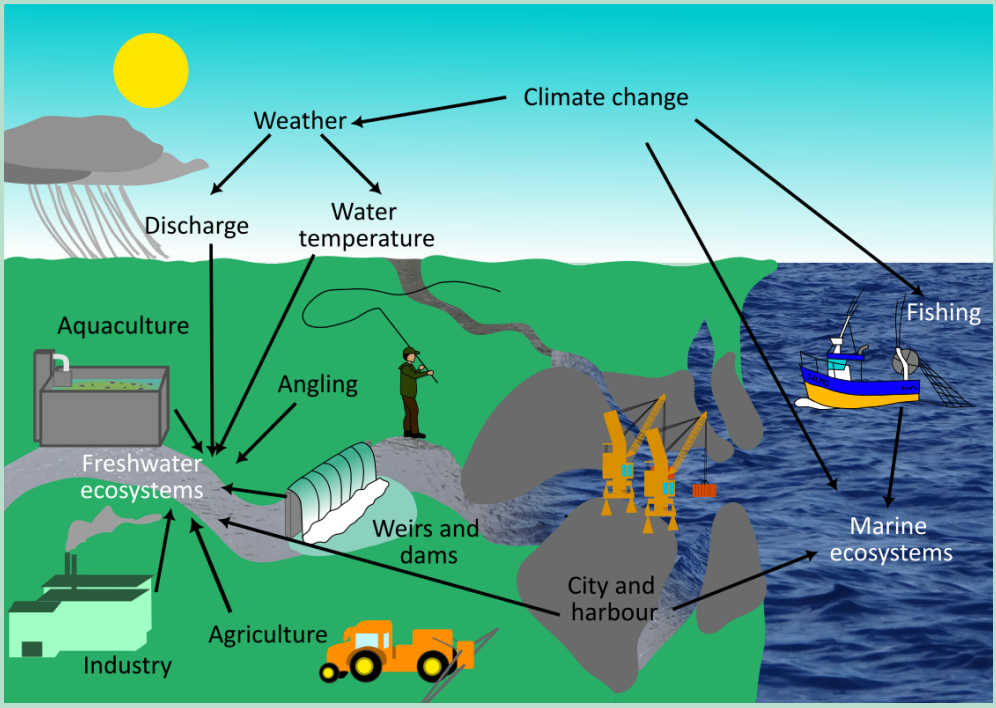
Migration is also controlled by photoperiod (McCormick et al., 1998; McCormick et al., 2011), which does not change from year to year. To determine whether the trend towards earlier migration can persist, it would be interesting to know to what extent the photoperiod can constrain smoltification and the migration decision. This would give us an idea of the extent to which the timing of migration is plastic and how early it can be. Furthermore, salmons can adapt their behaviour to escape warm water, which could mitigate this trend somewhat.

Finally, it does not take into account the potential evolutionary adaptations of salmon. Adaptation could occur if earlier migration has an impact on the salmon fitness.

Perspective 3

Knowing the extent to which migration phenology is plastic could lead to better prediction.

Other influence on the phenology and its consequences



Climate change is just one of the more global changes taking place in the world as a result of anthropogenic pressures. And these other changes can also affect the phenology of species, either alone or in conjunction with climate change. They can also affect the consequences of the phenology such as the synchronicity with favorable environmental conditions for examples. Here some other factors than can impact the smolts migration in the Scorff.

The Scorff catchment area is mainly forested and agricultural, with a few towns and villages. Some industries also border the Scorff, as well as an aquaculture farm. This environment is accompanied by a number of agricultural, domestic, and industrial pollutants, which can affect fish migration and survival. For instance the atrazine, a molecule used in some pesticides (not anymore used in France) reduces the osmoregulation capacity of the smolts, which can increase the risk of mortality in the estuary and delay arrival at sea (Moore et al., 2008). Conversely, psychiatric drugs like oxazepam, by reducing fish anxiety, can increase migration speed (Hellström et al., 2016).This could also make fish bolder, raising the risk of predation (Bouchard et al., 2023; Klaminder et al., 2019).

Other influence on the phenology and migration conditions

There are several weirs and dams on the Scorff. Weirs and dams can impact the swimming performance of smolt, cause injury and delay their migration, that would reduce their migration success (Birnie-Gauvin et al., 2018; Silva et al., 2020; Thorstad et al., 2012).

The Scorff does not flow directly into the sea but into a roadstead, where another river, the Blavet, also flows. This roadstead is urbanised, with several towns and harbours, including the port of Lorient. In addition to the pollutants, the presence of towns and ports can causes perturbations such as artificial light.

Artificial light at night can have important impact on the migration: for instance, it can disorientate and disturb the migratory routes of birds (Newton, 2024b). This can also alter the migratory behaviour of fish, such as eel and salmon (Riley et al., 2012). Long term impact is not known but it could delay from some hours to a day the migration of smolts (Riley et al., 2012) and increase the predation level (Nelson et al., 2021), which is already a major mortality factor during migration.

Finally, other factors can affect survival during migration in rivers, but also on arrival in estuaries and at sea. Harbours are an important vector of introduction of alien invasive species (AIS) (e.g. Antajan et al., 2014), in particular because of the hull and ballast water of commercial vessels (Breton, 2014). AIS are one of the main threats on the biodiversity (Smith, 2020): these species can disturb the ecosystem, by parasitism, by introduction of diseases or by competition (for food or/and space). So, by disrupting the estuary and the marine ecosystem, they can have an impact on salmon food during their first few months at sea. River and sea fishing also disrupt the trophic networks (Hernvann et al., 2020). As a result, competition for food can intensify, as can predation pressure. Smolts and post-smolts can also be by-catch of these fishing activities.

4.4.1 Earlier = smaller?

Reminder

The phenology of smolt migration is important because it is linked to their size as post-smolts. The earlier they migrate, the smaller they are as post-smolts. Post-smolts size is thought to be an important factor in their survival at sea, which ultimately determines their fitness (see section 1.2.3)

Our model only describes the mechanisms behind salmon phenology, but does not address the consequences for their fitness. However, every smolts captured are measured and weighted, so we have a proxy of their fitness: their size and weight when arriving at sea.

To test whether the phenology of salmon correlates with smolts quality, depending on when they migrate during the outmigration window, I ran linear model as in the section 4.2 and 4.3. My explanatory variables are $q_{phen}25$, $q_{phen}50$, $q_{phen}75$ and $q_{phen}90$. I tested the relationship between these quantiles and smolt size, weight and condition. The condition is the Fulton coefficient (Ricker, 1975), calculated as follows: $K = W/(FL^3)$ where W is the weight of the fish and FL is its fork length. The aim is to check whether the quality of the smolts changes during the emigration period. Thus, for each of the 3 quantities, the size, the weight and the condition, I calculated the mean between t_0 and $q_{phen}25$, then between $q_{phen}25$ and $q_{phen}50$, between $q_{phen}50$ and $q_{phen}75$ and between $q_{phen}75$ and $q_{phen}90$. I tested only the 1+ smolts to assess only the effect of the phenology on smolts conditions, and not of the age at migration 1 or 2 on smolts conditions.

Neither fork length nor weight were significant for any of the relationships tested. On the contrary, the condition factor presents some significant relationship, illustrated by the table 4.4.1 and the figure 4.13. The relation is negative for all case: the earlier the phenology, the better is the smolt's body condition. The same trend emerges regardless of the time of departure during the emigration window: regardless of the time of departure relative to the migration period, an earlier phenology is associated with better condition.

The fact that an early phenology is associated with a better condition can be explained by what was seen in the previous sections. Phenology is earlier when growing conditions are better. So, if the growth rate is higher, this compensates for the fact that the fish have less time to grow.

My results are based on the average size of 1+ smolts. This makes it impossible to discern the various effects of life history strategy, inter-individual variability, etc. whereas A. salmon is known to present a large variety of strategies (Sigourney et al., 2013). Nevertheless, these results are in contradiction

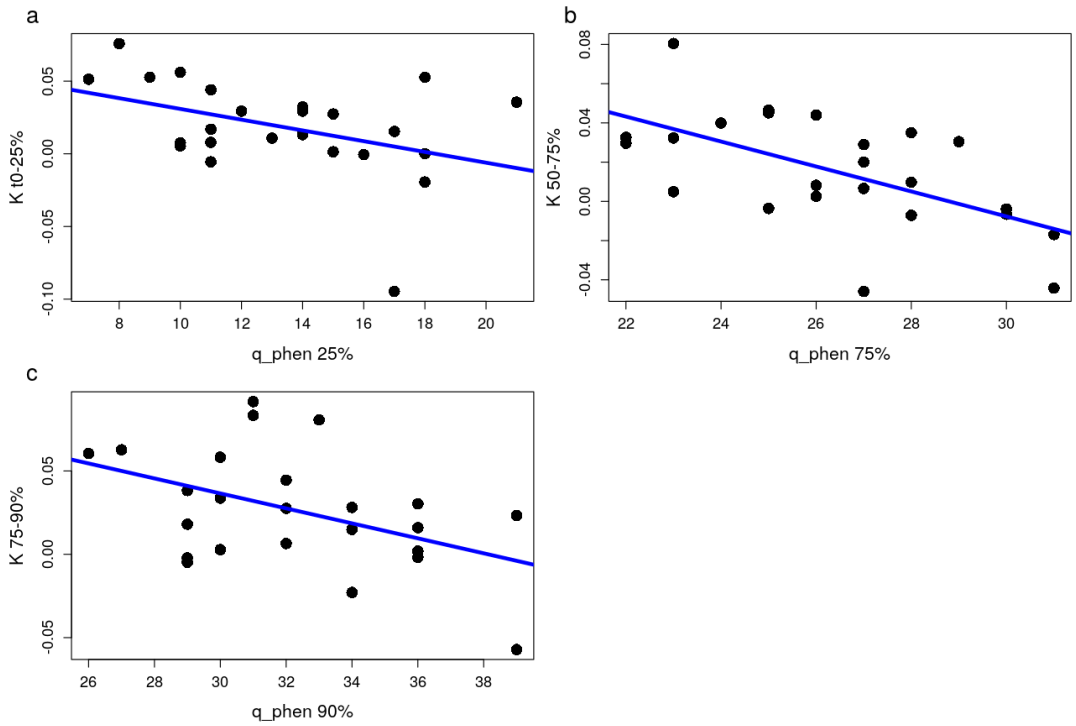


Figure 4.13 – **Factor condition K as function of the respective q_{phen}.** The straight line is that produced by the corresponding linear model. a. Coefficient condition K between t_0 and $q_{phen}25\%$. b. Coefficient condition K between $q_{phen}50\%$ and $q_{phen}75\%$. c. Coefficient condition K between $q_{phen}75\%$ and $q_{phen}90\%$.

Table 4.3 – Significant models explaining the condition (lines) by the phenology (columns). The stars indicate significance with $p-value < 0.01 : `***' p-value < 0.05 : `**', p-value < 0.1 : `*'$. Note that the explanatory variables are not the same for each response variable because they are averaged between t_0 and the quantile of interest.

Symbol	q_{phen}	R^2
$log(K_{t_0-25\%})$	-0.003 *	0.16
$log(K_{25\%-50\%})$		
$log(K_{50\%-75\%})$	-0.006 ***	0.32
$log(K_{75\%-90\%})$	-0.004 **	0.20

with the general hypothesis, that earlier phenology is associated with smaller smolts (Arevalo et al., 2021; Munsch et al., 2019; Simmons et al., 2021a). However, this hypothesis is rarely tested. In addition, in Munsch et al., 2019, the study is based on Chinook salmon, on the salmon's most southerly range, in a system where the cold water supply depends on the snowpack, where the water temperature can exceed 15°C in April, (which is not the case of the Scorff, see fig. 4.10), and with a lot of human construction such as dams, reservoirs etc. All these differences may be at the root of very different dynamics. Authors suggest that in the hottest year, the water temperature was too high, so Chinook salmon preferred to migrate earlier to escape these temperatures. It may be that the temperature in the Scorff has not (yet?) reached a sufficiently high level to cause a period of "truncated" growth, but rather, for the time being, to reinforce growth.

Warmer waters in late winter and early spring in the Scorff appear to promote both larger smolts and earlier migration. For maintaining their size at migration, they must still have a sufficient period of growth/preparation before migrating. If the water temperature in the Scorff warms up in winter, what is projected to happen, allowing growth at that time, then perhaps this growth will compensate for the early migration and maintain a sufficiently large size. On the other hand, if the rise in temperature triggers a migration that is too early, thereby truncating the growth period, the trend could be reversed.

To conclude this section, the earlier migration of smolts does not appear to correlate with a negative impact on the body condition of salmon in the Scorff for the time being. As size is an approximation of the fitness of post-smolts, we can therefore assume that there is no reduction in the fitness of post-smolts due to advanced phenology.

4.4.2 Possible impact on the fitness during migration

In Munsch et al., 2019, authors found that departure data is not correlated with the date of arrival at sea. This adds even more nuance. If the smolt is triggered by the rise in temperature to migrate, but is not completely ready, it may take longer to arrive at sea. Some smolts have been observed waiting and making numerous trips back and forth between the river and the estuary (Holm et al., 1982; Lacroix et al., 1996; Renkawitz et al., 2012; Lilly et al., 2022; Artero et al., 2020; Halfyard et al., 2013). Some of these behaviours have been linked to their progress in smoltification (Lacroix et al., 1996): the least smoltified smolts were more prone to these behaviours. It is conceivable that if the smolt is triggered too early to migrate, it can continue to grow and prepare itself before actually arriving at sea by reducing its migration speed. This would compensate for the early departure. However, this could be accompanied by a higher risk of predation during migration, particularly near the estuary, where there are many predators for smolts. As a result, by growing before reaching the sea, they would reduce their risk of predation at sea, but increase it in rivers and estuaries. Nevertheless, this behaviour of staying at the entrance to the estuary was not observed for the Scorff population during acoustic monitoring (C.Artero pers.com).

4.4.3 Possible mismatch and asynchrony

Reminder

It is also assumed that the phenology of smolt migration is important because it allows post-smolts to encounter conditions that will enable them to grow and survive during their first few months at sea. These conditions are biotic (food abundance and quality) and abiotic (temperature for example).

I have no data or studies indicating the phenology of salmon prey along their migration routes. I have therefore not been able to look for a signal of a shift between their phenology and that of their prey. Nevertheless, it is likely that the phenology of post-smolt prey is shifting as a result of climate change. For example, herring larvae (one of the salmon prey) are developing earlier and earlier in the Baltic Sea, associated with warmer conditions (Weigel et al., 2021). Pelagic fish have quite similar ecology, so we might expect changes in their phenology to follow the same pattern. But as phenological changes vary between fish species (Walraven et al., 2017), this remains to be explored. Especially as post-smolts are opportunist (Rikardsen et al., 2010), they can probably manage a mismatch with some of their prey by turning to others. So, how quickly the salmon's prey modifies (or not) their phenology is essential to know in order to be able to study the existence of a mismatch between the arrival of post-smolts at sea and the availability of food. Thus, we have few information on both the salmon marine phase and post-smolt preys phenology

shifting, which can explain why no study have directly tested the mismatch hypothesis.

Perspective 4

The phenology of salmon is changing, and it would seem that the phenology of its prey is changing too. Data and studies on changes in the phenology of salmon prey would make it possible to analyse whether or not their phenological shift follow the same rhythms.

Studies have used indirect indicators of the availability of salmon prey: the index of primary production (Olmos et al., 2020) and the energy of zooplankton available for forage fish larvae (Tyldesley et al., 2024), and have found that survival at sea is indeed partly linked to these indicators. Furthermore, Mäntyniemi et al., 2002 found that smolt survival correlated with herring recruitment, suggesting that herring abundance is a key determinant of smolt survival. Therefore, post-smolt survival does seem to be linked with their food abundance. This is particularly important given that climate change and fishing are altering species composition, such as in the Celtic sea (Hernvann et al., 2020). Scorff post-smolts pass close to the Celtic Sea. These trends are worrying for the survival of post-smolts. However, the abundances of blue whiting, one of the main prey species of post-smolts in this region (Utne et al., 2022), have changed less in recent years compared with other species (Hernvann et al., 2020). Therefore, whether declining survival is due to the mismatch between post-smolts and their prey, or to the general decline in prey abundance (with potentially increased competition for the resource) is not known. It could also be, at least in part, that these common declining trends of prey abundance and post-smolts survival are the result of general deteriorated environmental conditions.

Furthermore, plankton phenology is linked with its quality as food: shorter and earlier planktonic bloom is associated with lower zooplankton energy available to forage fish larvae (Tyldesley et al., 2024). We can therefore assume a cascading effect: if the quality of the plankton (by modifying the species in the assemblage) decreases, the fish larvae quality could decrease too, which could ultimately have an impact on the quality of the post-smolts. This has been observed for pilchard (*Sardina pilchardus*) and anchovies (*Engraulis encrasicolus*), which are becoming smaller and smaller, which seems to be linked to changes in the abundance and quality of food, as well as potentially increased competition for these resources (Brosset et al., 2016). Note that salmon also consume plankton, so it can also be directly impacted by the change in plankton quality.

However, we do have indirect results suggesting the importance of prey abundance and quality on post-smolt survival. Thus, even if smolts are able to feed on numerous prey, they may not be able to cope with the downward trend in

several of their preferred prey, and a mismatch would add to the difficulty of finding sufficient food.

Sea temperature at the post-smolt entry is assumed to be one of the important factors for the post-smolt survival (Hvidsten et al., 1998; Olmos et al., 2019). The sea temperature at the end of the Lorient roadstead in both March and April seems to be increasing (Fig 4.14). Earlier migration may allow smolts to follow lower seawater temperatures, i.e. to maintain synchrony with the favorable seawater temperatures. The mean river water temperature in April and the seawater temperature are quite well correlated (Pearson correlation: 0.86). Thus, for now, the river temperature seems to be a reliable cue of the seawater temperature at the beginning of their oceanic migration. Therefore, we can assume that for now, there is no asynchrony between the arrival at sea and the favorable temperature conditions. However, for this phenomenon to persist, the correlation between the temperature of the river water and the temperature of the sea water must be maintained, which is not certain.

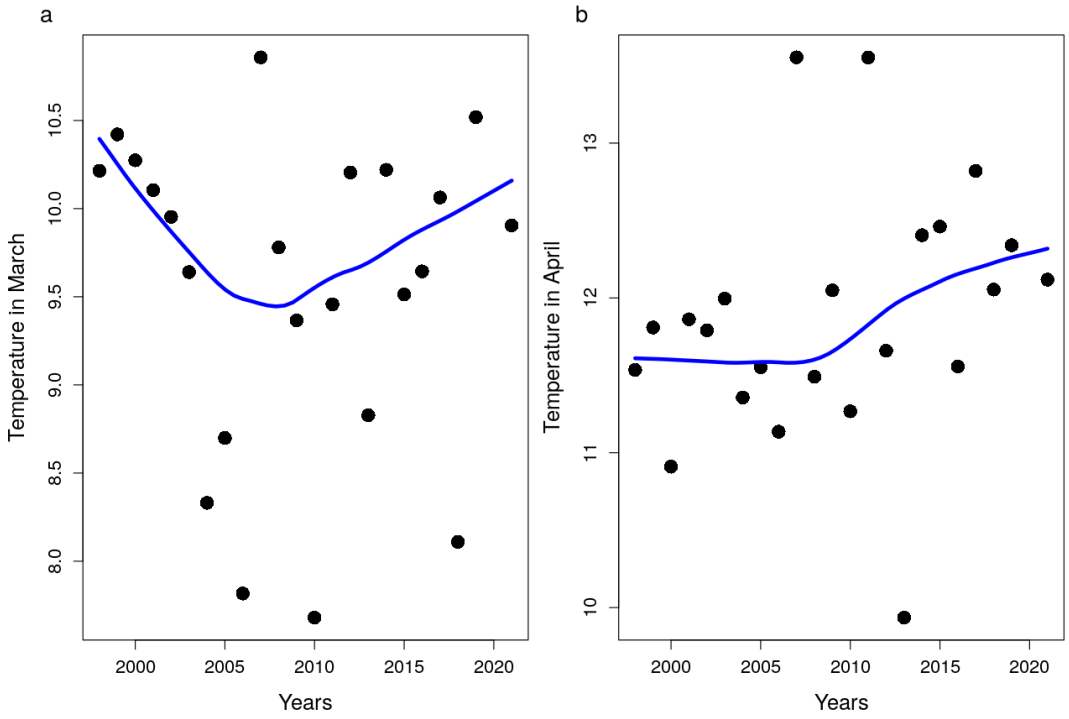


Figure 4.14 – **Temperature at the sea entry in March and April**. The blue line is the "loess" line. Temperature at 0.5m in a. March and b. April. The data come from EU Copernicus Marine Service information - https://marine.copernicus.eu. This is the temperature of the 1st of each month from 1998 to 2021, excluding 2020.

The temperature on arrival at sea is not the only important temperature: the temperature along the migration route could have an impact on post-smolt survival. To assess the impact of early migration on asynchronism with optimal seawater temperature, we could examine the sea temperature along the migration route of the post-smolt. This could be done using a modelled reconstruction with an assumed route, but also using a data storage tag, as in Woillez et al., 2016. This would allow tracking of the temperatures that the post-smolts encounter and a better idea of their route. However, this type of data storage tag is quite heavy for post-smolts and may not be retrieved.

4.4.4 Conclusion

The advancement of salmon phenology is correlated with better body condition, which seems to be linked to better growth conditions, according to section 4.2. Due to lack of data, no mismatch or asynchrony can be demonstrated. Thus, we cannot detect any negative effect of the advancement of phenology due to climate change on salmon fitness. However, climate change, and the socio-political choices that will be made regarding water management and land-use planning, could reinforce the modification of smolts phenology in the future, which could have consequences for post-smolts fitness.

4.5 Personal reflections on modelling and climate change: friend or foe?

Nowadays, many scientists are questioning how they work and conduct their career in relation to climate change. For example, some are questioning their use of transport for their career, particularly air travels (Limburg et al., 2021), while others are advocating scientific activism (Racimo et al., 2022). Indeed, there is a paradox: while science makes it possible to study global change, it is also a source of pollution. Let us take the example of modelling. Digital tools make it possible to carry out calculations that would be (almost) impossible to do by hand (Bayesian statistics are a good example), and therefore offer infinite modelling possibilities. Models to understand complex phenomenon can be developed, incorporating a wide range of data and knowledge. This is why modelling using numerical tools is necessary to address certain issues concerning anthropogenic pressures on climate and biodiversity. For example, the IPCC's models incorporate a wealth of knowledge to provide a better understanding of the changes underway and make reliable projections (IPCC, 2014). This enables the IPCC to advise political decision-makers (IPCC, 2023). Models have also become indispensable in fisheries management. Stock assessment models are used to advise political decision-makers on the measures to be applied, such as quotas. In some cases, this makes a major contribution to maintaining wild fish stocks (Gascuel, 2019).

In the same time, digital is a major source of pollution. One of the causes of this pollution is the production and transport of computer hardware. Other causes are the use of these energy-hungry equipment (Than Oo et al., 2023). As we develop more complex models, we need more powerful devices. As we advocate for more data, we need more stockage capacity. Add to that all the tools on which we are increasingly dependent, such as the Internet, Artificial Intelligence (Than Oo et al., 2023)... This has impacts on the environment. My thesis is part of this paradox, because to study a species in decline, I ran models for hours, even days, sometimes on several computers at the same time. I made extensive use of IT tools for bibliographic research, coding, communication, writing, etc. In addition, I have travelled multiple times, for example to go to the Scorff, several hundred kilometres from the laboratory, or to attend training courses and conferences. Without even considering the potential impact of data collection on the environment, carrying out my thesis has repercussions.

Some may think that this is a necessary cost of producing knowledge. After all, science has to produce knowledge and findings that can then lead society to 'lucidity' (Jacquard et al., 2005). Therefore, this is a necessity to know more about climate change if we are to combat it. On the other hand, some scientists think that they "have a responsibility to act towards a reduction of [their] carbon load" (Limburg et al., 2021). It is also our responsibility to use new technologies wisely, and our duty not to use all the powers they offer us (Jacquard et al., 2005).

It is certainly possible to adapt our practices, or to direct our research in a different direction to reduce their impacts. Perhaps one day, due to the need to save energy and share it more effectively, or with society's growing awareness of the impact of digital tools, we will see the emergence of ethical laws/recommendations governing the use of digital technology in science, as is the case today with bioethics laws. However, digital impacts on the environment are quite "invisible" and abstract to the public (Than Oo et al., 2023). Therefore, there is no demand for such laws. In this case, the responsibility for adapting practices lies with the researcher. In other words, the researcher is responsible for its use of technologies. Whether or not they question these uses depends on their sensitivity and their awareness of the impacts of their scientific practices. It also depends on whether they think they should be exemplary for the rest of society, or whether their role is above all to produce knowledge. Added to this, the pressure on researchers to publish more and more ("publish or perish") can prevent them from being able of make such changes, or even questioning their practices. Modelling is at the heart of the changes to come.

4.6 General conclusion

Our results suggest that the capture process can have a significant impact on the results. This study therefore adds to the existing literature to warn that the observation process in biological studies must be carefully examined. This thesis has demonstrated that mechanistic modelling approach enable a better understanding of the A. salmon migration dynamics. This model can be extended to examine the role of the migration phenology in the current decline in A. salmon populations. I also believe that the methodological approaches used in this thesis could serve as a basis for studying the migration phenology of other organisms.

Appendices

Appendix A: CMR model code, in Nimble (Valpine et al., 2024)

```
model.obs <- nimbleCode({

 # DESCRIPTION ####

 # i: day of marking

 # j: day of recapture

 # y: year

 ## Data  ##

 # n_rec[i,j, y]: number of fish marked on day i and recaptured on day j in year y

 # dis[i, y]: standardized discharge at day i in year y


 ## Migration process ##

 # nu[i, j, y]: numbers of individuals marked on day i and passing at trap2 from day j in year y

 # pi[i, j, y]: probability for an individual marked on day i to pass at trap 2 on day j  in year y

 # lambda[i, j, y]: hazard, represents the intensity of passage of marked individuals at trap2

 # mu[y]: average migration time between traps in year y

 # w[j,y]: is a weighing factor comprised between $0$ and $1$, reflecting daily variations in both the
schedule of trap checks  and the within-day timing of smolts passage at trap.


 ## Recapture process ##

 # p_trap2[j,y]: the capture probability at trap 2 on day j in year y

 # beta_trap2[1,y]: the mean capture probability in year y

 # beta_trap2[2,y]: the effect of the standardized environmental covariate X[j,y] (here, discharge dis)

 # eta_trap2[y]: over-dispersion parameter in year y.

 # rho_trap2[y] is a positive correlation coefficient indicating the degree of aggregation of the
individuals at capture



 ### PRIORS ####

 # Prior for marking effect

 #standard deviation

 pre_sigma_mark ~ dchisq(5)

 sigma_mark <- pre_sigma_mark/5

 tau_mark <- 1/sigma_mark^2
```

```
# Prior for migration effect
#standard deviation
pre_sigma_migr ~ dchisq(5)
sigma_migr <- pre_sigma_migr/5
tau_migr <- 1/sigma_migr^2

# Prior for weighting factor
mean_w_all ~ dbeta(2.5, 2.5)
inv_a_b_1_w_all ~ dbeta(2.5, 47.5)# 1/(alpha + beta + 1), entre ]0, 1[
# donne des valeurs entre 1 et 4 principalement
a_w_all <- ((1 - inv_a_b_1_w_all) * mean_w_all)/inv_a_b_1_w_all
b_w_all <-  a_w_all * (1 - mean_w_all)/mean_w_all


# Prior for intensity of passage
mean_mu ~ dbeta(2.5, 7.5)
rho_mu ~ dbeta(2.5, 47.5)
a_mu <- ((1 - rho_mu) * mean_mu)/rho_mu
b_mu <-  a_mu * (1 - mean_mu)/mean_mu


# Prior for regression coefficient
# intercept
mean_beta_trap2_1 ~ dbeta(2.5, 2.5)
inv_a_b_1_beta_trap2_1 ~ dbeta(2.5, 47.5)
a_beta_trap2_1 <- ((1 - inv_a_b_1_beta_trap2_1) * mean_beta_trap2_1)/inv_a_b_1_beta_trap2_1
b_beta_trap2_1 <-  a_beta_trap2_1 * (1 - mean_beta_trap2_1)/mean_beta_trap2_1
```

```
# slope
mean_beta_trap2_2 ~ dnorm(0, 1)
pre_sigma_beta_trap2_2 ~ dchisq(5)
sigma_beta_trap2_2 <- pre_sigma_beta_trap2_2 * 1/5
tau_beta_trap2_2 <- 1/sigma_beta_trap2_2^2

# Prior for sigma_trap2
pre_mean_sigma_trap2 ~ dchisq(5)
mean_sigma_trap2 <- pre_mean_sigma_trap2/5
pre_shape_sigma_trap2 ~ dchisq(5)
shape_sigma_trap2 <- pre_shape_sigma_trap2 + 2


#hyperparams eta_trap2 # Over-dispersion parameter
mean_rho_trap2 ~ dbeta(2.5, 7.5)
inv_a_b_1_rho_trap2 ~ dbeta(2.5, 47.5)# 1/(alpha + beta + 1), entre ]0, 1[
a_rho_trap2 <- ((1 - inv_a_b_1_rho_trap2) * mean_rho_trap2)/inv_a_b_1_rho_trap2
b_rho_trap2 <-  a_rho_trap2 * (1 - mean_rho_trap2)/mean_rho_trap2

## Probability to lose tags ##
p_lost ~ dbeta(lost, det)

# LIKELIHOOD ####
# Loop over years
for(y in 1:n_years){#year

 ## 1. MIGRATION PROCESS ####
 ### Migration and timing of passage of marked individuals at trap2  ####
 for (i in 1:D) {
   nu[i, i:(i + 9), y] ~ dmulti(pi[i, 1:10, y], size = n_mark[i, y])
 }
```

```
  ### Probability pi for individual marked on day i to pass at trap 2 on day j in year y  ####
  for (i in 1:D) {
   pi[i, 1, y] <- 1 - exp(- w[i, y] * lambda[i, 1, y])
   for(j in 2:9){
     pi[i, j, y] <- (1 - sum(pi[i, 1:(j - 1), y])) * (1 - exp(- w[i + j - 1, y]*lambda[i, j, y] - (1 - w[i + j - 2, y]) *
lambda[i, j - 1, y]))
    }
   pi[i, 10, y] <- 1 - sum(pi[i, 1:9, y])
  }

  ### Intensity of passage of marked individuals at trap2  ####
  for (i in 1:D) {
   for (j in 1:9) {
     log_lambda[i, j, y] <- alpha_base[y] + alpha_mark[i, y] + alpha_migr[i + j - 1, y]
     lambda[i, j, y] <- exp(log_lambda[i, j, y])
   }
  }

  # Average intensity of passage at trap2
  #mean
  pre_mu[y] ~ dbeta(a_mu, b_mu)
  mu[y] <- 9 * pre_mu[y]
  alpha_base[y] <- log(1/mu[y])


  # Day of marking effect
  for (i in 1:D) {
   alpha_mark[i, y] ~ dnorm(mean = 0, sd = sigma_mark) #marking
  }
```

```
  # Day of passage effect
  for (i in 1:(D + 9)) {
   alpha_migr[i, y] ~ dnorm(mean = 0, sd = sigma_migr) #migr
  }

  # Weighting factor: weights may reflect daily variations in both the schedule of trap checks and the
within-day timing of smolts passage at trap2
  for(i in 1:(nd + 9)){
   w[i, y] ~ dbeta(a_w_all, b_w_all)
  }


  ## 2. RECAPTURE PROCESS ####
  #Regression coefficients for the probability of capture at trap 2
  exp_beta_trap2[y] ~ dbeta(a_beta_trap2_1, b_beta_trap2_1)
  beta_trap2[1, y] <- logit(exp_beta_trap2[y])
  beta_trap2[2, y] ~ dnorm(mean_beta_trap2_2, tau_beta_trap2_2)

  # Precision and standard deviation for the probability of capture at trap 2
  sigma_trap2[y] ~ dgamma(shape = shape_sigma_trap2, scale =
mean_sigma_trap2/shape_sigma_trap2)
  tau_trap2[y] <- 1/sigma_trap2[y]^2

  # Over-dispersion parameter
  rho_trap2[y] ~ dbeta(a_rho_trap2, b_rho_trap2)
  eta_trap2[y] <- (1 - rho_trap2[y])/rho_trap2[y]
```

```
  ### Recapture of marked individuals at trap2 ####
  for (i in 1:(D - 9)) {
   for (j in i:(i + 8)) {
     n_rec[i, j, y] ~ dbetabin(alpha = alpha_trap2[j, 1, y], beta = alpha_trap2[j, 2, y], size = nu[i, j, y])
   }
  }
  for (i in ((D - 9) + 1):D) { # Last steps
   for (j in i:D) {
     n_rec[i, j, y] ~ dbetabin(alpha = alpha_trap2[j, 1, y], beta = alpha_trap2[j, 2, y], size = nu[i, j, y])
   }
  }

  ### Probability of capture at trap2  ####
  for (i in 1:D) {
   logit_p_trap2[i, y] ~ dnorm(beta_trap2[1, y] + beta_trap2[2, y] * dis[i, y], tau_trap2[y])
   p_trap2[i, y] <- 1/(1 + exp(-logit_p_trap2[i, y]))

   alpha_trap2[i, 1, y] <- p_trap2[i, y] * (1 - p_lost) * eta_trap2[y]
   alpha_trap2[i, 2, y] <- eta_trap2[y] - alpha_trap2[i, 1, y]

  }
 }#year

})
```

Apendix B: Number of migrants model code, in Nimble (Valpine et al., 2024)

```
model.obs <- nimbleCode({

 # DESCRIPTION ####
 # i: day
 # y: year
 # ni: beginning of the abundace estimation in year y
 # nd: end of the abundace estimation in year y

 ## Data  ##
 # n_capt[i, y]: number of fish captured on day i in year y
 # dis[i, y]: standardized discharge at day i in year y

 ## Recapture process ##
 # p_trap2[j,y]: the capture probability at trap 2 on day j in year y
 # eta_trap2[y]: over-dispersion parameter in year y.

 ## Number of migrants##
 # mean_theta[y]: mean number of unmarked individuals passing at trap2 in year y
 # n_unmarked[i, y]: number of fish migrating unmarked at day i in year y
 # ntot[y]: total number of migrants in year y

  #hyperparameters
  shape_theta ~ dgamma( 1,  1)
  mean_n ~ dnorm(log(28.5), 1)

  pre_sigma_mean ~ dchisq(5)
  sigma_mean <- pre_sigma_mean/5
  tau_mean <- 1/sigma_mean^2

  ## Probability to lose tags ##
```

```
    p_lost ~ dbeta(lost, det)

   for(y in 1:year){#year

     mean_theta[y] ~ dlnorm(mean_n, tau = tau_mean)

     prob[y] <- shape_theta / (shape_theta + mean_theta[y])



     for (i in ni[y]:nd[y]){#days

       # Number of fish migrating unmarked
       n_unmarked[i, y] ~ dnegbin(prob = prob[y], size = shape_theta)

       ## Beta-Binomial
       alpha_trap2[1, i, y] <- eta_trap2[y] * p_trap2[i, y]
       alpha_trap2[2, i, y] <- eta_trap2[y] * (1- p_trap2[i, y])
      n_capt[i, y] ~ dbetabin(alpha = alpha_trap2[1, i, y], beta = alpha_trap2[2, i, y], size =
n_unmarked[i,y])



       # Number of fish marked (did not lose their tags)
       n_mark_unlost[i, y] ~ dbinom(1 - p_lost, n_mark_tot[i, y])
     }#end days

     # total migrants
     ntot[y] <- sum(n_unmarked[ni[y]:nd[y], y]) + sum(n_mark_unlost[ni[y]:nd[y], y])

   }#year

}) # end model
```

Apendix C: phenological model code, in Nimble (Valpine et al., 2024)

```
model.phen <- nimbleCode({
 #### DESCRIPTION ####
 # i: day
 # y: year

 ## Data  ##
 # n_trap1[i, y]: number of fish captured on day i in year y in trap 1
 # n_trap2[i, y]: number of fish captured on day i in year y in trap 2
 # dis[i, y]: standardized discharge at day i in year y
 # var_dis[i, y]: standardized variations (difference between time step) of the discharge
 # temp[i, y]: standardized temperatures

 ## Migration process ##
 # preparation
 # t0[y]: starting date in year y
 # m[y]: median of the Weibull distribution in year y
 # q90[y]: quantile 90% of the Weibull distribution in year y
 # lambda_r_0[y]: hazard at time step 0
 # lambda_r[i, y]: hazard at day i in year y
 # p_r_0[y]: probability to be ready at time step 0 in year y
 # p_r[i, y]; probability to be ready at day i in year y

 #migration
 # p_migr_0: probability of departure at time step 0
 # p_migr[i, y]: probability of departure at day i year y

 #phenology
 # psy_0: time lag from one trap to the next at time step 0
 # psy: time lag from one trap to the next
 # p_pheno_0[y]: probaibility to be in migration at time step 0 in year y
 # p_pheno[i, y]: probaibility to be in migration at day i in year y
```

```
## Capture process ##

# p_trap1[i,y]: the capture probability at trap 1 on day i in year y

# beta_trap1[1,y]: the mean capture probability in year y at trap 1

# beta_trap1[2,y]: the effect of the standardized environmental covariate X[j,y] (here, discharge dis) at trap 1

# eta_trap1[y]: over-dispersion parameter in year y.

# rho_trap1[y] is a positive correlation coefficient indicating the degree of aggregation of the individuals at capture


# p_trap2[i,y]: the capture probability at trap 2 on day i in year y

# beta_trap2[1,y]: the mean capture probability in year y

# beta_trap2[2,y]: the effect of the standardized environmental covariate X[j,y] (here, discharge dis)

# eta_trap2[y]: over-dispersion parameter in year y.

# rho_trap2[y] is a positive correlation coefficient indicating the degree of aggregation of the individuals at capture




Q <- log(log(10)/log(2)) #constant


#### Hyperparameters for phenology process #####

## preparation ##

#90% quantile

mean_q90 ~ dbeta(2.5, 2.5)

rho_q90 ~ dbeta(2.5, 47.5)

a_q90 <- ((1 - rho_q90) * mean_q90)/rho_q90

b_q90 <-  a_q90 * (1 - mean_q90)/mean_q90


#median

mean_m ~ dbeta(2.5, 2.5)

rho_m ~ dbeta(2.5, 47.5)
```

```
a_m <- ((1 - rho_m) * mean_m)/rho_m
b_m <-  a_m * (1 - mean_m)/mean_m

#psy_0 and psy
psy_0 ~ dbeta(2.5, 2.5)
psy ~ dbeta(2.5, 2.5)

#t0
mean_t0 ~ dbeta(2.5, 2.5)
rho_t0 ~ dbeta(2.5, 47.5)
a_t0 <- ((1 - rho_t0) * mean_t0)/rho_t0
b_t0 <-  a_t0 * (1 - mean_t0)/mean_t0

#standard deviation
sigma_p_r <- 0.1
tau_p_r <- 1/sigma_p_r^2

##Departure ##
# beta discharge
beta_migr_dis ~ dnorm(0, 1)
#beta discharge variation
beta_migr_var ~ dnorm(0, 1)
#beta temperature
beta_migr_temp ~ dnorm(0, 1)

#beta intercept
beta_migr_mean ~ dnorm(0, 1)

#p migr_0
p_migr_0 ~ dbeta(2.5, 2.5)#shape, rate
logit_p_migr_0 <- logit(p_migr_0)
```

```
#standard deviation
pre_sigma_migration ~ dchisq(5)
sigma_migration <- 1/5 * pre_sigma_migration
tau_migration <- 1/sigma_migration^2


##### Capture process #####
## trap1 ##
#intercept
mean_beta_trap1_1 ~ dbeta(2.5, 2.5)
rho_beta_trap1_1 ~ dbeta(2.5, 47.5)
a_beta_trap1_1 <- ((1 - rho_beta_trap1_1) * mean_beta_trap1_1)/rho_beta_trap1_1
b_beta_trap1_1 <-  a_beta_trap1_1 * (1 - mean_beta_trap1_1)/mean_beta_trap1_1

#informative prior
mat_trap1[1:4] ~ dmnorm(mat_mean_trap1[1:4], mat_prec_trap1[1:4, 1:4])
rho_trap1 <- 1/((1 + exp(- mat_trap1[1])))#rho trap 1
eta_trap1 <- (1 - rho_trap1)/rho_trap1
sigma_trap1 <- exp(mat_trap1[2])#standard deviation trap 1
tau_trap1 <- 1/sigma_trap1^2
mean_beta_trap1_2 <- mat_trap1[3] #hyperparameter discharge effect
sigma_beta_trap1_2 <- exp(mat_trap1[4])#hyperparameter discharge effect
tau_beta_trap1_2 <- 1/sigma_beta_trap1_2^2


## trap2 ##
#informative prior
mat_dispersion[1:2] ~ dmnorm(mat_mean_od[1:2], mat_prec_od[1:2, 1:2])
rho_trap2 <- 1/((1 + exp(- mat_dispersion[1]))) #rho trap 2
eta_trap2 <- (1 - rho_trap2)/rho_trap2
```

```
sigma_trap2 <- exp(mat_dispersion[2]) #standard deviation trap 2
tau_trap2 <- 1/sigma_trap2^2

## Probability to lose tags ##
p_lost ~ dbeta(lost, det)

for(y in 1:year){#loop year

 ## 1. Weibull parameters ####
 #median
 pre_m[y] ~ dbeta(a_m, b_m)
 m[y] <- pre_m[y] * 30  # April
 #90 quantile
 pre_q90[y] ~ dbeta(a_q90, b_q90)
 q90[y] <- pre_q90[y] * (min(60 - t0[y], (q50[y]/(log(2)/log(10))))-q50[y]-5) + q50[y] + 5
 quant_ratio[y] <- q50[y]/q90[y]
 q50[y] <- m[y] - t0[y]

 #shape
 k[y] <- Q/log(1/quant_ratio[y]) #>1

 #starting date
 pre_t0[y] ~ dbeta(a_t0, b_t0)
 t0[y] <- pre_t0[y] * 30 - 30.5#March


 ## 2. Pr ####
 #hazard
 log_lambda_r_0[y] ~ dnorm(log(log(2)/q50[y]^k[y]) + log( (- 0.5 - t0[y])^k[y]), tau_p_r)
 lambda_r_0[y] <- exp(log_lambda_r_0[y])
```

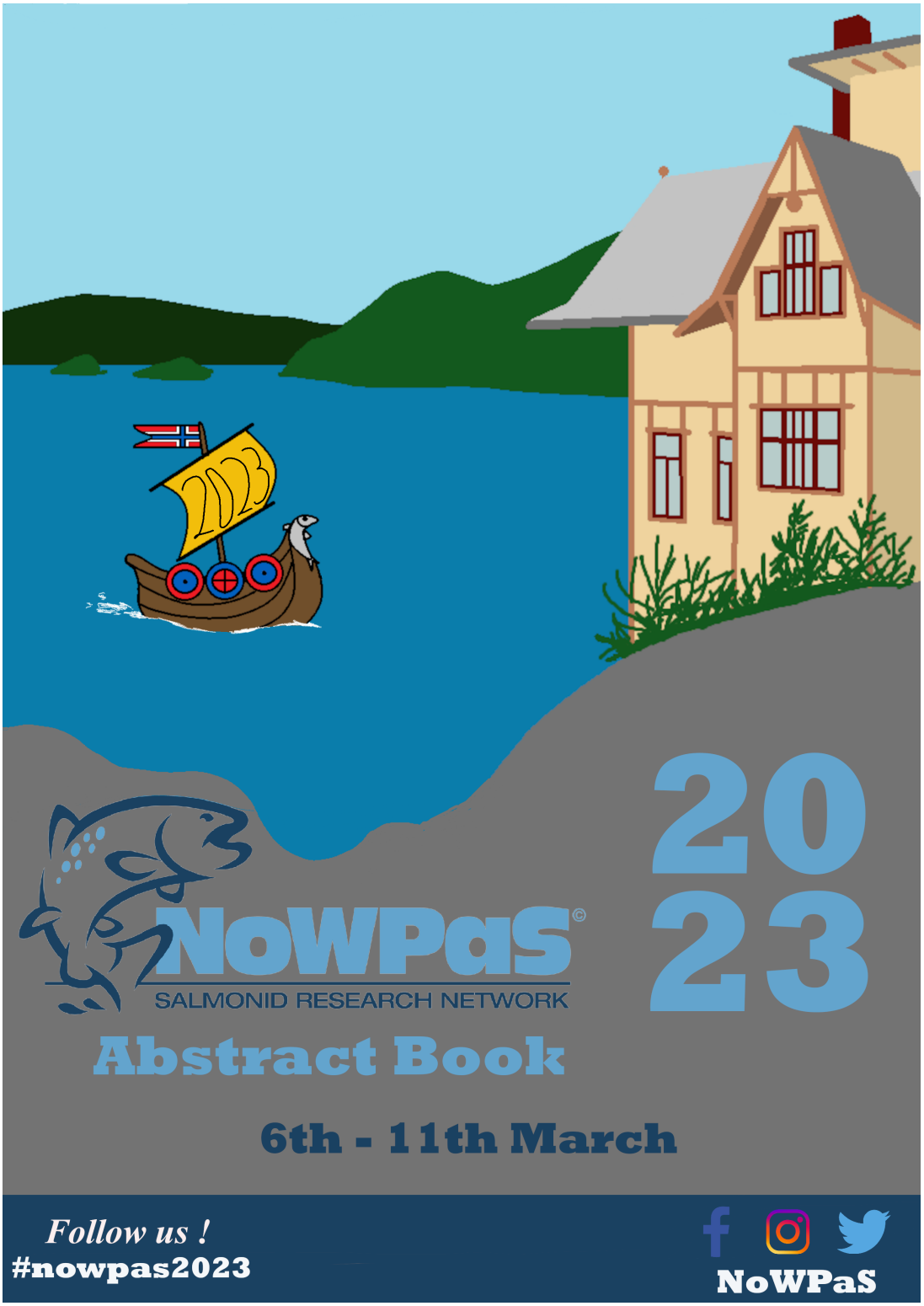
```
  for(i in 1:(D)){

    log_lambda_r[i, y] ~ dnorm(log(log(2)/q50[y]^k[y]) + log(((i - 0.5 - t0[y])^k[y] - (i - 1.5 -
t0[y])^k[y])), tau_p_r)

    lambda_r[i, y] <- exp(log_lambda_r[i, y])

  } #end loop days

  #proba

  p_r_0[y] <- 1 - exp(-lambda_r_0[y])

  p_r[1 , y] <- (1 - exp(-lambda_r[1, y])) * exp(-lambda_r_0[y])

  for (i in 2:(D - 1)){

    p_r[i, y] <- (1 - exp(-lambda_r[i, y])) * exp(-(sum(lambda_r[1:(i - 1), y]) + lambda_r_0[y])) #proba
de migrer jour i * celle de ne pas avoir migré avant

  }

  p_r[D, y] <- 1 - (sum(p_r[1:(D - 1), y]) + p_r_0[y])



  ## 3. P migr ####

  #proba

  for (i in 1:D) {

    logit_p_migr[i, y] ~ dnorm(beta_migr_mean + beta_migr_dis * dis[i, y] + beta_migr_var *
var_dis[i, y] + beta_migr_temp * temp[i, y] , tau_migration)

    p_migr[i, y] <- (1/(1 + exp(-logit_p_migr[i, y])))

  }



  ## 4. Phenology ####

  p_tot_r[1, y] <- p_r_0[y] * (1- p_migr_0) + p_r[1, y]

  p_pheno_0[y] <- p_r_0[y] * p_migr_0

  for (i in 1:(D - 1)){

    p_pheno[i, y] <- p_tot_r[i, y] * p_migr[i, y]

    p_tot_r[i + 1, y] <- p_tot_r[i, y] * (1 - p_migr[i, y]) + p_r[i + 1, y]

  }

  p_pheno[D, y] <- 1 - (sum(p_pheno[1:(D - 1), y]) + p_pheno_0[y])
```

```
### 5. Capture process ####

# trap1

#Prior for trap 1

exp_beta_trap1[y] ~ dbeta(a_beta_trap1_1, b_beta_trap1_1)

beta_trap1[1, y] <- logit(exp_beta_trap1[y])

beta_trap1[2, y] ~ dnorm(mean_beta_trap1_2, tau_beta_trap1_2)


for (i in 1:D) {#days

 logit_p_trap1[i, y] ~ dnorm(beta_trap1[1, y] + beta_trap1[2, y] * dis[i, y], tau_trap1)

 p_trap1[i, y] <- 1/(1 + exp(-logit_p_trap1[i, y]))

 #proba to migrate the day i and to be captured at trap 1

 p_pheno_trap1[i, y] <- p_pheno[i, y] * p_trap1[i, y] * time_lag[i, y] # 1 if trap1 is running, 0
otherwise

} # end loop days


# Informative prior for trap 2

beta_trap2[1:2, y] ~ dmnorm(mat_mean[1:2, y], mat_prec[1:2, 1:2, y])


# trap 2

for (i in 1:D) {#days

 logit_p_trap2[i, y] ~ dnorm(beta_trap2[1, y] + beta_trap2[2, y] * dis[i, y], tau_trap2)

 p_trap2[i, y] <- 1/(1 + exp(-logit_p_trap2[i, y]))

} # end loop i
```

```
  ## P phen trap2 ####

    #proba to migrate the day 1 and to be captured at trap 2

    p_pheno_trap2[1, y] <- p_pheno[1, y] * (1 - p_trap1[1, y] + p_trap1[1, y] * r_no_tag[1, y] +
p_trap1[1, y] * p_lost) * psy * p_trap2[1, y] + p_pheno_0[y] * psy_0 * p_trap2[1, y]

    for (i in 2:D){#days

      #proba to migrate the day i and to be captured at trap 2

      #r_no_tag: ratio of unmarked

      p_pheno_trap2[i, y] <- ((p_pheno[i, y] * (1 - p_trap1[i, y] + p_trap1[i, y] * r_no_tag[i, y] +
p_trap1[1, y] * p_lost) * psy) + (p_pheno[i - 1, y] * (1 - p_trap1[i - 1, y] + p_trap1[i - 1, y] * r_no_tag[i
- 1, y] + p_trap1[1, y] * p_lost) * (1 - psy))) * p_trap2[i, y]

    } # end loop i


    # Normalized probabilities

    for (i in 1:D) {

      p_pheno_trap1_b[i, y] <- p_pheno_trap1[i, y]/(sum(p_pheno_trap1[1:D, y]))

      p_pheno_trap2_b[i, y] <- p_pheno_trap2[i, y]/(sum(p_pheno_trap2[1:D, y]))


      alpha_trap1[i, y] <- (p_pheno_trap1_b[i, y] * eta_trap1) + 1e-6 # to protect against 0 values

      alpha_trap2[i, y] <- p_pheno_trap2_b[i, y] * eta_trap2

    } # end loop i


    ## Dirichlet multinomial ####

    n_trap1[1:D, y] ~ ddirchmulti(alpha = alpha_trap1[1:D, y], size = ncapt1[y])

    n_trap2[1:D, y] ~ ddirchmulti(alpha = alpha_trap2[1:D, y], size = ncapt2[y])


  }# end loop year



}) # END MODEL
```

Apendix D: NoWPaS 2023

I had the opportunity to organise the NoWPaS 2023 workshop in Oslo and Drøbak with Mélanie Debelgarric, Mari Austad Brandt, Domniki Manousi, Coralie Moccetti, Paolo Moccetti and Spencer Weinstein. Here is the logo and the cover of the abstract book I designed for the event.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