In Atlantic salmon, space use of potential breeders stabilises population dynamics and shapes sexual selection

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> « Since all models are wrong the scientist cannot obtain a "correct" one by excessive elaboration. [...] Just as the ability to devise simple but evocative models is the signature of the great scientist so overelaboration and overparameterization is often the mark of mediocrity. »
> — Box 1976*

> « But all evolutionary biologists know that variation itself is natures only irreducible essence. Variation is the hard reality, not a set of imperfect measures for a central tendency. Means and medians are the abstractions. » — Jay Gould, 1991**

* Box, G.E.P 1976. *Science and Statistics.* — Journal of the American Statistical Association 71(356): 791- 799.

** Jay Gould, S. 1991 — *Bully for Brontosaurus: Reflections in Natural History*, W. W. Norton & Company, Inc.

Foreword

My thesis about salmon lasted two years and three months, while thesis are usually planned for three years in France. My first subject dealt with the mating behaviour of Allis shad (*Alosa alosa*). However, we were able to catch a too low number of individuals for the experiment to produce a reliable thesis. I decided with my thesis directors to change the subject and to work on Atlantic salmon during the remaining time of my thesis. Do not hesitate to ask me for a published version or a more recent version of any chapter of my thesis.

Remerciements

En tout premier lieu je souhaiterais remercier mes directeurs de thèses Agnès Bardonnet et Cédric Tentelier de m'avoir permis de réaliser cette thèse. Ce n'était pas le sujet initial, mais on est allé au bout! Merci à toi Cédric de ton soutien, de m'avoir laissé l'indépendance que je souhaitais tout en étant là si besoin. Merci de m'avoir fait confiance durant ces trois années. J'espère avoir l'occasion de retravailler avec toi avec un peu moins de pression!

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Summary

Habitat fragmentation and reduction in the availability of suitable habitats are significant threats to ecosystems in particularly for freshwater ones. For instance, accessibility, availability, and quality of breeding sites of Atlantic salmon, *Salmo salar*, can be restricting in some rivers due to human activities and dams. Such threats may affect the distribution of potential breeders because, after their up-river migration, salmon females distribute within available breeding sites. Spatial distribution of females determines the spatial distribution of breeder males. Dominant males try to monopolise several females, whereas subordinate males adopt a sneaky behaviour. Access to females by males depends on the spatial distribution of females and on males' movements within a river. The spatial distribution of females generates the spatial distribution of juveniles, aggregating them at some breeding sites. The latter aggregation of juveniles may raise the density-dependent mortality with potential consequences on population dynamics. The thesis aims to assess how space use of potential breeders, namely mature individuals able to spawn or fertilise eggs, influence population dynamics and sexual selection.

I combined different approaches and different temporal and spatial scales to potential effects of space use of potential breeders. Time series of stock (deposited eggs) and of recruitment (juveniles) for the salmon population of the Nivelle River were combined with measures of spatial aggregation of nests. The effects of displacements and spatial distribution of potential breeders on their participation in reproduction were tested through inferring the sexual network of the population.

I found that spatial aggregation of nests diminished the recruitment variability. The spatial aggregation of nests resulting from female aggregation affected the number of effective breeders through a U-shaped curve. Such relationships suggested mate monopolisation dependent on the spatial aggregation of females. The negative effects of the spatial isolation of females on their number of mates also suggest such mate monopolisation. Then, the inferred sexual network enabled me to highlight a local social structure within the population. The latter structure and social competitors impacted the reproductive success of anadromous males. The participation of mature parr increased the sexual competition faced by anadromous males. Spatial behaviours of mature parr were linked to their participation in reproduction.

Altogether my results show that space use of potential breeders affected both population dynamics and sexual selection. Then, spatial aggregation of females can be beneficial for population dynamics as shown by combining different temporal and spatial scales. Females seemed to aggregate within the best breeding sites with better environmental stability. The spatial distribution of females affected the ability of males to monopolise several females and participation of sneaky males. The availability of

suitable good breeding habitats seemed restricting in the Nivelle, potentially due to the presence of impassable upstream dams. The lack of suitable breeding sites seemed to impact the mating system of the population and the sexual selection operating in. Some management actions to improve the quality of breeding sites and their availability could be planned.

Keywords: Atlantic salmon, breeding sites, habitat fragmentation, mature parr, mating system, sexual network, sexual competition, social competition, spatial aggregation, stock-recruitment

Résumé

La fragmentation des habitats ainsi que la réduction de leur disponibilité sont des menaces importantes pour les écosystèmes, notamment aquatiques. La disponibilité et la qualité des sites de fraie du saumon Atlantique peut donc être limitante dans certaines rivières. Après la migration en rivière, les femelles saumon vont chercher à s'établir dans un des sites de fraie disponibles. La distribution spatiale des femelles va alors influer sur la distribution spatiale des mâles reproducteurs qui vont chercher soit à monopoliser plusieurs femelles (pour les mâles dominants), soit à les approcher en adoptant un comportement "furtif" (pour les mâles satellites). L'accès des mâles aux femelles va donc dépendre de la distribution spatiale des femelles et des déplacements des mâles dans la rivière. La distribution des femelles va également jouer sur la distribution spatiale des juvéniles, les concentrant à certains endroits. Cette concentration peut augmenter la mortalité densité-dépendante qui modifie la dynamique de la population. Cette thèse avait pour but d'évaluer comment l'utilisation de l'espace des potentiels reproducteurs, c'est à dire les individus matures, influence la dynamique de la population et la sélection sexuelle.

Des séries temporelles de stock (œufs déposés) et de recrutement (juvéniles) pour la population de saumon de la Nivelle ont été associées à des mesures de l'agrégation spatiale des nids creusés par les femelles. L'effet des déplacements et de la distribution des reproducteurs sur leur participation à la reproduction a notamment été testé via la reconstruction du réseau d'interactions sexuelles dans la Nivelle.

J'ai ainsi démontré que l'agrégation spatiale des nids diminua sur la variabilité du recrutement. Cette agrégation résultante de celles des femelles influait sur le nombre effectif de reproducteurs par une parabole positive. Le réseau d'interactions sexuelles a permis de mettre en évidence une structure sociale locale au sein de la population. Cette structure et les compétiteurs présents diminuaient le succès reproducteur des mâles. Notamment, les tacons matures qui participent à la reproduction avant de migrer en mer renforçaient la compétition sexuelle dont les mâles dominants faisaient l'objet. Les comportements spatiaux des tacons matures impactaient leur participation à la reproduction, l'étendue des domaines de vie et les déplacements vers l'amont augmentant la probabilité de rencontrer une femelle. Mes résultats m'ont permis de mettre en évidence l'effet de l'utilisation de l'espace des potentiels reproducteurs sur la dynamique de la population et sur la sélection sexuelle. Ainsi, il a été montré que l'agrégation des femelles pouvait être bénéfique pour la dynamique de la population. Il semble que les femelles tendent à s'agréger d'abord sur les meilleurs sites de fraie avec une plus forte stabilité en-

vironnementale. Cette distribution des femelles affecta la capacité des mâles à monopoliser plusieurs femelles, une agrégation modérée permettant une monopolisation. La participation des mâles furtifs anadromes ou tacons matures était également dépendante de l'agrégation des femelles. Il apparait que la disponibilité d'habitats adéquats pour la reproduction semble limitante dans la Nivelle et notamment du fait de la présence de barrages. Ce manque semble affecter le système d'appariement de la population et la sélection sexuelle y opérant. Des mesures visant à améliorer la qualité des sites de fraie déjà disponibles ainsi que leur accessibilité pourraient être envisagées.

Mots-clés : Agrégation spatiale, compétition sexuelle, compétition sociale, fragmentation de l'habitat, habitats de reproduction, saumon Atlantique, système d'appariement, réseau sexuel, stock-recrutement

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PART I

General introduction

General context

A∫ STUDYING INDIVIDUALS AND POPULATIONS WITHIN THEIR ENVIRONMENT: FROM HUNTERS TO THE DESCRIPTION OF ECOLOGICAL NICHE

Ecologists try to understand how and why individuals and populations interact with their environment. In this way, prehistoric men were probably the first ecologists. Hunter-gatherers, as predators, interacted with other species by hunting them and by observing them, thus developing exploitation of resources. Observations and descriptions of entities is a prerequisite to the description of interactions between these entities. After a long time gap, de Buffon (1749) and Linnæus (1753) tried to lay the foundations for a rigorous study of life and for the description of entities (i.e. taxa). These first works in ecology looked at interactions between taxa through the prism of consumers and resources. Malthus (1798) laid the concept of carrying capacity when the number of consumers raises more sharply than available resources by looking through this prism.

Studying laws and processes regulating populations was the early stage of ecology. The regulation of populations was deeply investigated and discussed by Darwin (1859). In his introduction to *The origin of species*, Darwin said: "This is the doctrine of Malthus applied to the whole animal and vegetable kingdom". He also said:

> « It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. » — Darwin 1859

The laws identified by Darwin were notably growth with reproduction (as Malthus), inheritance, variability, struggle for life, divergence of character, and extinction. The quotation of Darwin is a good illustration of observations of different taxa interacting and being linked together. Interactions between species were highlighted as a cornerstone of ecology by Haeckel in 1866: "By ecology we mean the body of knowledge concerning the economy of nature the investigation of the animal both to its inorganic and to its organic environment; including, above all, its friendly and inimical relations with those animals and plants with which it comes directly and indirectly into contact.". Ever since these works interactions between a species and its environment became a standard question in ecology aiming to understand why a species occupies an area, while another not.

Interactions between species were the definition of the ecological niche as formulated by Elton (1927): "The 'niche' of an animal means its place in the biotic environment, *its relations to food and enemies*". Elton determined the niche by what an animal is "*doing*" and its "*food habits*": "A fox carries on the very definite business of killing and eating rabbits and mice and some kinds of birds. Lions feed on large ungulates...", for example. The latter definition given by Elton only accounted for biotic environments of individuals. Before Elton, Grinnell defined the niche concept by focusing on abiotic environments of individuals. Hutchinson (1957) formulated the most widely accepted definition of the ecological "fundamental niche" drawing on works of Elton and Grinnell:

> « The niche is the set of biotic and abiotic conditions in which a species is able to persist and maintain stable population sizes. » — Hutchinson 1957

Hutchinson went further by defining the "realised niche", a subset of the "fundamental niche", as the conditions experienced by individuals.

B∫ RESOURCE DISTRIBUTION AS DETERMINISM OF SPACE USE: WHY IS THERE INDIVIDUAL HETEROGENEITY IN SPACE USE?

a. SCALES IN ECOLOGY

The notion of niche raises the question of scales. Defining how a species, a population, or an individual interacts with its environment requires to define a spatial scale[1]. The concern of spatial scales in ecology was notably highlighted by Levin (1992). For instance, a trendy current topic is to assess the impact of climate change on species or populations. Such a topic necessarily links two different spatial scales with a worldwide phenomenon and a finer scale when studying a species or a population. It is also probable that two researchers raise the same question by adopting two different approaches based on two different scales, leading to different results (Wiens 1989). Although Darwin (1859) or Humboldt & Bonpland (1814) described where species distribute during their explorations, Levin (1974) was the first accounting for spatial considerations when he defined the concept of "patches" in his paper discussing of competition in patchy environments of two species.

Spatial considerations in ecology arose from insular zoogeography. MacArthur & Wilson (1963) explained the number of species distributed in islands by the size of islands and distance to other islands. Their theory enabled to estimate an equilibrium balancing immigration and extinction rates of species. In this way, MacArthur continued to work on spatial scales in ecology and developed a model explaining the use of patchy environments (MacArthur & Pianka 1966). As islands, species' environment is constituted by several patches of suitable resources. MacArthur & Pianka adopted an adaptationist view based on economy (i.e. "an activity should be enlarged as long as the resulting gain in time spent per unit food exceeds the loss") to highlight an optimal use of this patchy environment.

[1]Here, I develop the idea of spatial scale, while the same may occur with time scale.

GLOSSARY I.i: Habitat and patches— from Morris (2003)

Habitat — A spatially-bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than an adjacent subsets.

Habitat selection — The process whereby individuals preferentially use, or occupy, a non-random set of available habitats

Patch — Spatial subset of habitat that is treated as a single homogeneous unit by the behaviour of an individual. A patch can be an artificial delimitation to better describe a behaviour or a real one leading to territories for example.

The work of MacArthur & Pianka (1966) was one of the first considering that species may have different abilities in exploiting resources. Authors linked different abilities among species to various strategies in resource utilisation. Before MacArthur & Pianka (1966), Skellam (1951) introduced the concept of critical patch size (see Box Glossary I.i). Skellam demonstrated the size of a patch is critical for the persistence of a species or a population living in. Yet, Skellam accounted for diffusion of individuals through boundaries of patches without accounting for the quantity of resources. More recently, Fahrig (2013) rediscussed the effects of patch size and isolation by proposing the *habitat amount* hypothesis: the species richness should increase with the amount of habitat in the local landscape. Whereas this hypothesis can be discussed, it goes back to the idea that heterogeneity occurs in the way of how species, populations, individuals use their habitats and subsequent patches.

The question about ultimate mechanisms driving habitat selection (see Box Glossary I.i) arose by combining ideas of patches, effects of patch size and optimal use of a patchy environment. Morris (1987) linked the local density of two Temperate Zone rodents to macrohabitat variations but not to microhabitat variations. Within each habitat type — e.g. foraging ones—, a habitat corresponds to the minimum area where

an individual performs an activity — e.g. forage in foraging habitats, Figure. I.i—. Within a macrohabitat, environmental characteristics (physical, chemical, biotic) distinguishing microhabitats may influence in time or energy allocated by an individual to each microhabitat (Morris 1987). In his study, Morris advocated to carefully separate the effects of macro and microhabitats in habitat selection because processes acting at these two spatial scales may be different. Usually in such models habitat use is evaluated by correlating abundance (or other similar metrics) to environmental variables defining each patch. Morris also argued that other factors may affect habitat selection. More recently, Morris reviewed habitat selection by adopting an evolutionary view which deals with the fitness gains or losses of each habitat as well as density effect (Morris 2003; 2011).

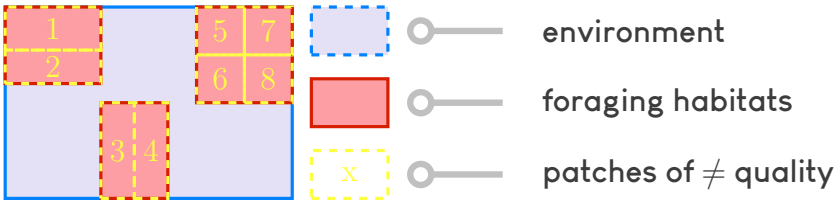


Figure. I.i: Scheme illustrating the difference in spatial scale between habitats and patches. The distinction between habitats and patches highlights processes that may act at macro- and micro-spatial scales.

b. SPACE USE THROUGH A BEHAVIOURAL POINT OF VIEW

Habitat selection, as in recent papers of Morris (2003; 2011), accounts for an evolutionary approach. An animal is supposed to condition its habitat choice to its expected fitness; the latter statement being the basis of behavioural ecology. Unlike the traditional ethology, behavioural ecology adopts an adaptationist point of view by attributing a central place to fitness (or other performance measurements) and a potential effect of selection on individuals and genes (Danchin *et al.* 2008, Krebs & Davies 2009). MacArthur & Pianka (1966) or Charnov (1976) adopted the adaptationist point of view in their approach when investigating how individuals use a patchy environment. Their work assumed that 1) individuals maximise their energy acquisition per time unit and 2) energy acquisition is directly linked to their evolutionary fitness. Selection should, thus, favour an optimal use of patchy environment in terms of the amount of food patches (i.e. where food is available) and of the amount of food types (i.e. different species).

Resource matching was the first determinant to explain distribution of individuals. Accounting for fitness or performances depending on available resources leads to consider Ideal Distributions. Whereas Charnov (1976) and MacArthur & Pianka (1966) identified this idea of resource matching, the first clear theory was the Ideal Free Distribution (IFD, Fretwell & Lucas 1969). As conceptualised by Fretwell & Lucas, individual distributions should match resource distributions and sometimes may lead to spatial aggregation of individuals (Sutherland 1983). Yet, individuals do not necessarily express the same abilities. These differences among individuals lead to accounting for individual heterogeneity as questioned by Parker & Sutherland (1986). This issue was notably dealt by Fretwell (1972) who defined the Ideal Despotic Distribution (IDD). First arrival or dominant individuals secure habitats whose the best and force other individuals (subordinate or late arrival) to distribute in less favourable habitats under IDD. Distributions such as the IDD assume differences between individuals.

C∫ CONSEQUENCES OF INDIVIDUAL HETEROGENEITY IN SPACE USE DURING REPRODUCTION

a. SPACE USE DURING REPRODUCTION

Habitat selection and habitat use correspond to a subset of individual space use. In both IFD and IDD, the term "ideal" denotes that individuals are able to assess patch quality, something difficult for individuals. For instance, individuals may assess patch or habitat quality by copying choices of other individuals which can generate aggregation (Boulinier & Danchin 1997, Danchin & Wagner 1997, Doligez *et al.* 2003). Habitat selection generating habitat use of species, populations, or individuals is not the only component of how individuals use space.

Space use can be viewed as species distribution or habitat selection, namely where are individuals but also how individuals move within and among habitats. The pattern of spatial distribution of individuals, their habitat preferences (Long *et al.* 2009, Starking-Szymanski *et al.* 2018), their movements between habitats (Starking-Szymanski *et al.* 2018), their movements within their habitats (Steingrímsson & Grant 2008), their home range (Moorcroft & Barnett 2008), or the covered distances (Long *et al.* 2009, Tentelier *et al.* 2016a) may be assessed by studying how individuals use space.

How individuals use space is often studied in relation to foraging. Foraging con-

text leads to questions about species co-existence, trophic networks, competition for resources. IFD, IDD or other concepts previously exposed were first defined concerning foraging resources. Yet, the same concept was defined by Parker (1970; 1974) in a reproductive context in parallel to the definition of IFD. Optimal uses of resources under a reproductive context was also dealt by Emlen & Oring (1977), or more recently by Shuster & Wade (2003). Emlen & Oring notably highlighted abilities of males to monopolise mates may drive the spatial distribution of breeders. Reproductive context leads to consider mating systems, sexual competition and selection, and recruitment. Individuals may, thus, exhibit specific space use in relation to reproduction. The most notable specific spatial behaviour in relation to reproduction is breeding migration occurring in a wide range of taxa (Pomeroy *et al.* 1994).

Different processes may modify individual space use in a reproductive context. First, breeding activity during breeding season may favour spatial aggregation in some species such as numerous marine mammals (Boulinier & Danchin 1997, Danchin & Wagner 1997, Pomeroy *et al.* 1994). Second, reproductive states may impact space use of individuals (Long *et al.* 2009). Third, searching mates rather than food may also modify home ranges of individuals (Preatoni *et al.* 2005, Quirici *et al.* 2010). Finally, individuals may adjust different spatial behaviours such as roamers and strayers (Sandell & Liberg 1992). All these examples highlight the modification of space use by reproduction. Feedbacks, which are effects of space use on reproduction, are also possible making it necessary to investigate how individuals use space during reproduction.

b. SOCIAL ENVIRONMENT AND REPRODUCTION

Space use may affect the participation of individuals in reproduction. As a first element, some individuals disperse while other exhibit philopatry in some taxa. Dispersal is beneficial in some conditions even if costs are associated (Coulton *et al.* 2011). However, dispersers and philopatric individuals may also exhibit similar reproductive success complicating identification of dispersion motivation (Davidian *et al.* 2016). At a narrower scale, movements among or within suitable breeding habitats may reduce or enhance probabilities finding a mate (South & Kenward 2001). Potential mates being a resource, individuals may express a diversity of behaviours to find them (Louâpre *et al.* 2015, Whitehead 1998). Overall, space use may affect the social environment of individuals (Formica *et al.* 2010) which consists in individuals encountered as either potential mates

or potential competitors. Social environments may affect mate choice (Callander *et al.* 2013, Formica *et al.* 2011) or sexual competition (Croft *et al.* 2005, McDonald *et al.* 2013) because both are relative processes. Sexual selection is operating when the value of an inheritable trait enhances success in sexual competition or in mate choice (Kuijper *et al.* 2012). Here, individuals participate in reproduction by i) being in the social environment of another individuals impacting, and ii) by producing juveniles. Space use of potential breeders may, thus, have consequences on their own participation to reproduction but also on the participation of other individuals.

c. A SPATIAL DISTRIBUTION OF BREEDERS GENERATING POPULATION REGULATION

Whereas resource demand and partitioning is usually applied to explain population regulation, space use of breeders may also affect population regulation. Dense populations are rarely stable in species requiring large home ranges; an effect highlighted a long time ago (McNab 1963). Such effects of home ranges on population regulation can be exacerbated when the distribution of breeders is under IDD, with some individuals monopolising best habitats and, thus, exhibiting a better reproductive success (Andren 1990). The distribution of produced juveniles is shaped by the distribution of potential breeders at least in species where juveniles exhibit low displacement abilities (Foldvik *et al.* 2010). In this case, high densities of juveniles engendered by aggregation of breeders may exacerbate local density-dependent mortality (Einum & Nislow 2005, Foldvik *et al.* 2010) regulating population. Space use may, thus, be used as a conservation tool because it may affect population regulation and individuals' participation in reproduction.

D∫ INTRAPOPULATION SPACE USE DURING REPRODUCTION AS A TOOL FOR MANAGEMENT OF POPULATIONS

Loss of breeding habitats and connectivity may be a strong pressure for a population. For instance, habitat loss may impose a relocation modifying home range of individuals (Judas & Henry 1999), while habitat connectivity may play a key role in viability of populations (Cushman 2006). In their study, Baldwin *et al.* (2006) advocates accounting for movements and migration between connected habitat elements to improve conservation planning for amphibian species. Fahrig (1998) demonstrated habitat fragmentation is problematic for species where breeding habitats cover less than 20 % of landscape, or for species exhibit high fidelity to breeding sites. Sutherland (1996) used a game-theoretical approach to estimate that a loss of 1 % of breeding habitat produces a population decline of the oystercatcher (*Haematopus ostralegus*) at 0.31 %. Examining habitat selection

and movements among habitats during reproduction is an essential current question due to habitat loss and fragmentation.

Studying space use during reproduction allows researchers to improve management policies. Studying space use during reproduction may highlight which habitats should be restored. Hunt *et al.* (2018) compared nest success and chick survival of Piping Plover (*Charadrius melodus*) between natural breeding habitats and habitats engineered to dampen habitat loss. Authors showed that newly created breeding habitats did not offer a better survival or a better nest success. Spatial distribution of individuals among habitats is a key parameter which should be accounted as shown by López-Sepulcre *et al.* (2010) on the Seychelles magpie robin, *Copsychus sechellarum*. Authors shown that increasing resource quantity within habitats where individuals already aggregated raised competition among individuals for high quality breeding sites. As the study of López-Sepulcre *et al.* (2010) and based on the work of Emlen & Oring (1977), aggregation of potential breeders among some breeding habitats may increase competition between potential breeders. Offering new breeding habitats may, thus, diminish aggregation and competition of potential breeders which can increase genetic diversity (Bacles *et al.* 2018) and reduce competition for resources in juveniles López-Sepulcre *et al.* (2010).

Migratory species using specific habitats to reproduce can be valuable organisms to study effects of habitat loss or fragmentation because individuals have to select habitats and move among them. Habitat loss or fragmentation may impact their migration and their subsequent use of available habitats to breed (Meixler *et al.* 2009, Sutherland 1996). Constrains of habitat loss or fragmentation may result in a skewed spatial distribution but also in constrained movements of individuals. Studying space use of individuals and the repercussions at both an individual **and** a population level may provide valuable information for conservation and population management. At an individual level, space use of potential breeders may shape individuals' participation in reproduction in terms of inclusion in the social environment of conspecific and reproductive success. At a population level, space use of potential breeders may affect the genetic diversity of the population and population dynamics.

Here, I propose the Atlantic salmon, *Salmo salar*, as species to investigate how space use of potential breeders affects population dynamics and sexual selection through the

participation of individuals in reproduction. Elements justifying the choice of Atlantic salmon will be presented with the thesis aims and hypotheses in a last section (page 31). I will firstly present the species (page 13) and the studied population (page 25).

An aquatic nomad as a biological model: Atlantic salmon[2]

Atlantic salmon *Salmo salar*, belonging in the Salmonidae family, was first described by Linnæus in 1758. The Web of Science database listed 16, 891[3] publications concerning Atlantic salmon with at least 800 items per year since 2010. Most of these publications concern fisheries or marine freshwater biology (Figure. I.i). The economic value as an exploited species for many decades triggered this high number of scientific publications. The strong studying pressure leads to a large amount of knowledge concerning biology, ecology, or population dynamics in Atlantic salmon.

[2]this title was adapted from the chapter 1 in Aas *et al.* (2011), the term "aquatic nomad" being well appropriated for atlantic salmon, especially in a thesis talking about space.

[3]Research "*Salmo salar*" was performed September 26, 2018

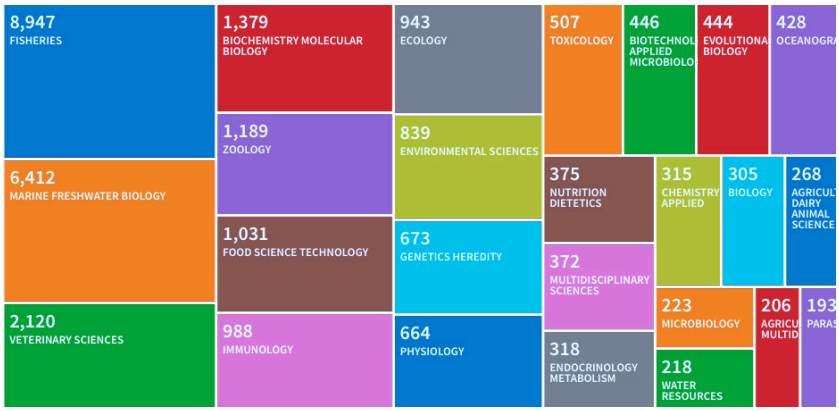


Figure. I.i: The first 25 categories assigned to the 16, 891 publications in the Web of Science© database concerning Atlantic salmon. The research "*Salmo salar*" was performed September 26, 2018.

E∫ LIFE CYCLE

Atlantic salmon exhibits a complex and variable life history. Variations in life history and phenology occur between individuals and between populations accordingly to latitude. Individual heterogeneity in life history leads to consider Atlantic salmon as a suitable biological model in ecology and evolution. Atlantic salmon usually uses two different environments: ocean and river. Yet, landlocked populations with migration in lakes exist; some are located in the Southern Hemisphere (MacCrimmon & Gots 1979). One of the southernmost populations is located in the French Kerguelen Islands (Lecomte *et al.* 2013). Few landlocked populations without migration in lakes and with a complete freshwater cycle also exist (Kazakov 1992).

The usual life cycle (Figure. I.ii) involves a reproduction in rivers and a growth at sea leading to name as *anadromous* individuals salmon accomplishing such life cycle. Growth at sea has multiple advantages such as bringing out a large growth and a higher fecundity. Such advantages are achieved due to a large amount of foraging resources at sea in comparison to river productivity (Gross 1987). Marine phase also has high associated costs (Gross 1987). Individuals struggle to maintain a healthy homoeostasis leading to high energetic costs associated with their osmoregulation (Gross 1987, Hansen & Quinn 1998). Shifts of environments involve two osmoregulatory adaptations throughout an anadromous life cycle. Marine phase is also associated with survival costs due to a high number of predators and the rising sea surface temperature (Hansen & Quinn 1998).

Anadromous (Figure. I.iii — d), which exhibit schooling and pelagic behaviour at sea, migrate to their home rivers (homing) after a period varying between one and four sea winters (Aas *et al.* 2011, Hansen & Quinn 1998). Variations in duration of the marine phase are potentially specific to each river population (Aas *et al.* 2011, Hansen & Quinn 1998). Southern populations of the Atlantic salmon (Figure. I.iv) exhibit only one and two sea winters individuals. Homing behaviour is strong in Atlantic salmon with less than 10 % of individuals straying to other rivers (Jonsson *et al.* 2003). Homing phenomena may spatially isolate small populations leading to a local adaptation (Taylor 1991). Homing migration could involve an orientation phase from feeding areas to coasts and after a more precise orientation phase near estuaries (Hansen & Quinn 1998). Despite little knowledge about homing mechanisms, homing migration denotes high abilities of Atlantic salmon to orientate and navigate in space.

Timing of the upstream migration in rivers varies between rivers depending on genetic component (Hansen & Jonsson 1991). For instance, salmon in Norway migrate from May to October, while Scottish populations exhibit migration during all months of the year (Hansen & Quinn 1998). Southern populations in France, exhibit two peaks of migration: one in spring and one in late autumn. In populations with two peaks, multiple sea winters individuals usually migrate before one sea winter individuals (Jonsson *et al.* 1990). Although breeding season occurs in winter, multiple sea winter individuals may, thus exhibit advantages being first arrival individuals at future breeding sites. In all cases, such individual variation in timing of arrival may generate a specific structure in encounters and in settlement at breeding sites. Upstream migration involves three different phases affecting displacements of individuals (Finstad *et al.* 2005): 1) a migration phase during which individuals cover the longer distance to potential spawning sites; 2) a search phase during which individuals exhibit short and repeated upstream and downstream movements at or close to the future selected spawning site; and 3) a holding phase without displacements until spawning. The second phase generates displacements at small scale leading to potential different space use between individuals.

Atlantic salmon usually spawn in rivers from September to February depending on latitude. Southern populations spawn later than northern ones. Egg development becomes faster as water temperature raises (Aas *et al.* 2011). Females spawn in a nest (a *redd*) and recover eggs with gravels. Eggs hatch in the following spring after

$430 - 480 \frac{°}{\text{day}}$ (Dumas & Darolles 1999). Hatching fish, named *alevins* (Figure. I.iii — a) and measuring 15-25 mm, remain in the surface layer of gravels during the first 3-8 weeks until the complete resorption of their yolk sac. Fish emerge from the gravel during March or April in the southern populations $840 - 1040 \frac{°}{\text{day}}$ (Dumas & Darolles 1999). Emerged individuals — called *fry* — start to feed on drifting invertebrates and face to a critical period during which the low survival leads to a bottleneck (Nislow *et al.* 2004). This bottleneck is directly linked to a strong density-dependent mortality due to food availability and differences in body length. Competition between individuals is strong and is dependent of local density, directly associated to local aggregation. At the fry stage, aggregation of individuals is directly linked to aggregation of redds due to the weak swimming abilities of individuals. The emerging date is under a strong selection. Early-emerging individuals are bigger than late-emerging individuals and, thus, exhibit an advantage in competition increasing their survival (Einum & Fleming 2000). At the opposite, early-emerging individuals are also more likely to face a mismatch with resources, thereby decreasing their survival (Kennedy *et al.* 2008).

Fry stay near redds during their first 10 days after emergence (Gustafson-Greenwood & Moring 1990) and, then, disperse downstream between 20 m to 100 m (Beall 1994, Crisp 1995, Einum & Nislow 2005). Individuals called *parr* compete to establish their feeding territories. High aggregation of individuals may, thereby, exacerbate density-dependent competition. Salmon parr are multiple-central foragers and move between different feeding stations within their feeding territories. For instance, Steingrímsson & Grant (2008) found that individuals use around 12 stations (median) within a territory of around 0.9 m^2 by studying 50 Atlantic salmon 0+. The terms "0+" or Young of the Year (YOY) define individuals in their first year of life.

At the next spring, the majority of one year parr (1+, Figure. I.ii & Figure. I.iii — b) leave the river and smoltify but some stay in the river to smoltify the next year (2+). In some populations, individuals may stay in the river for eight years (Aas *et al.* 2011). Individuals usually measure between 10 and 20 cm (range: 7-30 cm Aas *et al.* 2011) when they smoltify (Figure. I.ii & Figure. I.iii — c). This physiologically and morphologically transformation into *smolts* is energetically costly; the short period after smoltification being another bottleneck (Aas *et al.* 2011). Atlantic salmon being an iteroparous species, anadromous individuals also migrate at sea after spawning (named *kelt*, Figure. I.ii).

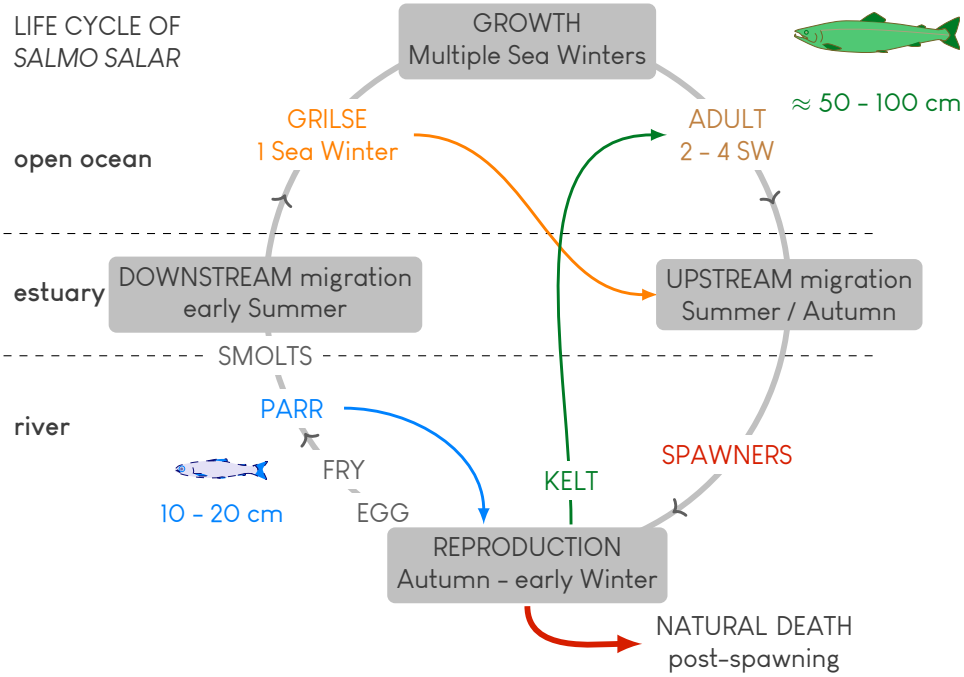


Figure. I.ii: Life cycle of Atlantic salmon. Individuals surviving to reproduction are called "kelt" (→), while one sea winter fresh runners are named "grilse" (→). Some parr mature before the smolt stage and participate in reproduction (→).

Yet, in southern populations, the majority of individuals are semelparous and die after spawning (Aas *et al.* 2011). Mating success and reproductive success are determining factors of fitness for these semelparous individuals.

(a) Salmon alevin (≈ 15-25 mm).

(b) Salmon parr (≈ 10-20 cm).

(c) Salmon smolt (≈ 10-20 cm).

(d) Female anadromous salmon (≈ 50-100 cm).

Figure. I.iii: Photographs of salmon at different life stages. ©INRA — S. Glise

F∫ DISTRIBUTION RANGE

a. NATURAL RANGE

The distribution range of Atlantic salmon corresponds to the North Atlantic Ocean with populations in the west coasts of Europe, Greenland, Canada and the United States (MacCrimmon & Gots 1979, Figure. I.iv). Yet, almost 90 % of known sustainable populations are found in only four countries: Norway, Island, Scotland, and Ireland (WWF 2001); whereas 85 % of the populations are categorised as vulnerable, endangered or critical (WWF 2001). Little is known about distribution in the open ocean despite the strong economic value and the high number of publications. A recent study highlighted diversity in migration routes and foraging areas either in Norwegian sea or Barents sea with individuals originating from the same river (Strøm *et al.* 2018).

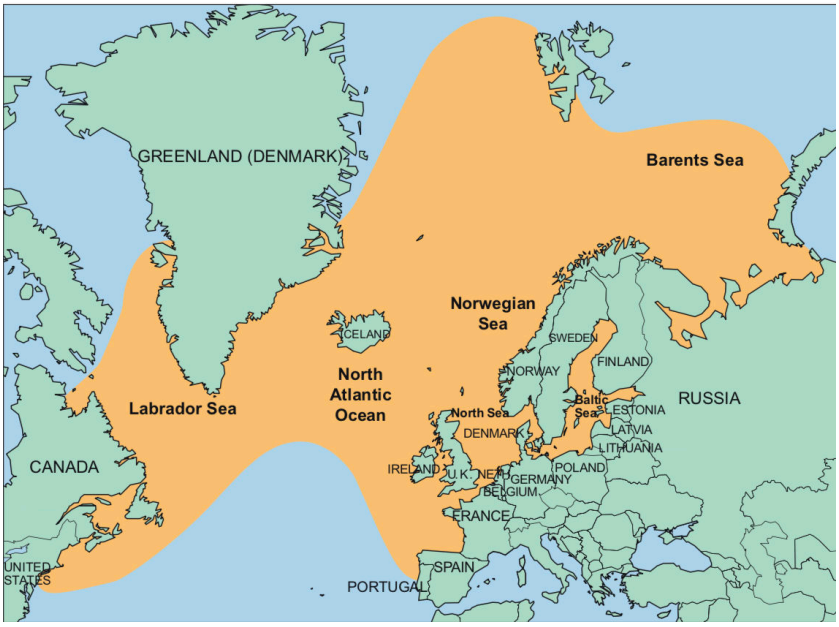


Figure. I.iv: Distribution range of Atlantic salmon from Aas *et al.* (2011). The map displays the countries that hold natural spawning populations of Atlantic salmon (given with names) and the assumed marine distribution of the Atlantic salmon in the North Atlantic Ocean. Atlantic salmon occur in watersheds both along the east coast of North America and the west coast of Europe, and feed over large areas of the North Atlantic Ocean. (Figure designed by Kari Sivertsen.)

b. COLONISATION, INTRODUCTION AND FARMS

One natural colonisation occurred in the Faroe Islands, while lots of introductions failed in establishments of anadromous sustainable populations in the Southern Hemisphere (MacCrimmon & Gots 1979). Escapements of individuals from fish farms occur and

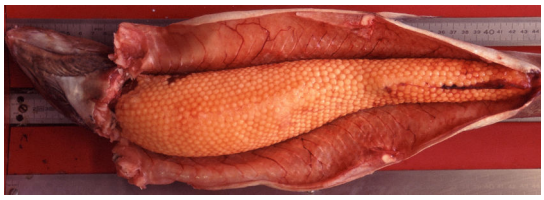


Figure. I.v: Eggs inside the body of a female anadromous salmon in the Nivelle. ©INRA — S. Glise

are probably underestimated (Skilbrei *et al.* 2015, Zhang *et al.* 2013). Farm salmon may reproduce in natural populations but exhibit a lower reproductive success which may affect population recruitment (Fleming *et al.* 2000). Mature parr originated from farms are good vehicles for introgression of farm salmon traits in natural populations (Garant *et al.* 2003). Despite the potentially lower fitness of farm salmon, recent river colonisations by farm pink salmon (Mo *et al.* 2018) raise the question about similar future colonisations by Atlantic salmon.

G∫ REPRODUCTION

a. REPRODUCTION PROCESS

Reproduction occurs from late autumn to February depending on the river's latitude (Aas *et al.* 2011). Once females become mature, time is counted to spawn their stock of eggs (Figure. I.v) which depends on their body mass (Fleming 1996). Mortality and malformations increase as the number of days since maturation increases (de Gaudemar & Beall 1998). The short duration of the spawning season generates temporal aggregation of spawning females that may raise competition for breeding sites.

Females select breeding sites according to morphodynamic characteristics (Louhi *et al.* 2008, Moir *et al.* 2004; 2006). Suitable breeding habitats correspond to the upstream side of riffles or gravel bars (Aas *et al.* 2011). The short duration of the breeding season associated with such necessary characteristics of breeding sites raise competition for breeding sites generating spatial aggregation of potential breeders at available breeding sites (Moir *et al.* 1998). The shallow water and the accelerating current through the gravel enables oxygenation of future deposited eggs as well as a low deposition of sediments (Aas *et al.* 2011, Moir *et al.* 2004; 2006). Multiple females usually clump their nests despite the high number of potential suitable breeding habitats (Aas *et al.* 2011, Moir *et al.* 1998). Redd superimposition or overdigging occurs when the same female or another one digs its redd over another redd (Taggart *et al.* 2001) raising the spatial

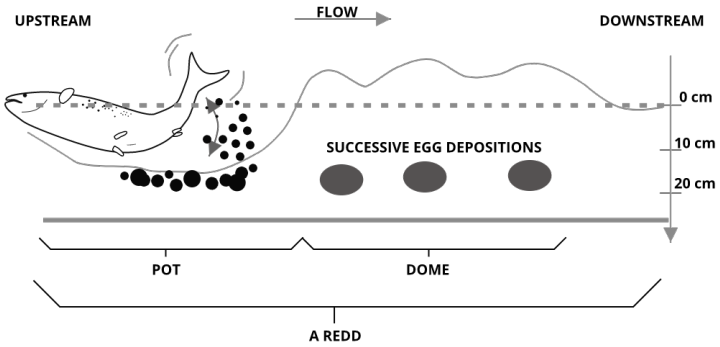


Figure. I.vi: Scheme of a female digging in the gravel to spawn. The dome due to previous diggings is visible, as well as three previous egg depositions. Dashed line indicates the initial level of gravels.

aggregation of nests.

Females use the accelerating current to dig a nest[4] in river bed through movements of their caudal (Figure. I.vi, de Gaudemar & Beall 1999). The caudal movements associated with the current move gravel and pebbles. Females deposit their eggs in the nest while male(s) fertilise(s) them (de Gaudemar & Beall 1999). After this spawning event, females cover eggs also by creating a depression through movements of their caudal (Figure. I.vi, de Gaudemar & Beall 1999). A redd is composed by an upstream "pot" and a downstream dome (Figure. I.vi) and can measure until 3 m long and around 1 m wide (de Gaudemar *et al.* 2000, Moir *et al.* 1998). Eggs are deposited at a depth between 10 cm to 30 cm (de Gaudemar *et al.* 2000, Moir *et al.* 1998). A female may spawn until 11 times in a single redd or in different redds (de Gaudemar & Beall 1999, de Gaudemar *et al.* 2000).

b. REPRODUCTIVE TACTICS & MATING SYSTEM

The major part of individuals is semelparous in southern populations even though Atlantic salmon is an iteroparous species. Differences in life history traits between populations also happen in age at maturity. In Atlantic salmon, age at maturity ranges from one year to ten years when considering both mature parr and anadromous (Hutchings & Jones 1998). Differences between populations also occur when focusing on anadromous individuals. The youngest average age at maturity is found in southern populations (3.21 in the Nivelle River, France) whereas the oldest is found in northern populations

[4]As a simplification, the term ”nest” may define a redd after in the thesis while here it defines one egg deposition.

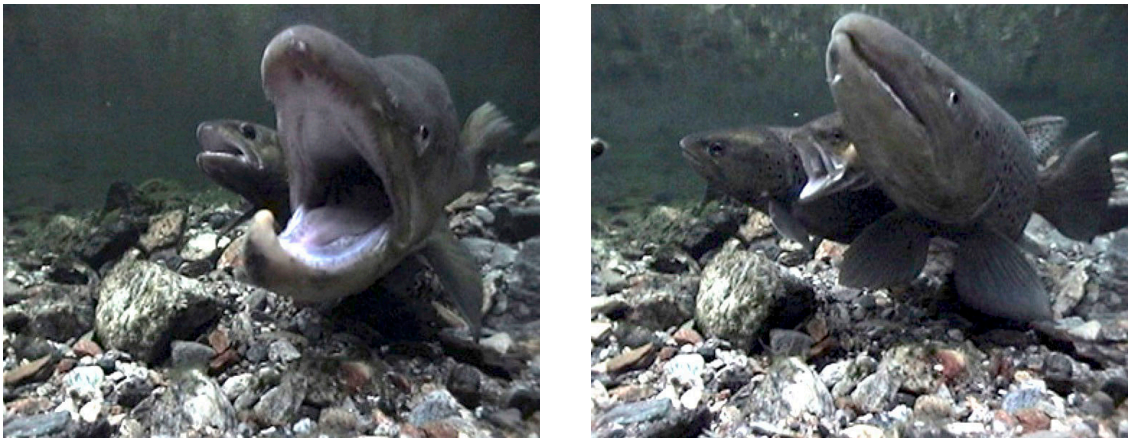
(8.80 years in George River, Quebec, Hutchings & Jones 1998).

Variations in age at maturity are likely based on genetic components (Aas *et al.* 2011) indicating adaptive differentiation among populations and a potential local adaptation (Garcia de Leaniz *et al.* 2007). Local environment seems to play an important role in Atlantic salmon selection. For instance, distance of migration select stronger individuals due to the high expenditures of migration in large river systems (Aas *et al.* 2011). Flow conditions may also affect selection by selecting small individuals in tributaries or rivers where discharges are less than 40 $m^3.s^{-1}$ (Aas *et al.* 2011).

Body size is a preponderant individual character in mating system of Atlantic salmon. In females, larger individuals exhibit higher fecundity and a better access in best breeding sites. Larger females may select breeding sites deeper and faster-flowing waters as well as with coarser substrates (Aas *et al.* 2011, Moir *et al.* 1998) Larger females also exhibit advantages in agonistic interaction when competing for breeding sites (Aas *et al.* 2011). Atlantic salmon males, which migrate 1-5 days before females, invest less in reproduction than females and the operational sex ratio is often male-biased (Aas *et al.* 2011). Males, thus, compete to access and secure females. In males, body size also confers an advantage in agonistic interaction leading to an establishment of a dominance hierarchy around a nesting female (Fleming 1996, Järvi 1990). A dominant male may, therefore, increase its mating success (see Box Glossary I.ii) by mating with the same female and/or with other females when it secures several females. Male-male competition leads to females not directly choosing their partners. Yet, females seem to exhibit indirect choices by, for instance, adapting the number of released eggs depending on the sperm depletion level which varies with mating history (Aas *et al.* 2011, Weir & Grant 2010).

Anadromous males may secure several females, especially because several females may clump their nests (Moir *et al.* 1998). Aggregation of females may favour or constrain such mate monopolisation. Females may also mate with different males along the breeding season leading to a polygynandrous mating system in Atlantic salmon (Aas *et al.* 2011, Garant *et al.* 2001, Taggart *et al.* 2001). Degree of polyandry (see Box Glossary I.ii) is also affected by the participation of anadromous satellite males. Despite the establishment of a dominance hierarchy, some anadromous males may stay downstream

an anadromous couple (i.e. a dominant male and a female) until the gamete emission (Fleming 1996, Järvi 1990). In this way, satellite males may be able to fertilise several eggs due to the duration of a spawning event (5-10 seconds, Figure. I.vii). Fertilisation success is notably dependent on mating history through sperm depletion, as well as proximity with females (Mjølnerød *et al.* 1998). Participation of satellite males may raise the sperm competition (see Box Glossary I.ii) faced by males. The mating system of Atlantic salmon is, thus, complex, variable, and potentially influenced by their space use and encounters between potential breeders.



(a) Anadromous pair. (b) A satellite male joins the pair.

Figure. I.vii: Photographs of a spawning anadromous salmon pair before and after the coming of a satellite male. ©Anders Lamberg

Participation of satellite males leads to a poor explanation of individual reproductive success (see Box Glossary I.ii) by body size for males (Fleming 1998). The participation of mature parr that are individuals maturing before their smoltification also explains the poor relationship between males body length and reproductive success (Figure. I.ii). Like anadromous satellite males, mature parr can have access to females, especially when they have the possibility to hide among pebbles (Aas *et al.* 2011, Jordan *et al.* 2007). Body size may enhance reproductive success of mature parr like in anadromous (Grimardias *et al.* 2010a), but habitat complexity and presence of pebbles favouring participation of mature parr (Grimardias *et al.* 2010b) diminishes the size advantage (Grimardias *et al.* 2010a).

GLOSSARY I.ii: Mating terms

Mating success — Number of mating events during which an individual has fertilised at least one egg. In this thesis such data was not available due to the sampling method of juveniles. Mating success was, thus, defined as the number of sexual partners (in the chapter 5).

Reproductive success — Number of juveniles sired by an individual.

Sperm competition — Here and thereafter, sperm competition denotes that several males may mate with a same female. Due to the lacking temporal dimension in parentage analysis, sperm competitors may define two males who mated with a same female during two different spawning events. Yet, males compete to fertilise eggs whose the number spawned by each female being a finite resource.

The Nivelle population

Contents

H∫ THE RIVER SYSTEM

The Nivelle River is a 39 km long river situated in the south west of France near the Spanish border (Figure. I.viii). The Nivelle watershed has an area of 238 km^2 mainly occupied by pastoral activities. The source of the Nivelle River is situated at 600 m height in Spain and the river flows into the Atlantic Ocean in the Bay of Saint-Jean de Luz (64, Figure. I.ix — a). Over the 39 km of the river, 7.5 km are subject to tidal influence. Water quality diminishes downstream from Saint-Pée sur Nivelle in the lower part of the Nivelle (Dumas & Darolles 1999, Dumas & Haury 1995, Dumas & Prouzet 2003).

Over the 39 km only around 20 km are available for salmon due to the presence of an impassable upstream dam (Figure. I.viii, Figure. I.ix — f). Along the 20 km, salmon may encounter two passable dams equipped with fish passes (Figure. I.viii): Uxondoa (Figure. I.ix — b) and Olha dams. At these two dams, all individuals passing through the fish pass are caught to be measured (body length and weight) and sampled (scales for age determination and a fin clip for genetic analyses). Some tributaries are also available

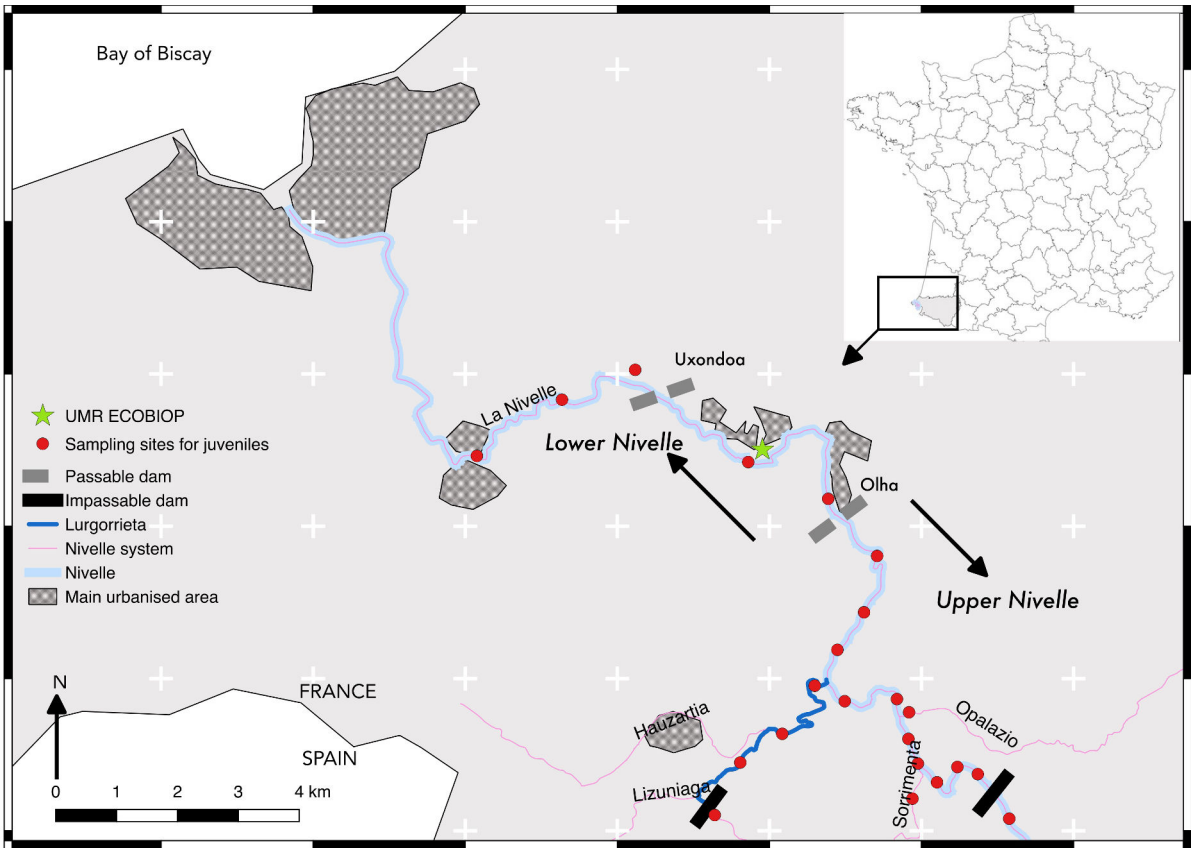
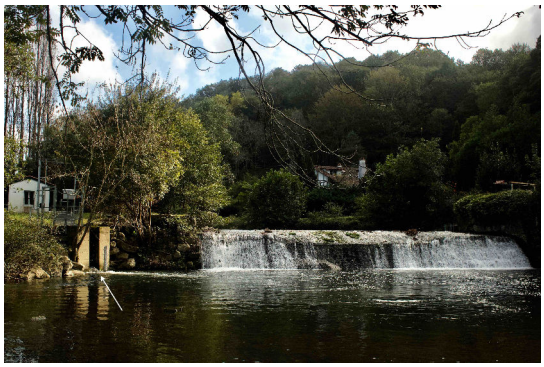


Figure. I.viii: Map of the Nivelle River. The dams "Uxondoa" and "Olha" are now equipped with a fish pass. The Olha dam marked the limit between the Upper Nivelle ("UN") and the Lower Nivelle ("LN"). The red dots correspond to the 22 sites where salmon juveniles are yearly sampled. The Lurgorrieta is the main tributary. Saint-Pée sur Nivelle is the urbanised area between Uxondoa and Olha dams. The yellow star indicates the geographic position of the UMR ECOBIOP.

for salmon: the Sorrimenta (Figure. I.ix — d), the Opalazio, and the Lurgorrieta which is the main tributary. Around 5 km (i.e. 4.7 km) are available for salmon in the Lurgorrieta but an impassable dam also constrains fish upstream displacements. The presence of dams enables to divide the Nivelle into three parts: i) the "Lower Nivelle" — LN — from the river mouth to the Olha dam; ii) the "Upper Nivelle" — UN — from the Olha dam to the upstream impassable dam on the main stream; iii) the "Lurgorrieta", the main tributary (Figure. I.viii). Such a small river system with a few tributaries enables researchers to easily work along the river and to set up monitoring, samplings, and experiments *in natura*.

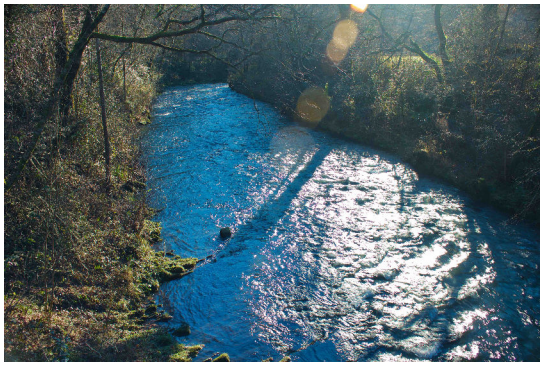
(a) River mouth



(b) Uxondoa dam with the entry of the fish pass at the left (white arrow)

(c) Part of the Upper Nivelle with the flow control dam

(d) Confluence with the Sorrimenta (right side) in the Upper Nivelle



(e) Part of the Upper Nivelle with river banks showing the source rock

(f) Upstream dam on the Nivelle River which is impassable for salmon

Figure. I.ix: Photographs of some points of interest of the Nivelle River (France).©C. Bouchard

I∫ HISTORY OF THE POPULATION

The Nivelle population of salmon is monitored since 1984 by the UMR ECOBIOP based at Saint-Pée sur Nivelle. Only the Lower Nivelle was accessible for salmon until 1992, the Olha dam being equipped in 1992 by a fish pass. In 1990 and 1991 some anadromous salmon were released in the Upper Nivelle, while juveniles were released in non-accessible parts from 1986 to 1995 (Brun 2011, Dumas & Prouzet 2003). Since 1992, the 20 km in the Nivelle and the 5 km in the Lurgorrieta are available, as well as the other tributaries. From 1996 to 2008 some juveniles were also released by the UMR ECOBIOP to compensate catches of anadromous individuals for experiments.

Since 1984, the number of anadromous breeders are moniroted in the Nivelle by accounting for catching probability at dams (chapter 2 for details). Since 1985 — corresponding to spawners in 1984 —, the recruitment in juveniles (number of 0+ or Young of the Year, see page 16) is monitored in the Nivelle by accounting for stocking and catching probability of juveniles during electro fishing (chapter 2 for details). Recruitment is assessed through electro fishings at 22 sites in the Nivelle (dots in Figure. I.viii, page 26). The number of anadromous breeders are available for the Upper Nivelle and the Lower Nivelle by means of Uxondoa and Olha dams (Figure. I.viii). Since 1985, the UMR ECOBIOP also monitors breeding activity through a redd mapping along the Nivelle. Number and location of redds in the Nivelle are, thus, monitored in parallel with the number of breeders (chapter 2 for details). The monitoring of the Nivelle population offers, thus, adequate time series data to work on population dynamics and where individuals spawn.

Number of anadromous salmon migrating in the Nivelle exhibits a strong drop-off since 2003. Since 2003, all the years displayed a number of returning individuals lower than the average yearly number at around 200 individuals (Figure. I.x). More worrying, the yearly number of returning anadromous is near 100 individuals for all years apart for 2010. Recreational fishing is probably not an important pressure for the population, only few individuals being caught. In contrast, the impact of professional fisheries in the Bay of Saint-Jean de Luz was never assessed, data being non-existent. Recent studies highlighted that upstream dams seem constraint both displacements of breeders and nest distribution (Tentelier *et al.* 2016a, Tentelier & Piou 2011), but the effects on population dynamics have never been assessed.

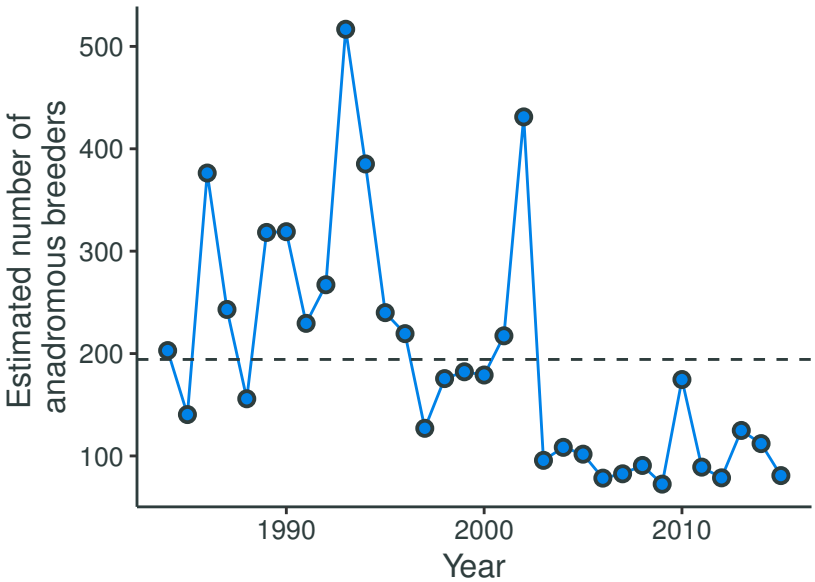


Figure. I.x: Yearly estimated numbers of anadromous breeders migrating in the Nivelle River (France) since 1984. The dashed line indicates the average value over the time series.

Thesis aims & outlines

J∫ KEY ASSUMPTIONS

My thesis aims to assess the effects of space use of potential breeders, namely mature individuals able to spawn or fertilise eggs, on population dynamics and on sexual selection (Figure. I.viii). Quantifying such effects involves working at different scales, i.e. local *versus* at population scale and individual *versus* population, leading to consider them separately. I merge different temporal and spatial scales to link individual space use to population dynamics as well as to sexual selection. I choose the Atlantic salmon population of the Nivelle which offers a suitable model to investigate such effects.

The use of specific habitats to spawn and the spatial distribution of potential breeders generate specific spatial distributions of nests and subsequent juveniles in Atlantic salmon (Einum *et al.* 2008, Foldvik *et al.* 2010). High densities of juveniles, increasing with their aggregation, lead to density compensation, namely density-dependent mortality for this species (Einum & Nislow 2005). A patchy distribution of nests may force juveniles to move over longer distances some weeks after they have emerged due to their territorial behaviour (Einum *et al.* 2006). The forced longer movements may affect the survival of juveniles increasing density-dependent mortality of juveniles. Spatial distribution of nests within a river could, thus, affect population dynamics by exacerbating the density-dependent mortality and diminishing survival. Increasing density-dependent mortality necessarily modifies the relationship between the number of eggs spawned in the river and the resulting number of juveniles.

However, females may select breeding sites according to habitat quality — i.e. quantity of resources and environmental stability — and aggregate their nests in best habitats. Aggregation of nests in habitats of high quality may buffer density-dependent mortality. Mortality should also be dampened in best habitats when environmental stability

comes into play in habitat quality. **The first aim of my thesis is thus to test how the spatial aggregation of nests affect the population dynamics.** I hypothesise that spatial aggregation should 1) diminish recruitment by raising density-dependent mortality and 2) stabilise recruitment depending on the habitat quality where females aggregate.

The use of specific habitats to spawn may generate clumping of salmon nests (Moir *et al.* 1998). Pre-copulatory competition between anadromous males occurs to access females and some males are able to monopolise several females (Fleming 1996, Järvi 1990). Post-copulatory competition happens when releasing of gametes, some anadromous males adopting a sneaky behaviour (Fleming 1996, Järvi 1990). High spatial aggregation of salmon females may favour the participation of sneaky males, whereas an intermediate value may enable anadromous males to monopolise females. Spatial aggregation of females should raise pre- and post-competition between males decreasing the number of males who access females.
The spatial distribution of females should also affect the displacements of males because males look for females. Movements of potential breeders determine their encounters because shaping their home range (Robert *et al.* 2012). Social environment relies on the number and the sex of encountered individuals. For males, other males in their social environment are competitors. The sexual selection looks for testing whether phenotypes or values of phenotypic traits affect accessing females and reproductive success (Kuijper *et al.* 2012). Such effects of a phenotype or trait values are relative, and the ones of neighbours may impact them (Gasparini *et al.* 2013). Sexual selection may, thus, be impacted by which competitors are present in social environment of individuals. Overall, the strength of sexual competition (i.e. pre- and post-copulatory competition) as well as sexual selection can be dependent of social environment. **Hence, the second aim is to test how spatial aggregation and movements of potential breeders influence the sexual competition and the sexual selection.** I hypothesise that 1) the participation of males in reproduction should vary with aggregation of females, and 2) the phenotype of competitors, belonging in the social environment of an individual, influences its reproductive success.

Atlantic salmon also offers the possibility to work on individuals exhibiting an alternative reproductive tactic. Mature parr exhibit sneaky behaviour and have to remain

hidden among pebbles (Aas *et al.* 2011, Jordan *et al.* 2007). Participation of mature parr in reproduction can sometimes reach high levels but is often assessed within some nests or in experimental facilities (Jordan *et al.* 2007, Martinez *et al.* 2000, Tentelier *et al.* 2016b, Thomaz *et al.* 1997). Aggregation of females could enhance participation of mature parr by raising the number of anadromous that compete with each other anadromous to access females. The participation of mature parr, which leads to egg fertilisation by them and not anadromous, should also raise sexual competition faced by anadromous through the post-copulatory competition.

Despite the potentially high participation of mature parr in reproduction, their movements throughout a breeding season remain unknown. In comparison, anadromous males exhibit various spatial behaviours with some individuals adopting a roaming tactic while others favour a staying tactic (Tentelier *et al.* 2016a), something usual when looking males' movements during reproduction (Forchhammer & Boomsma 1998, Sandell & Liberg 1992). **The third aim is to assess the influence of the participation of mature parr on sexual competition faced by anadromous, and the impact of the space use of mature parr on their participation in reproduction.** I hypothesise that 1) the participation of mature parr in reproduction should increase the sexual competition faced by anadromous, and 2) the space use of mature parr, which is engendered by their maturity states and variable among individuals, should influence their participation in reproduction.

Atlantic salmon, as a migratory species, offers a valuable opportunity to assess the effects of habitat fragmentation and habitat loss on space use by breeders. Whether anadromous females, anadromous males, or mature parr seek a resource: breeding habitats or females. The distribution of resources shapes spatial distribution and movements of individuals (MacArthur & Pianka 1966). However, the presence of dams may constrain movements of breeders and access to breeding habitats for females (Forget *et al.* 2018, Meixler *et al.* 2009). Remaining dams in the Nivelle may constrain movements of breeders. The dam opening during the monitoring of the Nivelle population offers the opportunity to evaluate how dams restrict breeders' movements. A satellite hypothesis of my thesis is that dams in such a small river system affect population dynamics by constraining breeders movements and nest placements.

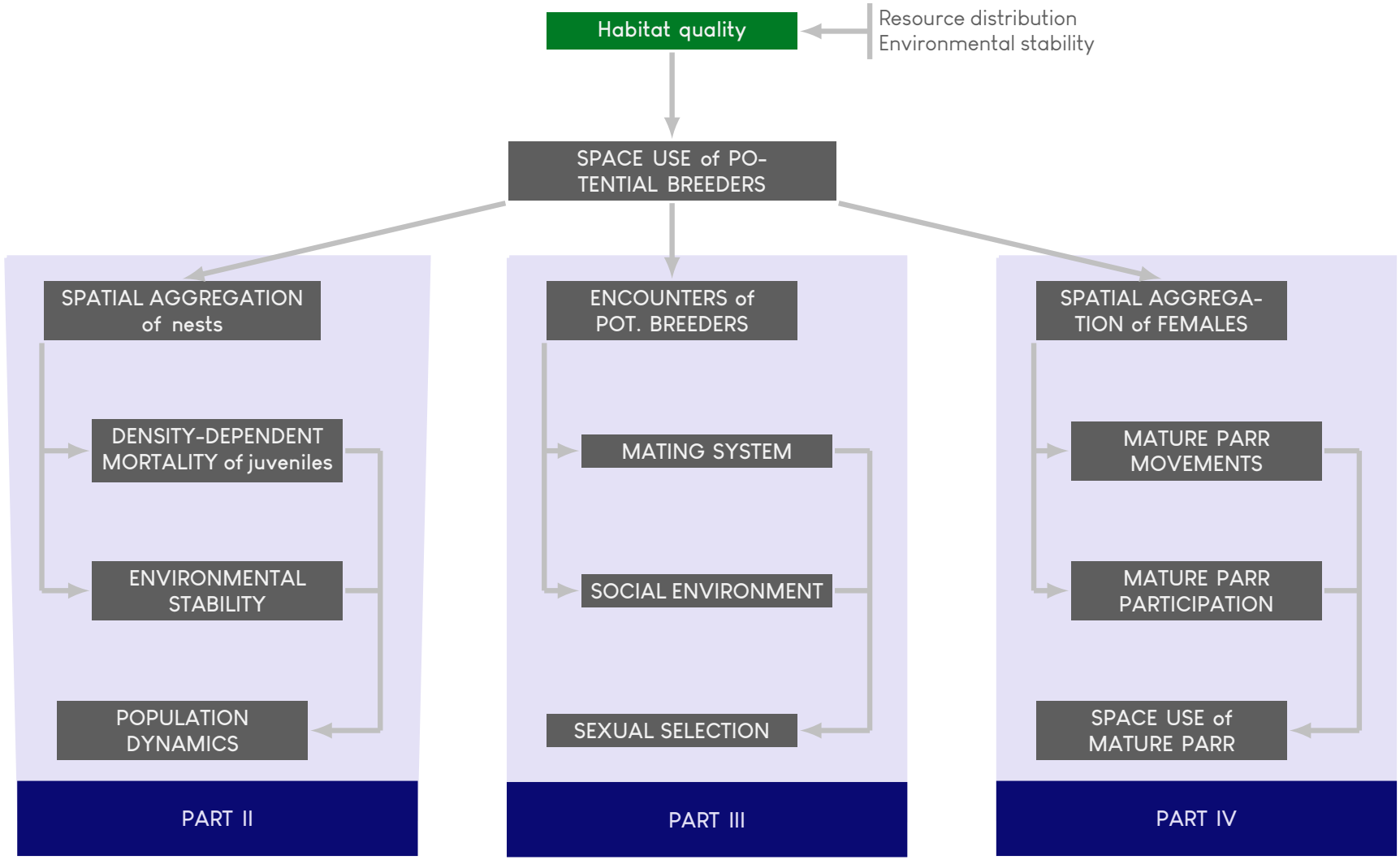


Figure. I.viii: Flow chart of the three parts of this thesis.

K∫ THESIS ORGANISATION

Five different parts make up the manuscript. The first one is the current part introducing the work done during the thesis. The three following parts (parts II, III, and IV) are each organised in three chapters: one main chapter — identified with this symbol: ● — and two satellite chapters (one before and one after the main chapter). Satellite chapters bring contextual information and other points of view or analyses to go further in the thinking. Because each part may focus or use specific tools, their bibliography is separated. The page corresponding to the next part is displayed before each bibliography to facilitate the reading: "Next section: ⇒ page 49"[5].

Part II (page 49) focuses on how spatial distribution of nests affects population dynamics. The first chapter of this part (chapter 1, page 57) is a methodological chapter raising the question of the measurement and appreciation of the spatial distribution through spatial aggregation. The central chapter of this part (chapter 2, page 65) incorporates the spatial aggregation of salmon nests within models relating the population recruitment (number of juveniles) to the population stock (number of eggs). The central chapter, corresponding to a published article in *Ecosphere*, discusses how the spatial aggregation influences the recruitment at the population level. To go further, the following chapter (chapter 3, page 101) reuses the same approaches at a finer spatial scale within Nivelle parts (Figure. I.viii).

The next part (part III, page 145) focuses on the local social structure of potential anadromous breeders created by their space use. The chapter 4 (page 153) links the spatial aggregation of nests to the effective numbers of breeders in the population. The following chapter (chapter 5, page 161), corresponding to an article in preparation, uses different sources of data to infer the sexual network of the population and the resulting sexual selection. Finally, the last chapter (chapter 6, page 199) adopts the females' point of view to assess how their spatial isolation notably influences their reproductive success.

Part IV (page 233) deals with the mature parr, their participation in reproduction, and their space use to access females. First, chapter 7 (page 241) discusses their influence on sexual selection and the mating system. Chapter 8 (page 257), which was submitted, evaluates their space use involved by their maturity level and links it to

[5]This indication, as well as all other, are clickable in the pdf file.

their potential participation in reproduction. Finally, the last chapter (chapter 9, page 283) compares their movements between the different habitat types with movements of immature individuals.

The last part (part V, page 315) corresponds to the general discussion of this work. The part opens by a criticism of the methodology used in the thesis. This final part discusses the principal findings of my thesis by connecting different chapters belonging to different parts. Finally, I discuss the potential implications within the small population of the Nivelle and the perspectives offered by my findings.

The numbering of floating objects (figures, tables, equations, boxes) incorporates the chapter number like Figure. 1.2. Floating objects displayed outside chapters (introduction and discussion of parts, general introduction, general discussion) are numbered within the part and with roman numbers like: Figure. I.iii. All along this manuscript some boxes (like the Box Glossary I.ii, page 23) are displayed. The different types of boxes are displayed below with their meaning.

GLOSSARY I.iii: Example

Glossary box.

BESIDE I.i: Example

Box to present an idea of further possible analyses with the data used in the thesis and in relation with aims of the thesis.

TOOLS I.i: Example

Box to deeply explain an analysis or a method.

DEEPER I.i: Example

Box to present a satellite analysis to go further and bring interesting information.

Next part: ⇒ page 49

Bibliography

Aas, O., Balshine, S., Klemesten & Skurdal (eds.) (2011) *Atlantic salmon ecology*. Blackwell Pub, Chichester ; Ames, Iowa.

Andren, H. (1990) Despotic distribution, unequal reproductive success, and population regulation in the jay *Garrulus Glandarius* L. *Ecology* **71**, 1796–1803.

Bacles, C.F.E., Bouchard, C., Lange, F., Manicki, A., Tentelier, C. & Lepais, O. (2018) Estimating the effective number of breeders from single parr samples for conservation monitoring of wild populations of Atlantic salmon *Salmo salar*. *Journal of Fish Biology* **92**, 699–726.

Baldwin, R.F., Calhoun, A.J.K. & deMaynadier, P.G. (2006) Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the wood frog *Rana Sylvatica*. *Journal of Herpetology* **40**, 442–453.

Beall, E. (1994) Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. *ICES Journal of Marine Science* **51**, 1–9.

Boulinier, T. & Danchin, E. (1997) The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology* **11**, 505–517.

Brun, M. (2011) *Aide à la décision pour la conservation des populations de saumon atlantique (Salmo salar L.)*. Ph.D. thesis, Pau.

Callander, S., Hayes, C.L., Jennions, M.D. & Backwell, P.R.Y. (2013) Experimental evidence that immediate neighbors affect male attractiveness. *Behavioral Ecology* **24**, 730–733.

Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology* **9**, 129–136.

Coulton, D.W., Clark, R.G., Howerter, D.W., Anderson, M.G. & Wassenaar, L.I. (2011) Costs and benefits of natal dispersal in yearling mallards Anas platyrhynchos. *Journal of Avian Biology* **42**, 123–133.

Crisp, D.T. (1995) Dispersal and growth rate of O-group salmon (*Salmo salar* L.) from point-stocking together with some information from scatter-stocking. *Ecology of Freshwater Fish* **4**, 1–8.

Croft, D.P., James, R., Ward, A.J.W., Botham, M.S., Mawdsley, D. & Krause, J. (2005) Assortative interactions and social networks in fish. *Oecologia* **143**, 211–219.

Cushman, S.A. (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* **128**, 231–240.

Danchin, E., Giraldeau, L.A. & Cézilly, F. (2008) *Behavioural ecology.* Oxford University Press, Oxford ; New York.

Danchin, E. & Wagner, R.H. (1997) The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution* **12**, 342–347.

Darwin, C. (1859) *The origin of species by means of natural selection, or, the preservation of favored races in the struggle for life.* OCLC: 934794833.

Davidian, E., Courtiol, A., Wachter, B., Hofer, H. & Höner, O.P. (2016) Why do some males choose to breed at home when most other males disperse? *Science Advances* **2**, e1501236.

de Buffon (1749) Histoire naturelle, premier discours: de la manière d'étudier et de traiter l'histoire naturelle. Paris.

de Gaudemar, B. & Beall, E. (1998) Effects of overripening on spawning behaviour and reproductive success of Atlantic salmon females spawning in a controlled flow channel. *Journal of Fish Biology* **53**, 434–446.

de Gaudemar, B. & Beall, E. (1999) Reproductive behavioural sequences of single pairs of Atlantic salmon in an experimental stream. *Animal Behaviour* **57**, 1207–1217.

de Gaudemar, B., Schroder, S.L. & Beall, E.P. (2000) Nest placement and egg distribution in Atlantic salmon redds. *Environmental Biology of Fishes* **57**, 37–47.

Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* **66**, 973–988.

Dumas, J. & Darolles, V. (1999) Caractéristiques environnementales et survie embryolarvaire du saumon Atlantique, *Salmo salar* L., dans un cours d'eau du piémont pyrénéen, la Nivelle (France). *Cybium* **23**, 29–44.

Dumas, J. & Haury, J. (1995) Une rivière du Piémont pyrénéen: la Nivelle (Pays basque). *Acta Biologica Montana* **11**, 113–146.

Dumas, J. & Prouzet, P. (2003) Variability of demographic parameters and population dynamics of Atlantic salmon (*Salmo salar* L.) in a south-west French river. *ICES Journal of Marine Science* **60**, 356–370.

Einum, S. & Fleming, I.A. (2000) Selection against late emergence and small offspring in atlantic salmon (*Salmo salar*). *Evolution* **54**, 628–639.

Einum, S. & Nislow, K.H. (2005) Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. *Oecologia* **143**, 203–210.

Einum, S., Nislow, K.H., Mckelvey, S. & Armstrong, J.D. (2008) Nest distribution shaping within-stream variation in Atlantic salmon juvenile abundance and competition over small spatial scales. *Journal of Animal Ecology* **77**, 167–172.

Einum, S., Sundt-Hansen, L. & H Nislow, K. (2006) The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos* **113**, 489–496.

Elton, C.S. (1927) *Animal ecology*. Sidgwick and Jackson, first edn.

Emlen, S.T. & Oring, L.W. (1977) Ecology, sexual selection, and evolution of mating systems. *Science* **197**, 215–223.

Fahrig, L. (1998) When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* **105**, 273–292.

Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* **40**, 1649–1663.

Finstad, A.G., Okland, F., Thorstad, E.B. & Heggberget, T.G. (2005) Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology* **67**, 919–930.

Fleming, I.A. (1996) Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries* **6**, 379–416.

Fleming, I.A. (1998) Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 59–76.

Fleming, I.A., Hindar, K., Mjolnerod, I.B., Jonsson, B., Balstad, T. & Lamberg, A. (2000) Lifetime success and interactions of farm salmon invading a native population. *Proceedings of the Royal Society B: Biological Sciences* **267**, 1517–1523.

Foldvik, A., Finstad, A.G. & Einum, S. (2010) Relating juvenile spatial distribution to breeding patterns in anadromous salmonid populations. *Journal of Animal Ecology* **79**, 501–509.

Forchhammer, M.C. & Boomsma, J.J. (1998) Optimal mating strategies in nonterritorial ungulates: a general model tested on muskoxen. *Behavioral Ecology* **9**, 136–143.

Forget, G., Baglinière, J.L., Marchand, F., Richard, A. & Nevoux, M. (2018) A new method to estimate habitat potential for Atlantic salmon (*Salmo salar*): predicting the influence of dam removal on the Sélune River (France) as a case study. *ICES Journal of Marine Science* .

Formica, V.A., Augat, M.E., Barnard, M.E., Butterfield, R.E., Wood, C.W. & Brodie, E.D. (2010) Using home range estimates to construct social networks for species with indirect behavioral interactions. *Behavioral Ecology and Sociobiology* **64**, 1199–1208.

Formica, V.A., McGlothlin, J.W., Wood, C.W., Augat, M.E., Butterfield, R.E., Barnard, M.E. & Brodie III, E.D. (2011) Phenotypic assortment mediates the effect of social selection in a wild beetle population. *Evolution* **65**, 2771–2781.

Fretwell, S.D. (1972) *Populations in seasonal environments.* Princeton University Press, Princeton, NJ.

Fretwell, S.D. & Lucas, H.L.J. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16–36.

Garant, D., Dodson, J.J. & Bernatchez, L. (2001) A genetic evaluation of mating system and determinants of individual reproductive success in Atlantic salmon (*Salmo salar* L.). *Journal of Heredity* **92**, 137–145.

Garant, D., Fleming, I.A., Einum, S. & Bernatchez, L. (2003) Alternative male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. *Ecology Letters* **6**, 541–549.

Garcia de Leaniz, C., Fleming, I.A., Einum, S., Verspoor, E., Jordan, W.C., Consuegra, S., Aubin-Horth, N., Lajus, D., Letcher, B.H., Youngson, A.F., Webb, J.H., Vøllestad, L.A., Villanueva, B., Ferguson, A. & Quinn, T.P. (2007) A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. *Biological Reviews* **82**, 173–211.

Gasparini, C., Serena, G. & Pilastro, A. (2013) Do unattractive friends make you look better? Context-dependent male mating preferences in the guppy. *Proceedings of the Royal Society of London B: Biological Sciences* **280**, 20123072.

Grimardias, D., Merchermek, N., Manicki, A., Chebaux, J., Gaudin, P., Jarry, M. & Beall, E. (2010a) Effects of habitat on individual reproductive success of mature male parr of Atlantic salmon *Salmo salar*. *Journal of Fish Biology* **77**, 2460–2466.

Grimardias, D., Merchermek, N., Manicki, A., Garnier, J., Gaudin, P., Jarry, M. & Beall, E. (2010b) Reproductive success of Atlantic salmon (*Salmo salar*) mature male parr in a small river, the Nivelle: influence of shelters: Mature male parr success and shelters. *Ecology of Freshwater Fish* **19**, 510–519.

Gross, M.R. (1987) Evolution of diadromy in fishes. *In American fisheries society symposium* **1**, 14–25.

Gustafson-Greenwood, K.I. & Moring, J.R. (1990) Territory size and distribution of newly-emerged Atlantic salmon (*Salmo salar*). *Hydrobiologia* **206**, 125–131.

Hansen, L.P. & Jonsson, B. (1991) Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* **38**, 251–258.

Hansen, L.P. & Quinn, T.P. (1998) The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 15.

Humboldt, A.d. & Bonpland, A. (1814) *Voyage aux régions équinoxiales du Nouveau Continent, fait, en 1799, 1800, 1801, 1802, 1803, et 1804, par Al. De Humboldt et A. Bonpland*, vol. 1. chez F. Schoell, Paris, France.

Hunt, K.L., Fraser, J.D., Friedrich, M.J., Karpanty, S.M. & Catlin, D.H. (2018) Demographic response of Piping Plovers suggests that engineered habitat restoration is no match for natural riverine processes. *The Condor* **120**, 149–165.

Hutchings, J.A. & Jones, M.E.B. (1998) Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 26.

Hutchinson, G.E. (1957) *Treatise on Limnology.* John Wiley and Sons.

Järvi, T. (1990) The effects of male dominance, secondary sexual characteristics and female mate choice on the mating success of male Atlantic salmon *Salmo salar. Ethology* **84**, 123–132.

Jonsson, B., Jonsson, N. & Hansen, L. (1990) Does juvenile experience affect migration and spawning of adult Atlantic salmon? *Behavioral Ecology and Sociobiology* **26**.

Jonsson, B., Jonsson, N. & Hansen, L.P. (2003) Atlantic salmon straying from the River Imsa. *Journal of Fish Biology* **62**, 641–657.

Jordan, W.C., Fleming, I.A. & Garant, D. (2007) Mating system and social structure. *The Atlantic salmon: genetics, conservation and management*, pp. 167–194, Blackwell Pub, Oxford.

Judas, J. & Henry, O. (1999) Seasonal variation of home range of collared peccary in tropical rain forests of French Guiana. *The Journal of Wildlife Management* **63**, 546.

Kazakov, R.V. (1992) Distribution of Atlantic salmon, *Salmo salar* L., in freshwater bodies of Europe. *Aquaculture Research* **23**, 461–475.

Kennedy, B.P., Nislow, K.H. & Folt, C.L. (2008) Habitat-mediated foraging limitations Drive survival bottlenecks for juvenile salmon. *Ecology* **89**, 2529–2541.

Krebs, J.R. & Davies, N.B. (2009) *Behavioural ecology an evolutionary approach.* Blackwell, Malden (Mass.); Oxford; Victoria, oCLC: 866999693.

Kuijper, B., Pen, I. & Weissing, F.J. (2012) A Guide to sexual selection theory. *Annual Review of Ecology, Evolution, and Systematics* **43**, 287–311.

Lecomte, F., Beall, E., Chat, J., Davaine, P. & Gaudin, P. (2013) The complete history of salmonid introductions in the Kerguelen Islands, Southern Ocean. *Polar Biology* **36**, 457–475.

Levin, S.A. (1974) Dispersion and population interactions. *The American Naturalist* **108**, 207–228.

Levin, S.A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* **73**, 1943–1967.

Linnæus, C. (1753) *Species plantarum*, vol. 1. Impensis gc nauk edn.

Linnæus, C. (1758) *Systema naturae*, vol. 1.

Long, R.A., Kie, J.G., Terry Bowyer, R. & Hurley, M.A. (2009) Resource selection and movements by female mule deer *Odocoileus hemionus*: effects of reproductive stage. *Wildlife Biology* **15**, 288–298.

López-Sepulcre, A., Kokko, H. & Norris, K. (2010) Evolutionary conservation advice for despotic populations: habitat heterogeneity favours conflict and reduces productivity in Seychelles magpie robins. *Proceedings of the Royal Society of London B: Biological Sciences* **277**, 3477–3482.

Louâpre, P., Fauvergue, X., van Baaren, J. & Martel, V. (2015) The male mate search: an optimal foraging issue? *Current Opinion in Insect Science* **9**, 91–95.

Louhi, P., Mäki-Petäys, A. & Erkinaro, J. (2008) Spawning habitat of Atlantic salmon and brown trout: general criteria and intragravel factors. *River Research and Applications* **24**, 330–339.

MacArthur, R.H. & Pianka, E.R. (1966) On Optimal Use of a Patchy Environment. *The American Naturalist* **100**, 603–609.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogreography. *Evolution* **17**, 373–387.

MacCrimmon, H.R. & Gots, B.L. (1979) World Distribution of Atlantic Salmon, *Salmo salar*. *Journal of the Fisheries Research Board of Canada* **36**, 422–457.

Malthus, T. (1798) *An essay on the principle of population*. J.Johnson, London.

Martinez, J.L., Moran, P., Perez, J., De Gaudemar, B., Beall, E. & Garcia-Vazquez, E. (2000) Multiple paternity increases effective size of southern Atlantic salmon populations. *Molecular Ecology* **9**, 293–298.

McDonald, G.C., James, R., Krause, J. & Pizzari, T. (2013) Sexual networks: measuring sexual selection in structured, polyandrous populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20120356–20120356.

McNab, B.K. (1963) Bioenergetics and the Determination of Home Range Size. *The American Naturalist* **97**, 133–140.

Meixler, M.S., Bain, M.B. & Todd Walter, M. (2009) Predicting barrier passage and habitat suitability for migratory fish species. *Ecological Modelling* **220**, 2782–2791.

Mjølnerød, I.B., Fleming, I.A., Refseth, U.H. & Hindar, K. (1998) Mate and sperm competition during multiple-male spawnings of Atlantic salmon. *Canadian Journal of Zoology* **76**, 70–75.

Mo, T.A., Thorstad, E.B., Sandlund, O.T., Berntsen, H.H., Fiske, P. & Uglem, I. (2018) The pink salmon invasion: a Norwegian perspective. *Journal of Fish Biology* **93**, 5–7.

Moir, H., Gibbins, C., Soulsby, C. & Webb, J. (2004) Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (*Salmo salar* L.). *Geomorphology* **60**, 21–35.

Moir, H.J., Gibbins, C.N., Soulsby, C. & Webb, J.H. (2006) Discharge and hydraulic interactions in contrasting channel morphologies and their influence on site utilization by spawning Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2567–2585.

Moir, H.J., Soulsby, C. & Youngson, A. (1998) Hydraulic and sedimentary characteristics of habitat utilized by Atlantic salmon for spawning in the Girnock Burn, Scotland. *Fisheries Management and Ecology* **5**, 241–254.

Moorcroft, P.R. & Barnett, A. (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology* **89**, 1112–1119.

Morris, D.W. (1987) Ecological scale and habitat use. *Ecology* **68**, 362–369.

Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia* **136**, 1–13.

Morris, D.W. (2011) Adaptation and habitat selection in the eco-evolutionary process. *Proceedings of the Royal Society of London B: Biological Sciences* **278**, 2401–2411.

Nislow, K.H., Einum, S. & Folt, C.L. (2004) Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon. *Journal of Fish Biology* **65**, 188–200.

Parker, G. & Sutherland, W. (1986) Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behaviour* **34**, 1222–1242.

Parker, G.A. (1970) The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae): II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. *The Journal of Animal Ecology* **39**, 205.

Parker, G.A. (1974) The reproductive behaviour and the nature of sexual selection *Scatophaga stercoraria* L. (Diptera: Scatophagidae). IX. Spatial distribution of fertilization rates and evolution of male search strategy within the reproductive area. *Evolution* **28**, 93–108.

Pomeroy, P.P., Anderson, S.S., Twiss, S.D. & McConnell, B.J. (1994) Dispersion and site fidelity of breeding female grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology* **233**, 429–447.

Preatoni, D., Mustoni, A., Martinoli, A., Carlini, E., Chiarenzi, B., Chiozzini, S., Van Dongen, S., Wauters, L.A. & Tosi, G. (2005) Conservation of brown bear in the Alps: space use and settlement behavior of reintroduced bears. *Acta Oecologica* **28**, 189–197.

Quirici, V., Castro, R.A., Ortiz-Tolhuysen, L., Chesh, A.S., Burger, J.R., Miranda, E., Cortés, A., Hayes, L.D. & Ebensperger, L.A. (2010) Seasonal variation in the range areas of the diurnal rodent *Octodon degus*. *Journal of Mammalogy* **91**, 458–466.

Robert, K., Garant, D. & Pelletier, F. (2012) Keep in touch: Does spatial overlap correlate with contact rate frequency? *The Journal of Wildlife Management* **76**, 1670–1675.

Sandell, M. & Liberg, O. (1992) Roamers and stayers: a model on male mating tactics and mating systems. *The American Naturalist* **139**, 177–189.

Shuster, S.M. & Wade, M.J. (2003) *Mating systems and strategies*. Monographs in behavior and ecology, Princeton University Press, Princeton.

Skellam, J.G. (1951) Random dispersal in theoretical populations. *Biometrika* **38**, 196.

Skilbrei, O.T., Heino, M. & Svåsand, T. (2015) Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages from farm sites in Norway. *ICES Journal of Marine Science* **72**, 670–685.

South, A.B. & Kenward, R.E. (2001) Mate finding, dispersal distances and population growth in invading species: a spatially explicit model. *Oikos* **95**, 53–58.

Starking-Szymanski, M.D., Yoder-Nowak, T., Rybarczyk, G. & Dawson, H.A. (2018) Movement and habitat use of headstarted Blanding's turtles in Michigan. *Journal of Wildlife Management* **82**, 1516–1527, wOS:000442501700018.

Steingrímsson, S.Ó. & Grant, J.W.A. (2008) Multiple central-place territories in wild young-of-the-year Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* **77**, 448–457.

Strøm, J.F., Thorstad, E.B., Hedger, R.D. & Rikardsen, A.H. (2018) Revealing the full ocean migration of individual Atlantic salmon. *Animal Biotelemetry* **6**.

Sutherland, W.J. (1983) Aggregation and the 'Ideal Free' Distribution. *Journal of Animal Ecology* **52**, 821–828.

Sutherland, W.J. (1996) Predicting the consequences of habitat loss for migratory populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **263**, 1325–1327.

Taggart, J.B., McLaren, I.S., Hay, D.W., Webb, J.H. & Youngson, A.F. (2001) Spawning success in Atlantic salmon (*Salmo salar* L.): a long-term DNA profiling-based study conducted in a natural stream. *Molecular Ecology* **10**, 1047–1060.

Taylor, E.B. (1991) A review of local adaptation in Salmonidac, with particular reference to Pacific and Atlantic salmon. *Aquaculture* **98**, 185–207.

Tentelier, C., Larranaga, N., Lepais, O., Manicki, A., Rives, J. & Lange, F. (2016a) Space use and its effects on reproductive success of anadromous Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 1461–1471.

Tentelier, C., Lepais, O., Larranaga, N., Manicki, A., Lange, F. & Rives, J. (2016b) Sexual selection leads to a tenfold difference in reproductive success of alternative reproductive tactics in male Atlantic salmon. *The Science of Nature* **103**.

Tentelier, C. & Piou, C. (2011) Obstacles to migration constrain nest distribution of Atlantic salmon. *Ecology of Freshwater Fish* **20**, 400–408.

Thomaz, D., Beall, E. & Burke, T. (1997) Alternative reproductive tactics in atlantic salmon: factors affecting mature parr success. *Proceedings of the Royal Society of London B: Biological Sciences* **264**, 219–226.

Weir, L.K. & Grant, J.W.A. (2010) Courtship rate signals fertility in an externally fertilizing fish. *Biology Letters* **6**, 727–731.

Whitehead, H. (1998) Male mating strategies: models of roving and residence. *Ecological Modelling* **111**, 297–298.

Wiens, J.A. (1989) Spatial Scaling in Ecology. *Functional Ecology* **3**, 385.

WWF (2001) The Status of Wild Atlantic Salmon. Tech. rep., WWF.

Zhang, Z., Glover, K.A., Wennevik, V., Svåsand, T., Sørvik, A.G.E., Fiske, P., Karlsson, S. & Skaala, ø. (2013) Genetic analysis of Atlantic salmon captured in a netting station reveals multiple escapement events from commercial fish farms. *Fisheries Management and Ecology* **20**, 42–51.

PART II

Effects of aggregation on population recruitment

Introduction of Part II

POPULATION REGULATION: FROM STOCK TO RECRUITMENT

In a wide range of taxa, population dynamics exhibit yearly variations. A key question in ecology and conservation is understanding whether and how to vary population dynamics. Indeed, identifying such variations in population dynamics and their causes allows highlighting potential conservation issues and implementing management plans (Dobson & Lees 1989, Milner-Gulland *et al.* 2003, Sydeman & Allen 1999). Demographic models constitute key instruments for managing populations as universally recognised (Morris *et al.* 2002, Norris 2004). For example, Elliott *et al.* (2011) highlighted a negative abundance impact on survival of bald eagle (*Haliaeetus leucocephalus*) due to the salmon depletion. Population size fluctuates according to variation in recruitment induced by variation either in stock or processes impacting the stock.

Recruitment as a result of processes acting on a stock. Processes either density-dependent or density-independent may positively or negatively affect the relationship between the stock (e.g. number of breeders or eggs, ...) and the recruitment (e.g. number of eggs, juveniles, or future breeders, ...), namely stock-recruitment models. Sometimes, a same environmental factor can affect recruitment through density-dependent and density-independent process. For example, temperature may decrease egg survival as found by Du & Ji (2006) in the northern grass lizard (*Takydromus septentrionalis*) by impacting embryonic development through density-independent cellular processes. On the other hand, temperature may lead to a mismatch with resource availability (Durant *et al.* 2007) by affecting phenology. A mismatch may exacerbate competition for resources, a density-dependent process. Density-dependent processes may also have positive effects on recruitment. Indeed, positive density-dependence arises when the density enhances survival or fecundity of individuals, whereas negative density-dependence happens when

the survival or fecundity decreases as abundance increases (Elliott *et al.* 2011, Herrando-Pérez *et al.* 2012, Neave 1953). Stock-recruitment models account for density-dependent and independent processes when linking recruitment to stock (box Tools II.i).

TOOLS II.i: Stock-recruitment models

Stock-recruitment models are a group of models linking the abundance of the reproductive stock — e.g. breeders or eggs — and the number of recruits — e.g. eggs or juveniles named 0+ or Young Of the Years (YOY, see 16) —. Indeed, they provide identification of some stock reference points such as the one maximising the recruitment (S_{Rmax}), or maximising a sustainable yield (S_{MSY}). These models also provide an estimate of the carrying capacity, namely the abundance of recruits that can be supported by a given environment. Hence, fishery scientists or stakeholders widely used stock-recruitment models.

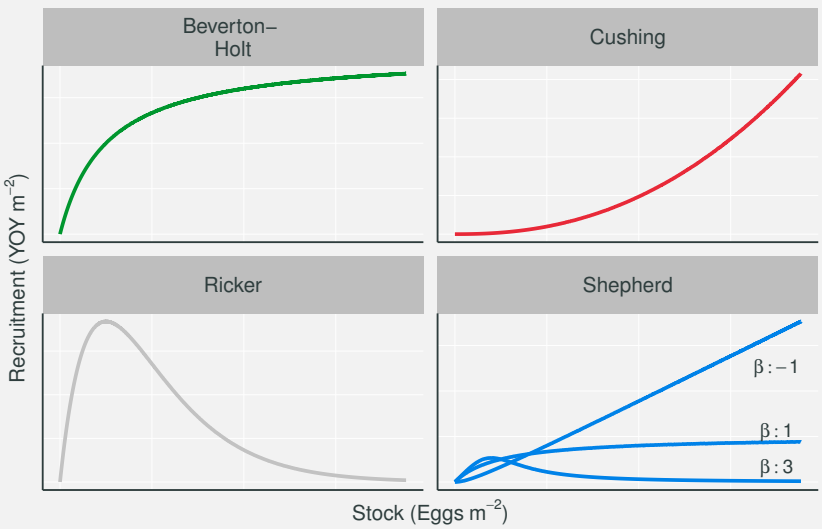


Figure. II.i: Example of stock-recruitment curves from the four mainly used models.

The most used models are those of Beverton & Holt (1957), Cushing (1973), Ricker (1954), and Shepherd (1982). Different assumptions on the density-dependent mortality differentiate the first three models. Indeed, stock-recruitment models link the recruitment to the stock by accounting for a density-independent term and density-dependent one. The

differences of assumptions are clearly visible when looking at the curve shapes generated by the models (Figure. II.i). The model of Cushing (1973) assumes a weak density-dependent mortality leading to an infinitely increasing curve. At the opposite, the model of Ricker (1954) assumes a weak density-dependent mortality at low density but a strong one when the stock reaches a threshold biomass. This model generates a dome-shaped curve. Between these two models, the one of Beverton & Holt (1957) gives an asymptotic curve. In Ricker's model the density compensation (increased mortality at high densities) was exacerbated compared to Beverton & Holt's model or to Cushing's one. Finally, the model of Shepherd (1982) enables to generate the three previous curves through another parameter β (Figure. II.i): *i*) $\beta < 1$ gives a Cushing-shaped curve, *ii*) $\beta = 1$ gives a Beverton-Holt-shaped curve, and *iii*) $\beta > 1$ gives a Ricker-shaped curve.

HABITAT SELECTION GENERATES POPULATION REGULATION AFFECTING POPULATION DYNAMICS

Breeding habitat selection generates spatial aggregation of potential breeders. Spatial aggregation occurs when individuals, or more generally items, are not regularly distributed in space (Figure. II.ii). Aggregation occurs even if individuals exhibit a random and uniform distribution (Figure. II.ii). Conspecific attraction, choice copying, colonial living, ..., are some processes generating aggregation in time or space in a wide range of taxa (Danchin & Wagner 1997, Doligez *et al.* 2003, Evans *et al.* 2016). Habitat choice related to reproduction also generates spatial aggregation in species using a specific breeding habitat (Doligez *et al.* 2003, Evans *et al.* 2016). Although the most visual example of such aggregation during reproduction remains harems and leks, some species exhibit aggregation of potential breeders due to the spatial distribution of the breeding sites. For example, Almada *et al.* (1994) linked the spatial aggregation of potential breeders in *Salaria pavo* (Blenniidae) to the spatial distribution of available breeding sites. Produced juveniles usually stay at breeding sites during a variable period before to shift to another niche. Aggregation of juveniles at breeding sites already existed in dinosaurs (Forster 1990) and is common in fishes (Macpherson 1998). In fishes with external fecundation, mating, spawning, hatching and first stages of development

occur at the same location. The habitat choice of potential breeders may, thus, lead to aggregation of their juveniles.

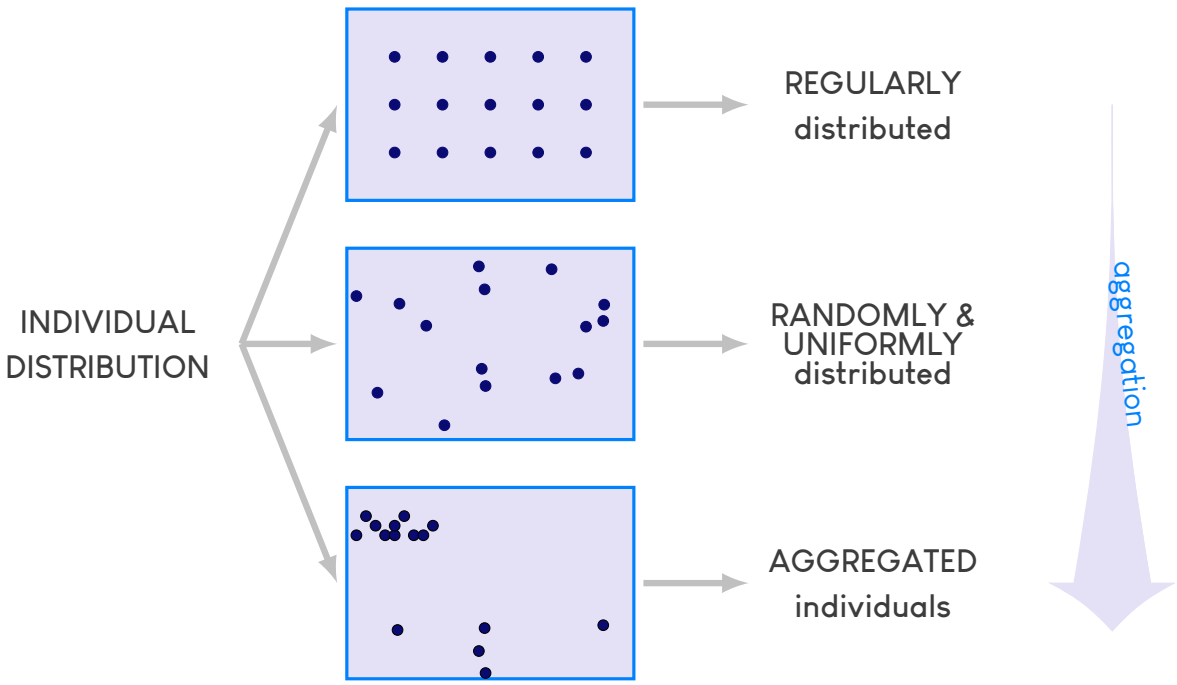


Figure. II.ii: Three patterns of individual spatial distribution. Positions denoting a random and uniform distribution were sampled from a uniform distribution.

Aggregation as a cause of population regulation. Spatial aggregation may affect recruitment by impacting the survival of eggs and juveniles. As in metapopulations, aggregated nests may compensate for losses of recruitment in a nest meaning that aggregation of nests stabilises population recruitment (Murdoch *et al.* 1992). In contrast, recruitment may be more variable when aggregated nests suffer environmental stochasticity so that local perturbations with positive or negative impacts hits many nests at a time (Engen *et al.* 1998, Lande 1993, Sæther 1997). Concerning a loss of recruitment, aggregation may exacerbate density-dependent compensation or mortality (Clotfelter & Yasukawa 1999, Griffiths *et al.* 2003). Aggregation may increase recruitment when kins form the major part of aggregated individuals as such an aggregation of kins favours antipredator responses in some fishes (Ward & Hart 2003). Spatial aggregation of nests may, thus, generates a loss or a gain of recruitment but also stabilises or varies the recruitment.

STOCK-RECRUITMENT AND SPATIAL AGGREGATION

Atlantic salmon is a good candidate to study effects of aggregation on recruitment. Atlantic salmon exhibit habitat choice for breeding sites (Louhi *et al.* 2008) which may favour nest aggregation. Some environmental factors such as floods may also favour nest aggregation by diminishing the number of suitable habitats which are accessible (Moir *et al.* 1998, Parry *et al.* 2018, and Figure. II.iii page 125). Stock-recruitment models have been mainly used to study population dynamics (Brun 2011, Jonsson *et al.* 1998, Prevost 2003, Prévost *et al.* 1996, Rivot *et al.* 2004). Whereas the spatial structure has been studied at small scale (e.g. at the nest scale, Einum & Nislow 2005, Finstad *et al.* 2009), the effects of local spatial aggregation on population recruitment remain poorly appreciated.

Accounting for spatial aggregation in stock-recruitment models supplements accounting for density-dependent processes. The current part aims to test whether spatial aggregation of nests modifies population dynamics by impacting stock-recruitment relationships. Chapter 1 (page 57) compares mean density to two spatial aggregation indices by simulating nest distribution to test whether spatial aggregation indices bring another information than mean density accounted in stock-recruitment models. Chapter 2 (page 65) implements the spatial aggregation of nests computed for the entire population into stock-recruitment models. I assessed the potential effects of aggregation either on the mean or the variability of the recruitment at a population level. Finally, density-dependent processes linked to the spatial distribution of nests may act at a narrower scale than the population level. The same method was, thus, applied within river zones (Lower Nivelle, Upper Nivelle, and Lurgorrieta) in chapter 3 (page 101).

CHAPTER 1

Spatial aggregation to go further than the mean density

Within populations, some individuals may aggregate in space even if they exhibit uniform and random distribution (Figure. II.ii). Investigating the causes of spatial aggregation remains difficult, aggregation involving both costs and benefits (Danchin & Wagner 1997). However, some authors tried to quantify the spatial aggregation of individuals to link it with their environment. Although the conceptualisation and the formulation of aggregation remain difficult (Gokhale 1975), Lloyd (1967) was one of the first trying to assess spatial aggregation. He justified his work by saying:

> « ...there is one thing about the habitat that can be measured and is undoubtedly important to the centipedes [of Wytham Woods], namely, the other centipedes in their immediate vicinity. » — Lloyd 1967

His main idea was to investigate how the number of competitors was significant for individuals. In this way, a measure of the number of competitors experienced by an average individual is a better way to assess competition and interactions than the mean density (Lloyd 1967, Wade *et al.* 2018). The idea developed by Lloyd on the importance of the number of competitors was one of the justifications of the current chapter. Another justification was that mean density is already accounted for in stock-recruitment relationships through density-dependent compensation. Aggregation pattern and density may carry different information on the distribution of individuals.

I selected two different indices measuring spatial aggregation: space selectivity from Petitgas (1998) and patchiness as defined by Lloyd (1967). These two indices enable me to assess spatial aggregation within an environment divided into patches. Although some indices use distances between items to assess aggregation, the data concerning salmon nests did not allow me to utilise them (chapter 2, page 2). This short methodological

chapter aims to graphically compare these two indices to ensure that one of these indices could be used to assess the spatial aggregation of salmon nests. In addition, these indices were compared to mean density what highlighted mean density did not well depict spatial distribution of redds (salmon nests).

1.1 SPATIAL AGGREGATION INDICES

1.1.1 SPACE SELECTIVITY

Space selectivity (Ss) has been firstly defined for mineral exploitation (Mathéron 1981). In his study, Petitgas (1998) generalised this index to assess aggregation of pelagic fishes from their spatio-temporal distribution. This index was based on :

- $z(x)$ the fish density at point x and A the total area occupied by the fish population,
- T: proportion of A where the number of fish is $>$ to $z(x)$ (from 0 to 1),
- Q: density of fish found into T compared to A.

T and Q allow users to generate aggregation curves enabling a better understanding and to visualise fish aggregation. The Ss was computed from the area under the curve $Q(T)$ (Figure. 1.1). In my case, fish were replaced by redds and A by the total number of patches where redds were found.

1.1.2 PATCHINESS

Patchiness was defined by Lloyd (1967) from the mean number of neighbours per individual in the same patch, the "mean crowding" — $\overset{*}{m}$, Figure. 1.2. Patchiness was simply the ratio $\frac{\overset{*}{m}}{m}$, where m is the mean density (general formula page 73). The reference value of 1 indicates a uniform and random distribution (Figure. II.ii, page 54) while values upper 1 indicate an aggregated one.

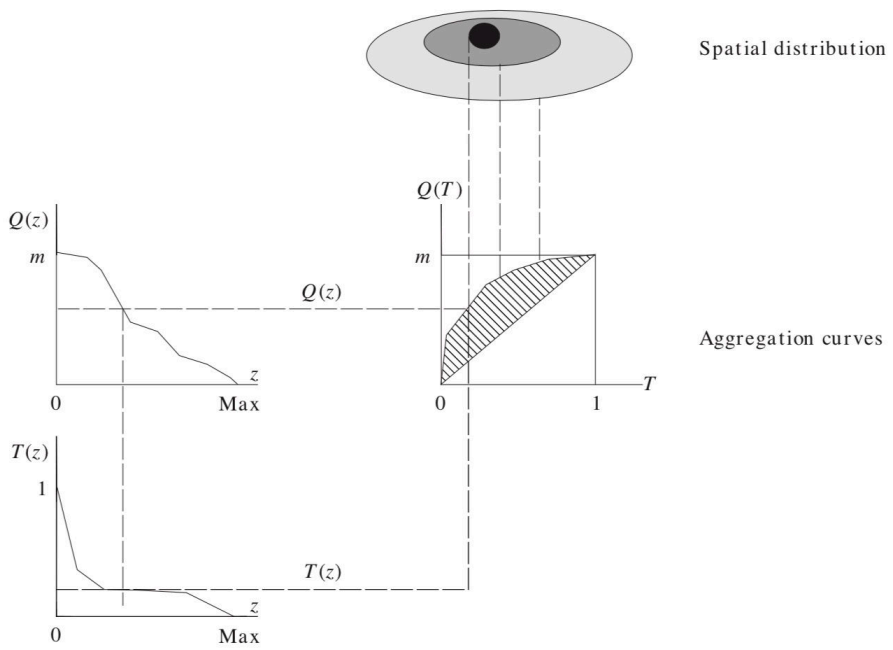


Figure. 1.1: Graphical construction of the geostatistical aggregation curve Q(T) with the curves Q(z) and T(z) for a schematic spatial distribution. Density values are denoted by z. T(z) is the proportion of the total fish presence area where the density is greater than z. Q(z) is the fish biomass that is on the area T(z) where density is higher than z. The curve Q(T) relates Q(z) to T(z) and gives the maximum biomass that can be in any proportion T of the total area. The hatched zone under the Q(T) curve represents half of the space selectivity (concentration) index Ss (from Petitgas 1998).

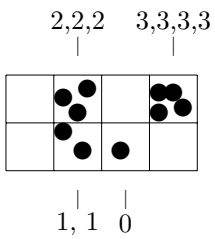


Figure. 1.2: Examples of individual distribution among patches to compute the mean number of neighbours in the same patch. The number of neighbours per individual is displayed for each patch where at least one individual is present (•).

Table. 1.1: Table of the different scenarii used to depict the difference between two spatial aggregation indices (space selectivity and patchiness) and mean density.

Scenario	Available patches	N redds	Spatial distribution of redds
1	$x_1 = 93$	$n_1 = 233$	same number of redds per patch
2	$x_2 = 14$	$n_2 = 105$	same number of redds per patch
3	$x_2 = 14$	$n_1 = 233$	same number of redds per patch
4	$x_2 = 14$	$n_3 = 20$	same number of redds per patch
5	$x_1 = 93$	$n_1 = 233$	random distribution of redds among all patchs
6	$x_1 = 93$	$n_1 = 233$	random distribution of redds among $\frac{1}{4}$ patchs
7	$x_2 = 14$	$n_3 = 20$	random distribution of redds among $\frac{1}{4}$ patchs
8	$x_1 = 93$	$n_3 = 20$	random distribution of redds among $\frac{1}{4}$ patchs
9	$x_1 = 93$	$n_1 = 233$	$\frac{1}{4}$, $\frac{1}{2}$, $\frac{1}{8}$, $\frac{1}{8}$ individuals in four patchs
10	$x_1 = 93$	$n_3 = 20$	$\frac{1}{4}$, $\frac{1}{2}$, $\frac{1}{8}$, $\frac{1}{8}$ individuals in four patchs

1.2 TEN SCENARII TO DEPICT DIFFERENCES

I defined ten different theoretical scenarii to depict differences between Ss, patchiness (and the mean crowding), and mean density. The different scenarii were based on two different numbers of available patches ($x_1 = 93$ and $x_2 = 14$), as well as three different numbers of redds ($n_1 = 233$, $n_2 = 105$, and $n_3 = 20$ — Table. 1.1). x_1 corresponds to the number of patches in the Nivelle (under a threshold length of 50 m, see methods of chapter 2 at page 73 for details) and x_2 is the number of patches in the Lower Nivelle (see chapter 3). The number of redds corresponds to the minimal number of redds found in the Nivelle (n_3), the maximal number (n_1), and an intermediate value (n_2). The spatial distribution of redds varied among patches to depict contrasted situations (Figure. 1.3). For a considered number of available patches (x_1) and a considered number of redds (n_1), spatial aggregation should be higher for the scenario 9 where redds are distributed in only four patches than for the scenarii 1, 5, and 6. Scenarii exhibiting the same patterns of distribution of redds should also exhibit similar values of aggregation. In this way, similar values of spatial aggregation should be found for: i) scenarii one, two, three, and four; ii) scenarii six, seven, and eight; and iii) scenarii nine and ten. Scenario five should exhibit values of spatial aggregation near the values of scenarii one, two, three, and four.

For each scenario, Ss, mean crowding, patchiness, mean density and variance of density were computed. First, the highest values of mean density were found for scenario one, two, and three when the redds were uniformly distributed among patches (Figure. 1.4). Variance of density was highly dependent on the number of redds (see scenario 9, Figure. 1.4). Spatial aggregation gave, thus, more information than the only

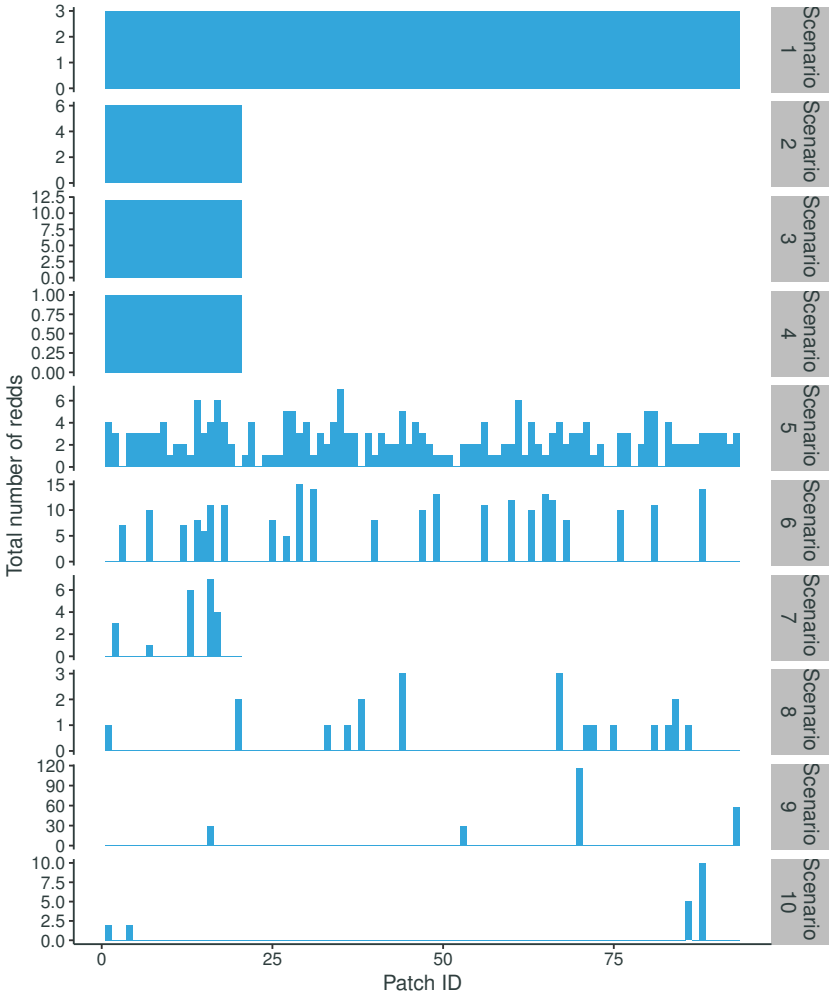


Figure. 1.3: Repartition of redds among available patches under the ten theoretic scenarii (Table. 1.1).

mean density and this whatever the index (mean crowding, patchiness, or Ss — Figure. 1.4). The mean number of neighbours is also a better metric than density (mean or variance) to describe each spatial distribution between scenarii. Second, mean crowding and space selectivity varied in the same way between scenarii. Patchiness well exhibited the fact that redds were concentrated within four patches under the scenarii 9 and 10. In addition, under the scenarii 9 and 10, only the number of redds was different, and patchiness was the only measure giving similar aggregation values between these two scenarii. In this way, the scenarii 9 and 10 enabled to see that Ss and mean crowding seemed influenced by the number of redds.

Density (mean and variance) provides very little information when the question is about to characterise the spatial distribution of individuals among patches. All other

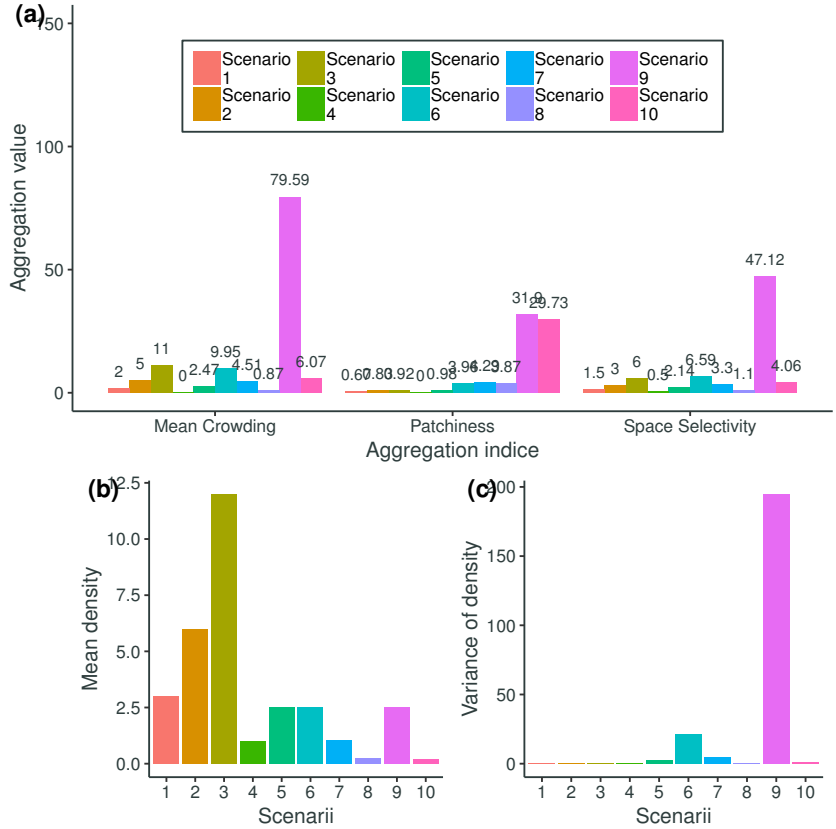


Figure. 1.4: a) Aggregation values computed with the Space selectivity and the patchiness under the ten theoretic scenarii (Table. 1.1). b) Mean density values and variance of density (c) under the same scenarii.

indices displayed variations between scenarii and can be used to characterise spatial distribution among patches. Mean crowding and Ss were influenced by the number of redds which logically increased the number of neighbours. The space selectivity (Ss) is dependent of the density due to the way of its calculation (Figure. 1.1). At the opposite, patchiness seemed less influenced by the number of redds because it divides the average number of neighbours per the mean density which accounts for the total number of individuals.

Beyond this work, the current chapter raises the question of using mean density in ecological studies to depict heterogeneous spatial distribution. In addition, the rare use of patchiness since the study of Lloyd (1967) also remains an open question. Indeed, some studies and books discussed the use of different aggregation measures some years after the work of Lloyd (Gokhale 1975, Simon *et al.* 1981, Young & Young 1998), but most of the recent studies use the term "spatial aggregation" without properly assessing

it. Indeed, 68% of papers citing the Lloyd's patchiness really investigated the spatial distribution of one species or taxon (Wade *et al.* 2018). Despite this, a new study for the 50-year anniversary of Lloyd's work, rediscusses measures of spatial aggregation (Wade *et al.* 2018).

> « We have shown that Lloyds formulation of mean crowding is intrinsic to some of the most important metrics and processes in ecology and evolutionary biology. » — Wade *et al.* 2018

To my concerns, patchiness seems to be the best way to investigate patterns of aggregation of salmon's nests. Density is already considered in stock-recruitment models through density compensation terms and should not be implemented in such models to prevent having two times the same information. The current chapter also clearly justifies why density cannot give a good overview of the spatial distribution and, therefore, cannot be employed to investigate such questions.

HIGHLIGHTS OF CHAPTER 1

- The widely used mean density failed to discriminate among ten simulated scenarii of redd distribution...
- ...whereas mean crowding, patchiness, and space selectivity provided valuable information to characterise the different scenarii.
- The total number of redds influenced the mean crowding, the space selectivity and the mean density.
- Patchiness seems to be the best metric to measure accurately spatial aggregation of redds among different patches.

CHAPTER 2

Effects of spatial aggregation of nests on population recruitment: the case of a small population of Atlantic salmon

This chapter corresponds to an open-access article published in Ecosphere. The layout of the text and figures have been modified for a better incorporation in the thesis. You can access the entire paper either by scanning the following QR-Code with your smartphone or by directly clicking on the QR-code in the pdf file. Two supplementaries files were available with this article, and are displayed at the end of this chapter.

Authors: Bouchard, C., A. Bardonnet, M. Buoro, and C. Tentelier

Abstract: Spatial aggregation within a population is a widespread phenomenon which may both exacerbate local competition and the stochastic effect of local environmental perturbations. In particular, the spatial aggregation of nests may strongly affect recruitment and hence population dynamics. Although the negative effect of local density on local recruitment has often been theoretically extended to population dynamics, very few studies have demonstrated the effect of local aggregation on the whole population recruitment. Using a long-term survey of a small Atlantic salmon population, we tested the effect of spatial aggregation on the whole population recruitment and whether accounting for population stock is important or not when explaining the population recruitment. We found that accounting for population stock is necessary and that spatial aggregation of nests improved estimates of population recruitment. The spatial aggregation of nests did not impact the average population recruitment; however, a

stronger aggregation diminished the variability of population recruitment. Our findings suggest that the aggregation of nests among some breeding areas does not necessarily impair the whole population recruitment, and significantly reduces the stochasticity of the recruitment. In addition, the aggregation of nests seems to be the result of an Ideal Distribution of females, selecting the best-breeding sites. Our results also indicate that females select breeding sites on environmental risk to spawn within the safest sites. This study warns against the extrapolation of local density-dependence observations to the population level, and advocates for investigating the effect of aggregation on the demographic and evolutionary population dynamics; a clear contribution of aggregation on population dynamic processes being found in the Nivelle population.

Keywords: Beverton-Holt, breeding site, clustering, density compensation, environmental stochasticity, patchiness, population dynamic, spatial distribution, spatial heterogeneity

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2.1 INTRODUCTION

Individuals within populations are rarely randomly or uniformly distributed over space but tend to aggregate in the most favorable habitats among available ones. Spatial aggregation arises in many taxa such as mammals (Moll *et al.* 2016), birds (Clotfelter & Yasukawa 1999), crustaceans (Broly *et al.* 2012), fishes (Hoare *et al.* 2004), or plants (Lara-Romero *et al.* 2016). Although density is a widely and preferentially used metric in ecology, the concept of spatial aggregation has been defined in two different ways, *i.e.* the number of neighbors within a habitat unit (Lloyd 1967) or on the distance to the nearest neighbor (Clark & Evans 1954). Assessing if individuals are clumped in space is the main use of aggregation indexes and this despite the potential effects of aggregation on population processes; such effects remaining rarely investigated.

Spatial aggregation of individuals may notably arise when they feed or breed in specific habitats (Clotfelter & Yasukawa 1999, Danchin & Wagner 1997, Sergio *et al.* 2003 , Tregenza 1995, Wagner & Danchin 2003). Individuals select such habitats by assessing either the habitat quality in term of resources (Boulinier & Danchin 1997),

environmental perturbations (Doligez *et al.* 2003) and the safety of a site (Winandy *et al.* 2017), or the density of conspecifics (Doligez *et al.* 2003, Falcy 2015) to maximize their fitness leading to adaptive choices (Hendry *et al.* 2001, Morris 2003). However, these choices may be constrained by agonistic interactions between individuals, social status, site accessibility and limited information on habitat quality (Falcy 2015, Hendry *et al.* 2001, López-Sepulcre *et al.* 2010, Morris 2003, Tentelier & Piou 2011). Because these constraints are dynamic, the resulting aggregation pattern at the population level can vary in space and time.

Spatial aggregation may affect population dynamic and recruitment at the population level through density-dependence of recruitment. Reasons are twofold and closely related. First, the aggregation of breeders diminishes breeder survival or parental investment by exacerbating competition between them (*e.g.* to settle in breeding sites; Adkison *et al.* (2014), McPeek *et al.* (2001), Wong *et al.* (2007)). Second, the aggregation of nests leads to aggregation of early life stages (recruits) with limited dispersal abilities, thereby raising local competition for resources and diminishing their survival (Einum & Nislow 2005, Finstad *et al.* 2009, Steingrimsson & Grant 1999). However, competition between juveniles, caused by aggregation, may be compensated by habitat quality (Fretwell & Lucas 1969, Hendry *et al.* 2001, Schlaepfer *et al.* 2002), or exacerbated by it when breeders select an ecological trap leading to a mismatch between quality and attractiveness (Schlaepfer *et al.* 2002, Weldon & Haddad 2005). Therefore, the effect of nest aggregation on recruitment through local competition is context-dependent, the intensity of aggregation and habitat quality where breeders distribute themselves being key factors.

Spatial aggregation might also modify the variability of population recruitment through the effect of spatial environmental stochasticity. If individuals choose breeding sites irrespective of environmental stability, the aggregation of individuals may dampen the effects of environmental perturbations occurring randomly in space (Kallimanis *et al.* 2005) or exacerbate these effects when perturbations are auto-correlated (Kallimanis *et al.* 2005). Thereby, random local perturbations such as a scouring of fish nests (Gauthey *et al.* 2017) or a falling of a tree supporting hollow-dependent marsupial (Lindenmayer *et al.* 1997) may either affect many individuals if occurring in an aggregate or none if occurring in an empty patch. The resulting recruitment at the population level

is thus, more variable over time (Murdoch *et al.* 1992). On the contrary, if individuals can forecast local disturbances and choose the safest sites, or have cues of habitat quality, aggregation on these sites may buffer against environmental stochasticity and then dampen recruitment variability.

Atlantic salmon (*Salmo salar*) is a relevant biological model to investigate the effects of aggregation on population dynamic processes. The choices of breeding sites dependent on physical characteristics of habitat, and a short duration of the reproductive season (from November to January) lead to spatial aggregation of nests dug by females (de Gaudemar *et al.* 2000, Louhi *et al.* 2008). Spatial aggregation of nests reflects aggregation of breeders and competition for breeding sites and mates; this competition being costly in terms of fecundity and survival (Jonsson *et al.* 1998). Nest aggregation also affects both the aggregation of eggs and emerging fry, diminishing their survival through density-dependent and independent processes. Such density-dependent processes correspond to nest over-digging by other females, competition for oxygen under gravel substrate, disease spread, and competition for feeding territories (Aas *et al.* 2011, Armstrong & Nislow 2006, Crisp 1995, Gustafson-Greenwood & Moring 1990, Nislow *et al.* 2004). On the other hand, aggregation may exaggerate or dampen the effect of random local perturbations such as nest scouring or predation of young stages (Lapointe *et al.* 2000, Palm *et al.* 2009).

However, the potential effects of spatial aggregation on the whole population recruitment remain poorly appreciated and rarely investigated. Indeed, the existing literature on the nest distribution of Atlantic salmon correlates the local density of nests in a river stretch to either local environmental variables (Louhi *et al.* 2008, Parry *et al.* 2018) or local recruitment (Foldvik *et al.* 2010); this in order to respectively infer ecological determinants of nest placement and to test negative density-dependence. The potential effects of spatial aggregation on the whole population recruitment remain to be investigated empirically (Einum *et al.* 2007 for a simulation-based approach). An explanation of this rare investigation may be the extensive amount of data required to investigate these effects: long time series of spatial aggregation and population recruitment. This is unfortunate because assessing the influence of aggregation on recruitment should improve our understanding of population dynamics and resilience to environmental perturbations.

The main goal of this study was to test the effects of nest spatial aggregation on the yearly recruitment of a small Atlantic salmon population. In this way, we capitalized on a long-term dataset (31 years) collected in the Nivelle river, France, consisting of the spatial distribution of nests, the expected number of deposited eggs (stock), and the abundance of juvenile individuals in nursery stretches (recruitment, Dumas & Prouzet 2003). We used a hierarchical model testing direct effects of aggregation on the whole population recruitment. Because the recruitment is primarily dependent on the stock (Prévost & Chaput 2001, chap. 2), we also evaluated the influence of nest aggregation on demographic processes using stock-recruitment models (Iles 1994, Prévost & Chaput 2001). Such models take into account the density-dependent (competition) and the independent (environmental stochasticity) mortality occurring on a stock. Here we tested two alternative hypothesis. First, we predicted that a strong aggregation should diminish recruitment according to the negative density-dependence theory (Einum & Nislow 2005, Finstad *et al.* 2009, Foldvik *et al.* 2010, Steingrimsson & Grant 1999). Alternatively, we predicted that aggregation should not modify recruitment level if females aggregated their nests in the best and safest breeding sites (Fretwell & Lucas 1969, Hendry *et al.* 2001, Schlaepfer *et al.* 2002), but should lead to steadier recruitment by buffering environmental stochasticity (Kallimanis *et al.* 2005).

2.2 METHODS

2.2.1 STUDY AREA AND DATA COLLECTION

The Nivelle is a 39 km long river, with a drainage area of 238 km^2 located in France near the Spanish border, and flowing into the Bay of Biscay (Figure. 2.1). The study area corresponds to the river portion starting from the estuary to 19 km, plus 4.5 km on the main tributary (the Lurgorrieta). The river is a typical succession of pools and riffles, with an average depth of 48 cm, an average width of 10 m, and an average annual discharge of 5.4 m^3/s^1 (Dumas & Prouzet 2003). The study area was divided into 624 stretches of different lengths, defined by habitat features such as dams, bridges, confluences, or river morphodynamic changes (Tentelier *et al.* 2016). Two dams are equipped with fish-passes and traps: Uxondoa dam (12 km from the river mouth) equipped in 1984, and Olha dam (16.7 km from the river mouth) in 1992 (Figure. 2.1). The area of suitable and available river habitats for salmon reproduction (h) was therefore smaller before 1992 ($h = 15,011\ m^2$ against $h = 56,575\ m^2$ after 1992, Dumas & Prouzet (2003)). Suitable river habitats correspond to the favorable areas for the production of

juveniles (nursery stretches), namely shallow running water flowing over a coarse bottom substrate (Marchand *et al.* 2017), wherein available ones define those accessible for salmon (Prévost *et al.* 1996).

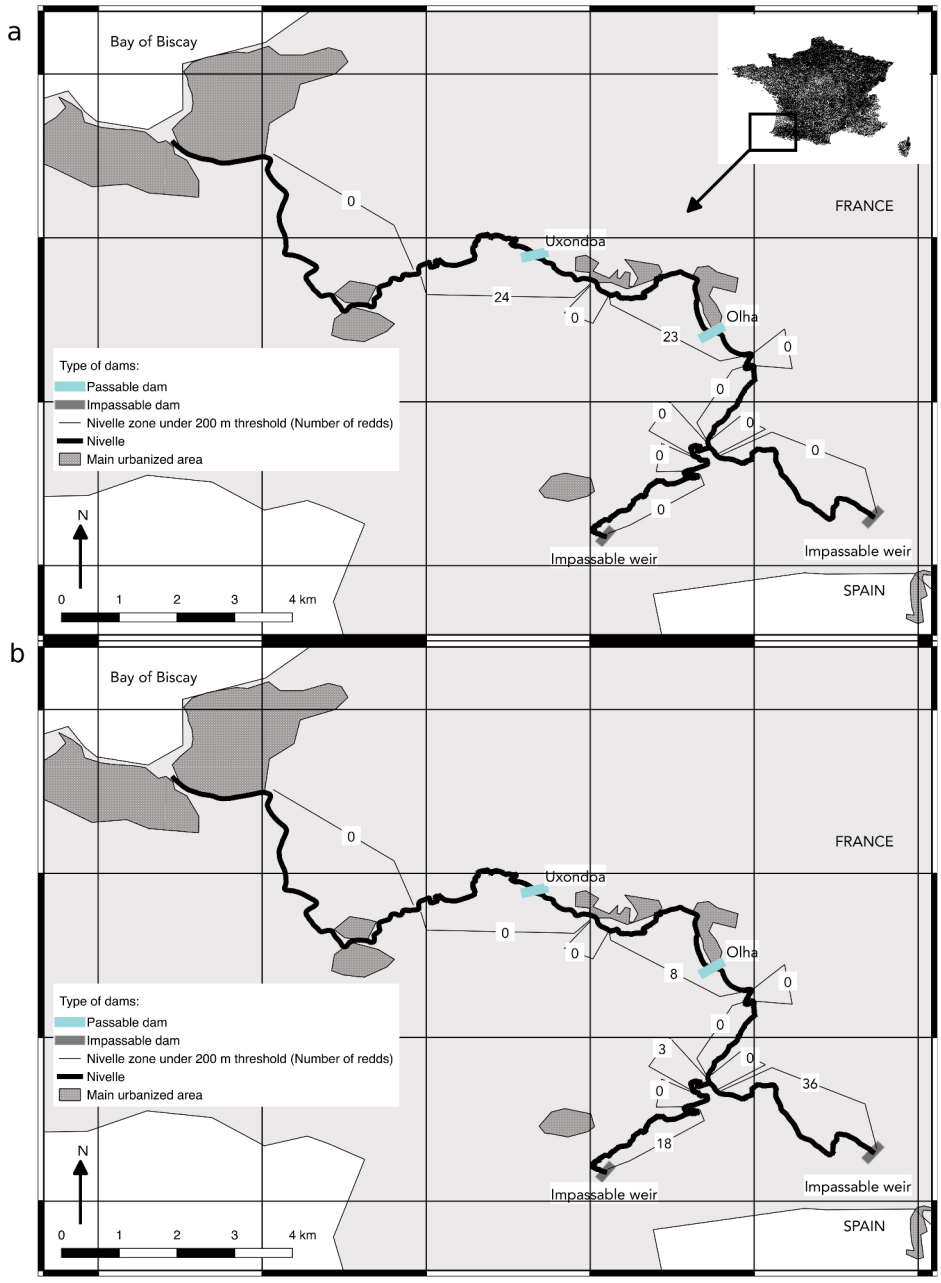

Figure. 2.1: Maps of the Nivelle river system available for Atlantic salmon. Four dams are indicated, including those equipped with fish passes: Uxondoa and Olha. Gray areas correspond to the major urbanised areas near the Nivelle. (a) Nest distribution in 1986 which corresponds to the year with the lowest aggregation under a 50 m threshold length: 4.20. (b) Nest distribution in 2012, the year with the higher aggregation: 27.46.

We used a long-term (31 years: 1984-2015) monitoring program to assess yearly recruitment and yearly stock, and nest mapping that we used to compute the spatial aggregation of nests. This monitoring has been carried out by the Environmental Research Observatory (ERO) on Diadromous Fish in Coastal rivers (DiaPFC) [1]. First, the recruitment, *i.e.* the yearly juvenile number, was estimated from electrofishing within suitable river habitats for juveniles, previously described as shallow running water flowing over a coarse bottom substrate (Marchand *et al.* 2017). Twelve sites were yearly sampled from 1985 to 2002, and 22 from 2003 to 2015. The area sampled on these 22 sites represents more than 21% of suitable river habitats available for salmon juveniles in the Nivelle (Appendix S1: Table. 2.5, Marchand *et al.* (2017)). The estimates of juvenile densities at each sampling site permitted the quantification of the relationship between juvenile density and the area of suitable river habitat at each sample site. Juvenile density for the whole river was thereafter estimated from the total area of suitable habitats in the river. Second, the stock, *i.e.* the yearly number of deposited eggs in the Nivelle, was estimated from the abundance of females in each age class. In this way, the two fish-traps allow the capture and mark of anadromous salmon on both sites in the Nivelle. This generates a capture-mark-recapture dataset allowing the estimate of the number of anadromous salmon in each age class (1 or 2 sea winters) and each sex from a N-mixture model using hierarchical Bayesian modeling approach (Brun *et al.* 2011, Servanty & Prevost 2016). These estimates of abundance encompass catch probability, which was estimated at 0.9 (Appendix S1, Servanty & Prevost 2016). Then, fecundities were attributed to each age class: 4500 eggs/kg and 7200 eggs/kg for one and two sea-winters respectively (Appendix S1, Servanty & Prevost 2016). The estimates of stock and recruitment are based on standardized sampling protocols and hierarchical Bayesian models taking explicitly into account assessments of uncertainties such as capture or detection probabilities (Brun *et al.* 2011, Dauphin *et al.* 2009, Prévost & Baglinière 1995, Servanty & Prevost 2016). Here, the estimates of deposited eggs were considered from 1984 to 2014, and the estimates of juveniles from 1985 to 2015 (juveniles from year j stem from eggs of year $j-1$).

Finally, the nest survey was repeated two or three times per spawning season (from mid-December to January). Because of the length of the study site, each complete survey was carried out directly in the water in 1-3 walking days. Over a decade, surveys were conducted by a same duo of observers after training; experience and training shrink-

[1] ERO DiaPFC: https://www6.inra.fr/diapfc

ing nest count errors (Dunham *et al.* 2001). Nests were visually detected as a typical depression-dome succession where algae and silt were removed during digging by the females. The location of each nest was recorded as the *id* number of the stretch where the nest was discovered.

2.2.2 AGGREGATION OF NESTS

Nest aggregation of the spawning season of year j was assessed by computing the patchiness index developed by Lloyd (1967). Patchiness is a spatial aggregation index computed by dividing the "mean crowding" ($\overset{*}{m}_j$) by the mean density (noted m_j, Eq. 2.2). The mean crowding ($\overset{*}{m}_j$) is defined as the mean number of neighbors per nest in the same patch (Eq. 2.2), while the mean density (m_j) is the total number of nests divided by the total number of patches. Then, according to Lloyd (1967):

$$\overset{*}{m}_j = \frac{\sum_{i=1}^{N_j} X_{i,j}}{N_j}$$

$$\overset{*}{m}_j = m_j + \left(\frac{\sigma^2}{m_j} - 1\right), \qquad \text{(Eq. 2.1)}$$

$$\text{Patchiness}_j = P_j = \frac{\overset{*}{m}_j}{m_j} \qquad \text{(Eq. 2.2)}$$

with N_j: the total of nests discovered during the spawning season of year j, $X_{i,j}$: the number of nests found in the same patch as nest i during the spawning season of year j, $\overset{*}{m}_j$: the mean crowding of the spawning season of year j. When the number of neighboring nests ($\overset{*}{m}_j$) is similar to the mean density (m_j), patchiness equals 1, the only reference value of this index. Yearly nest aggregation, noted P_j for Patchiness, was computed from 1984 to 2014 (31 years).

We grouped the 624 initial stretches to buffer fine scale changes in habitat throughout the study period. In this way, each patch was defined as a group of stretches including at least one nest during the study period, and that was separated from other stretches by a defined threshold length of habitat never used for spawning (Appendix S1: Figure. 2.7). We varied the threshold length of unused habitat for separating patches from 20 m to 500 m, reflecting the biological low probability that salmon fry cross such a length of unfavorable habitat during their first weeks of life (Beall 1994, Crisp 1995, Einum & Nislow 2005, Einum *et al.* 2006, Garcia de Leaniz *et al.* 2000, Gustafson-Greenwood & Moring 1990). Aggregation of nests was computed with patches defined as 624 initial

stretches but also patches defined under threshold lengths varying from 20 m to 500 m (Appendix S1 for details).

2.2.3 EFFECTS OF AGGREGATION ON POPULATION RECRUITMENT

Two approaches were used to meet the main objective of this study, namely to test the effect of aggregation of nests on recruitment. First, the direct effect of aggregation on population recruitment was tested regardless of the stock. Second, the aggregation effect on recruitment was tested within a stock-recruitment relationship to assess whether accounting for population stock is important or not.

In this study, yearly stock was the estimated number of deposited eggs (noted E_j), and yearly recruitment was the estimated number of juveniles in September (noted Y_j). Since the suitable and available river habitat (noted h) was different before and after 1992 (opening of Olha), E_j and Y_j were divided by h to obtain the density of deposited eggs (E_j^*), and of juveniles (Y_j^*) per river habitat area h.

Population recruitment as a function of aggregation The direct effect of nest aggregation on recruitment at population level was firstly tested by modeling yearly recruitment (Y_j^*) as a function of the yearly aggregation of nests (P_j). Four different models were tested (Table. 2.1):

- a null model without effect of aggregation on mean and variance (noted $\mathcal{M}_0$),
- a model with both simple and quadratic effects of aggregation on the mean μ_j (noted $\mathcal{M}_1$),
- a heteroscedastic model with an effect of aggregation on variance σ_j (noted $\mathcal{M}_2$), and
- a complete model combining $\mathcal{M}_1$ and $\mathcal{M}_2$ (noted $\mathcal{M}_3$).

Stock-recruitment models Stock-recruitment models were mainly developed for fisheries (*e.g.* Cushing (1973), Ricker (1954), Beverton & Holt (1957)). Shepherd's (1982) model is a versatile model that can imitate curves of Beverton-Holt, Ricker, or Cushing through a specific parameter. Simulations were firstly done with Shepherd's model for two reasons. First, this model allows data to drive the curve and not the opposite because the model is versatile. Second, this allowed us to avoid setting a specific *a priori*

model. Estimates of Shepherd's model corresponded to Beverton-Holt's curve, thus using Beverton-Holt's model allowed to save one parameter (Appendix S2: Table. 2.8). In addition, Beverton-Holt's model is widely used in studies on Atlantic salmon and was therefore chosen to run our analyzes (Brun 2011, Michielsens & McAllister 2004, Prévost & Chaput 2001).

Recruitment was modelled with a log-normal distribution where μ_j corresponded to the mean of recruitment, and τ to the precision parameter (inverse of variance) of recruitment:

$$Y_j^* \sim Log\mathcal{N}\left(\log\left(\mu_j\right), \frac{1}{\tau}\right), \qquad \text{(Eq. 2.3)}$$

A simple Beverton-Holt model was considered as the null model ($\mathcal{BH}_{\texttt{null}}$) because the question addressed here was whether aggregation affected the stock-recruitment dynamic. Therefore, μ_j in the Eq. 2.3 corresponded to:

$$\mu_j = \frac{a \times E_j^*}{1 + \frac{E_j^*}{K}} \qquad \text{(Eq. 2.4)}$$

where j is the considered year, a the parameter for density-independent contribution to fish mortality, $\frac{1}{K}$ the density-dependent contribution to fish mortality.

Effects of aggregation were computed in two ways. First, the direct effect of aggregation on recruitment, i.e. mean (μ_j), was assessed by elevating yearly aggregation (noted P_j) at power q (Eq. 2.5):

$$\mu_j = \frac{a \times E_j^*}{1 + \frac{E_j^*}{K}} \times P_j^q. \qquad \text{(Eq. 2.5)}$$

Second, the effect of aggregation on recruitment variability, i.e. dispersion parameter (τ, inverse of the variance), was estimated by elevating yearly aggregation (noted P_j) at power η (Eq. 2.6):

$$\tau = \delta \times P_j^\eta, \qquad \text{(Eq. 2.6)}$$

where, δ is the intercept of τ calculation. A complete model, noted $\mathcal{BH}_{\texttt{complete}}$, with effects of aggregation on mean (Eq. 2.5) and variance (Eq. 2.6) was fitted. In addition, semi-models were also fitted with an effect either on μ_j or on τ, by replacing μ_j with Eq. 2.5 ($\mathcal{BH}_\mu$) or τ with Eq. 2.6 ($\mathcal{BH}_\tau$), respectively. Effects of spatial aggregation were

modeled through multiplicative forms because an additive integration was biologically unrealistic, co-variables can only modulate recruitment (Aas *et al.* 2011, Iles 1994).

All models in this study were fitted under a Bayesian framework using HMC sampling applied by Stan through the R package RStan (Carpenter *et al.* 2016, Stan Development Team 2017). Little informative prior distributions were applied to parameters a, K, q, and η (Table. 2.2, Prevost 2003). Gamma distributions, which are more informative, were chosen for scale parameters δ and τ (Gelman *et al.* 2014, Prevost 2003). For each model, four independent chains were run to save 6,400 iterations after a warm-up of 2,000 iterations (per chain), and with a thin of 5. As all Bayesian models, chain convergence was assessed by visual checking, and parameter convergence was assessed with the Gelman & Rubin (1992) scale reduction factor: $\hat{r}$. Prior actualization by data was evaluated by comparing parameter posteriors and priors. Simulations of recruitment with the parameter estimates were made to test the accuracy of parameter estimates. A sample of 2,000 values over the 6,400 of each parameter estimates were extracted for each model. From these samples, 2,000 estimates of recruitment were computed for each value of stock to ensure the quality of the model. Parameter statistics are subsequently reported using median and Credible Interval at 95 % ($CI_{95\%}$). Assessment of models was done with the Widely Applicable Information Criterion (WAIC, Vehtari *et al.* 2017), a relevant criterion to rank stock-recruitment models (Subbey *et al.* 2014, Wang & Liu 2006) under a Bayesian framework.

Table. 2.1: Equations of the mean and variance of the four hierarchical models linking the yearly recruitment (Y_j^*) of the Atlantic salmon population to the spatial aggregation of nests (P_j). $\mathcal{M}_0$ was a null model. $\mathcal{M}_1$ was a model with a simple (parameter α) and a quadratic effect (parameter β) of aggregation on the mean of the recruitment (μ_j). $\mathcal{M}_2$ was a model with an effect of aggregation on the variance of the recruitment (σ_j, parameter γ). $\mathcal{M}_3$ was a complete model combining $\mathcal{M}_1$ and $\mathcal{M}_2$.

Model	Mean	Variance	Distribution
$\mathcal{M}_0$	$\mu_j = \text{intercept}$	$\sigma_j = \text{intercept}$	$Y_j^* \sim \mathcal{N}\left(\mu_j, \sigma_j\right)$
$\mathcal{M}_1$	$\mu_j = \text{intercept} + \alpha \times P_j + \beta \times P_j^2$	$\sigma_j = \text{intercept}$	$Y_j^* \sim \mathcal{N}\left(\mu_j, \sigma_j\right)$
$\mathcal{M}_2$	$\mu_j = \text{intercept}$	$\sigma_j = \text{intercept} + \gamma \times P_j$	$Y_j^* \sim \mathcal{N}\left(\mu_j, \sigma_j\right)$
$\mathcal{M}_3$	$\mu_j = \text{intercept} + \alpha \times P_j + \beta \times P_j^2$	$\sigma_j = \text{intercept} + \gamma \times P_j$	$Y_j^* \sim \mathcal{N}\left(\mu_j, \sigma_j\right)$

Table. 2.2: Summary of the main parameters and their prior distributions. Parameter K corresponds to the threshold biomass which indicates the carrying capacity when K is multiplied by a, the slope at origin. Parameters τ and δ are involved in the modelisation of the precision of Beverton model. Parameters q and η correspond to the effect of aggregation on the mean and the precision of Beverton model.

Parameter	Definition	Prior distribution
a	Eq. 2.4 and Eq. 2.5	$Log\mathcal{N}(0,2)$
K	Eq. 2.4 and Eq. 2.5	$Log\mathcal{N}(0,10)$
τ	Eq. 2.4	$\Gamma(0.01,100)$
q	Eq. 2.5	$\mathcal{N}(0,20)$
δ	Eq. 2.6	$\Gamma(0.01,100)$
η	Eq. 2.6	$\mathcal{N}(0,20)$

2.2.4 EFFECTS OF POPULATION SIZE ON MEAN DENSITY AND AGGREGATION OF NESTS

We also tested if the aggregation of nests (P_j) and the mean density of nests (m_j) was dependent of the anadromous population size (N_{pop}) using a linear regression (Eq. 2.7). Aims of this model were to assess i) whether aggregation solely reflects or not the anadromous population size so as to not put the same information in the stock-recruitment models twice (stock being dependent of N_{pop}), and ii) to know how aggregation varies with N_{pop}.

$$\begin{aligned} \mu_j &= intercept + \zeta \times N_{\text{pop}}, \\ m_j \text{ or } P_j &\sim \mathcal{N}\left(\mu_j, \sigma\right), \end{aligned} \qquad \text{(Eq. 2.7)}$$

Weakly informative priors were applied to parameters *intercept*, ζ, and σ with a Cauchy distribution ($\mathcal{C}(0,2.5)$, Gelman *et al.* (2008)). Four independent chains were fitted to save 6,400 iterations after a warm-up of 2,000 iterations, and with a thin of 5 values. The model was fitted to data of mean density and aggregation under each threshold length. We evaluated the confidence of whether the effect is positive or negative by calculating the proportion of the posterior values with a different sign as the median (noted "Bayesian p_{value}").

2.3 RESULTS

2645 nests were reported in the Nivelle river from 1984 to 2014. The yearly number of nests varied from 20 in 1985 to 233 in 1993, with approximately 80 nests per year over the last decade (Figure. 2.2). The number of adults varied from 72 individuals in 2009 to 516 in 1993 leading the adult density to fluctuate between 0.0013 adults/m^2 in 2009 and 0.0251 adults/m^2 in 1986. The stock varied between 3.34 eggs/m^2 in 2008 and 40.84 eggs/m^2 in 1990 (Figure. 2.6). Recruitment was steadier than stock, ranging between 0.04 juveniles/m^2 in 2006, and 0.28 juveniles/m^2 in 2012.

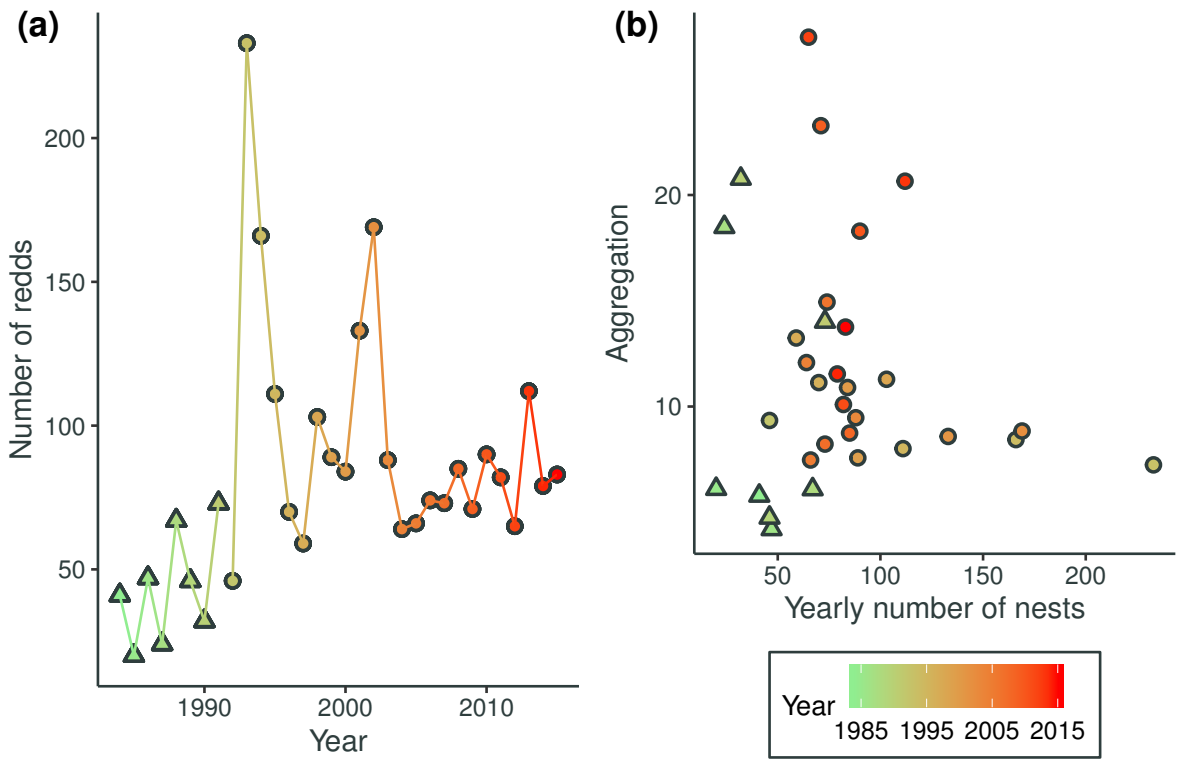

Figure. 2.2: (a) Plot of the yearly number of nests (N = 32 years and 2645 nests). (b) Yearly aggregation value (patchiness) as a function of the yearly number of nests (N = 32 years). Triangles indicate years before the opening of Olha, a dam equipped with a fish pass in 1992, and dots years after the opening.

2.3.1 AGGREGATION OF NESTS

Concerning aggregation of nests (patchiness), we displayed only results obtained with a threshold length of 50 m because 1) other threshold lengths provided qualitatively similar results (Appendix S2) and 2) previous studies found salmon fry disperse within a range of distances close to 50 m (Beall 1994, Einum & Nislow 2005). Therefore, we

decided that 50 m was a good candidate for resolving the trade-off between the number of patches and their lengths. The threshold length of 50 m led to 93 new patches (average length = 255.33 m, minimum length = 7.00 m, maximum length = 2929.60 m, Appendix S1: Table. 2.6).

Aggregation of nests (patchiness) was always higher than the reference value (equals to one) varying between 4.20 in 1986, and 27.46 in 2012 (Figure. 2.2). In addition, aggregation value was not linearly dependent of the number of nests (Figure. 2.2, Spearman: $rho = 0.001$, $S_{value} = 5450$, $p_{value} = 0.99$, $N = 32$). But, a negative trend was found between aggregation and the number of anadromous individuals ($\zeta = -0.0140$, $CI_{95\%} = [-0.0312; 0.0037]$, Bayesian $p_{value} = 0.06$, Figure. 2.3), while mean density of nests within occupied patches increased significantly as the number of anadromous individuals increased ($\alpha = 0.0055$, $CI_{95\%} = [0.0004; 0.0108]$, Bayesian $p_{value} = 0.02$, Figure. 2.3). No significant relationship was found between aggregation and flow (average, maximum, minimum, range or standard deviation) between September and December. Years with lowest aggregations were always before 1992, even though the yearly nest counts were not always lower and the available river habitat increased in 1992 due to the opening of Olha (Figure. 2.2). The proportion of used patches over available patches increased with the yearly number of nests, and the slope was steeper before 1992 than after, with a median estimated at 0.0037 ($CI_{95\%} = [0.0020; 0.0054]$) against 0.0012 ($CI_{95\%} = [0.0005; 0.0019]$, Figure. 2.4).

2.3.2 EFFECTS OF AGGREGATION ON POPULATION RECRUITMENT

Accounting for population stock and model selection The four models of Beverton-Holt taking the population stock into account ($\mathcal{BH}_{\texttt{null}}$, $\mathcal{BH}_{\mu}$, $\mathcal{BH}_{\tau}$ and $\mathcal{BH}_{\texttt{complete}}$) had a lower WAIC than models without the stock ($\mathcal{M}_0$, $\mathcal{M}_1$, $\mathcal{M}_2$, $\mathcal{M}_3$ - Table. 2.3) indicating models of Beverton-Holt were therefore better than models without the population stock (lowest WAIC is better). The model $\mathcal{BH}_{\tau}$ taking the population stock and an effect of aggregation on the variance of the population recruitment displayed the lowest WAIC, and was thus the best of all models tested in this study. Furthermore, the second best model was a model with a non-significant effect of the aggregation on the mean: $\mathcal{BH}_{\texttt{complete}}$ ($q = -0.0264$, $CI_{95\%} = [-0.3657; 0.3522]$, 55.52 % of q estimates lower than 0). Finally, the ranking of the best model was similar among each group of models. The model with just the effect of aggregation on the variance was the best model among those without the population stock. Because all models laid consistent results (Table. 2.3), we only

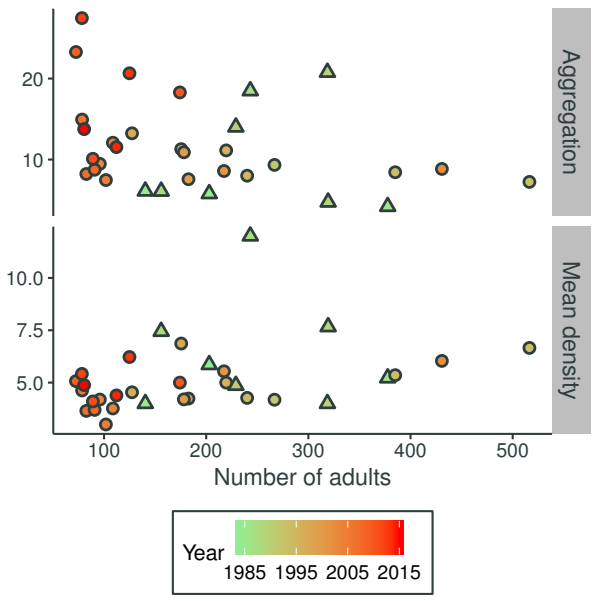

Figure. 2.3: Aggregation (patchiness) and mean density of nests as a function of the yearly number of anadromous salmon of the Nivelle. Triangles indicate years before the opening of Olha, a dam equipped with a fish pass in 1992, and dots years after the opening.

present the results of the best model $-\mathcal{BH}_{\tau}-$ in the rest of this section.

Effects of aggregation on demographic processes The $\mathcal{BH}_{\tau}$ model laid out a significant effect of aggregation on τ, parameter η being estimated at $\eta = 0.71$ ($CI_{95\%} = [0.03; 1.37]$ with 2.09 % of negative estimates of η over the 6,400) indicating a positive effect of aggregation on precision, corresponding to a decrease in variability (precision is the inverse of variance) when aggregation (P_j) increased (Figure. 2.5). According to parameters estimated with $\mathcal{BH}_{\tau}$ (best model), a two- or five-fold increase in aggregation did not have a direct effect on recruitment (median = 0.11 for each aggregation values, Table. 2.4), but really decreased the variability of recruitment. The range between lower and upper boundaries of the credible interval of recruitment diminished from 0.53 at minimum of aggregation, to 0.28 at twice times the minimum of aggregation, and 0.19 at five times this aggregation value (Table. 2.4).

The parameter a of fitted Beverton-Holt models (density-independent mortality) was estimated at $a = 1.23$ ($CI_{95\%} = [0.08; 46.96]$) for $\mathcal{BH}_{\texttt{null}}$, and $a = 1.20$ ($CI_{95\%} = [0.09; 46.79]$) for the best model with aggregation ($\mathcal{BH}_{\tau}$). Parameter K (inverse of the density-dependent mortality) was estimated at $K = 0.26$ ($CI_{95\%} = [0.00; 1.53]$) for

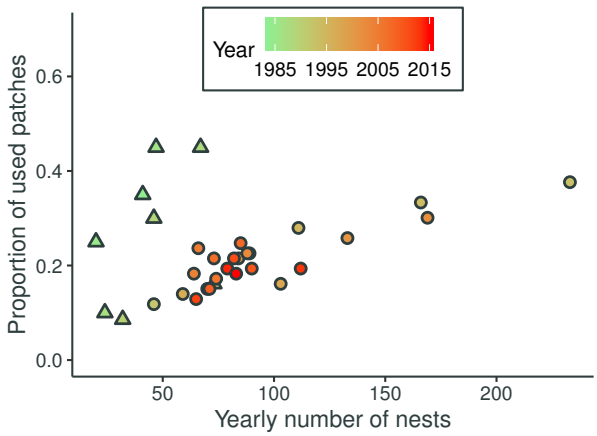

Figure. 2.4: Yearly proportion of patches used as a function of the yearly number of nests of the Nivelle. The yearly proportion of used patches corresponded to the number of patches where at least one nest was found divided by the number of patches in the available zone. Triangles indicate years before the opening of Olha, a dam equipped with a fish pass in 1992, and dots years after the opening.

$\mathcal{BH}_{\texttt{null}}$, and $K = 0.09$ ($CI_{95\%} = [0.00; 1.39]$) for $\mathcal{BH}_{\tau}$. These two parameters (a and K) allowed to compute the carrying capacity: $a \times K$ estimated at 0.12 juveniles/m^2 ($CI_{95\%} = 0.03; 0.26]$) for $\mathcal{BH}_{\texttt{null}}$ and 0.11 juveniles/m^2 ($CI_{95\%} = [0.09; 0.13]$) for the best model with aggregation ($\mathcal{BH}_{\tau}$, Figure. 2.5). There was no significant difference between the two carrying capacities (45% of differences between all the 6,400 estimates were lower than 0). With the best model ($\mathcal{BH}_{\tau}$) which took into account the aggregation effect on recruitment variability, the majority of yearly recruitment was well estimated, observed points being inside or close to the 95% credibility interval of estimates (Figure. 2.5).

Effects of the opening of Olha dam To test for the potential effect of the opening of Olha dam, we compared residuals of stock-recruitment models before and after 1992, for the null model without aggregation ($\mathcal{BH}_{\texttt{null}}$) and the best one ($\mathcal{BH}_{\tau}$). No particular pattern was graphically detected for residuals of both models before and after 1992 (Figure. 2.6). In addition, no significant difference in the yearly average residuals before and after the opening of Olha was detected (Wilcoxon: $W = 76$, $p_{value} = 0.49$, same results for $\mathcal{BH}_{\texttt{null}}$ and $\mathcal{BH}_{\tau}$).

Table. 2.3: Summary of the parameter estimates of the four models ($\mathcal{M}_0$, $\mathcal{M}_1$, $\mathcal{M}_2$, $\mathcal{M}_3$) explaining recruitment by the yearly aggregation of nests (patchiness).

Model	WAIC	α	β	γ
$\mathcal{M}_0$	-79.861	-	-	-
$\mathcal{M}_1$	-77.161	0.0027 ± 0.0090	-0.0001 ± 0.0003	-
$\mathcal{M}_2$	-82.335	-	-	-0.0019 ± 0.0013
$\mathcal{M}_3$	-82.628	0.0026 ± 0.0073	-0.0001 ± 0.0002	-0.0022 ± 0.0014

		q		η		δ	a	K
		Value	Test ≤ 0	Value	Test ≤ 0	Value	Value	Value
$\mathcal{BH}_{\texttt{null}}$	-90.4	-	-	-	-	1.95	6.88	0.26
$\mathcal{BH}_{\mu}$	-88.4	0.0584	39.23	-	-	1.9031	7.1576	0.2619
$\mathcal{BH}_{\tau}$	-93.9	-	-	0.7102	02.09	0.5398	6.4497	0.2419
$\mathcal{BH}_{\texttt{complete}}$	-91.5	-0.0211	55.52	0.7033	02.70	0.5485	6.8361	0.2585

Notes: α was the simple effect and β was the quadratic effect of aggregation on the mean of the yearly recruitment. γ was the simple effect of aggregation on the variance of the yearly recruitment. Results for the four Beverton-Holt models ($\mathcal{BH}_{\texttt{null}}$, $\mathcal{BH}_{\mu}$, $\mathcal{BH}_{\tau}$, $\mathcal{BH}_{\texttt{complete}}$): the null model with no effect of aggregation, the model including the effect of aggregation on recruitment mean only, the model including the effect of aggregation on recruitment variance only, the model including the effect of aggregation on both recruitment mean and variance. The value corresponds to the estimated ***mean*** *of parameter, and the column "test" to the percentage of parameter values which were ≤ 0 to test the parameter significance.*

Table. 2.4: Effects of aggregation increase on the recruitment (median with credible interval at 95 %, and mean) with the best Beverton-Holt model. Recruitment was computed with the average observed stock in the Nivelle: around 12 eggs per square meter. The three values of aggregation corresponded to the minimal value of aggregation, two times this value (around the mean), and five time this value (around the max).

Aggregation	Median $CI_{95\%}$	Mean
4.2013	0.1070 $CI_{95\%} = [9.10^{-04}; 0.5319]$	0.1902
8.4025	0.1070 $CI_{95\%} = [0.0231; 0.2778]$	0.1268
21.0063	0.1070 $CI_{95\%} = [0.0503; 0.1933]$	0.1128

2.4 DISCUSSION

Using stock-recruitment models we demonstrated the effect of the spatial aggregation of nests on population dynamics in two ways. First, spatial aggregation diminished the variability of the whole population recruitment, whereas no effect was found on the average recruitment. Second, aggregation did not modify the stock-recruitment

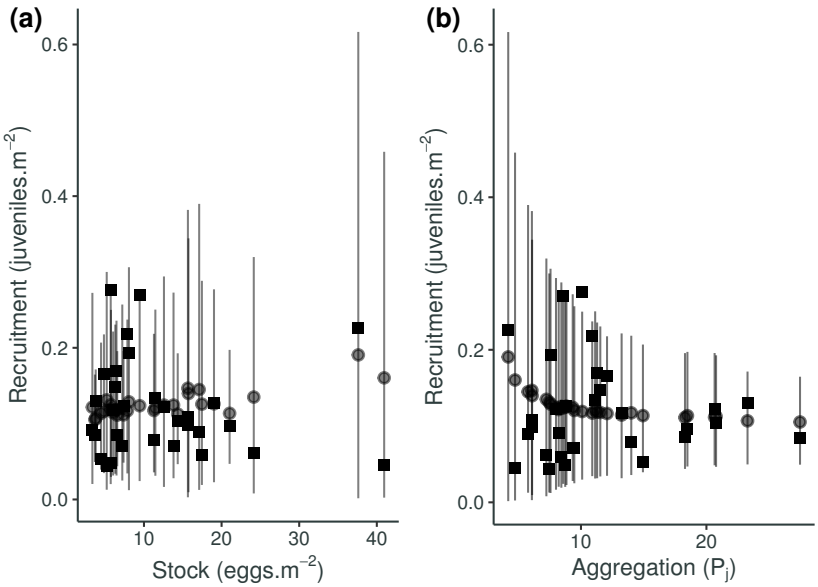

Figure. 2.5: (a) Stock-recruitment relationship of the Atlantic salmon population of the Nivelle river with the best Beverton-Holt model incorporating the effect of nest aggregation (patchiness) on the recruitment variability. Recruitment was the juvenile density in the river while the stock was the estimated density of deposited eggs. Black squares indicate the observed values of recruitment while black points and bars indicate the estimates of the model and corresponding credibility interval at 95 percent. (b) Plot of the recruitment of the Atlantic salmon population of the Nivelle river as a function of the aggregation (patchiness: P_j) acting on the variance. This plot displays the negative effect of aggregation on the recruitment variability within the stock-recruitment relationship.

relationship of the population, and the effects of spatial aggregation on the recruitment variability remained similar whatever the stock level. Moreover, we found a negative trend of anadromous population size on aggregation of nests, while the mean density of nests increased with population size. Altogether, these results suggest that i) aggregation is a way to dampen environmental stochasticity, and ii) salmon females choose their breeding sites on habitat quality and risk of disturbances.

2.4.1 CONSTRAINT OF DAMS

The most notable environmental change for the 31 years, the opening of Olha dam, did not impact stock-recruitment relationships. This opening in 1992 multiplied the length of river accessible to salmon by 1.5 and the available river habitat for spawning by four (Figure. 2.3). The surprising lower aggregation before than after 1992 could be explained by the more homogeneous distribution of nests among accessible spawning

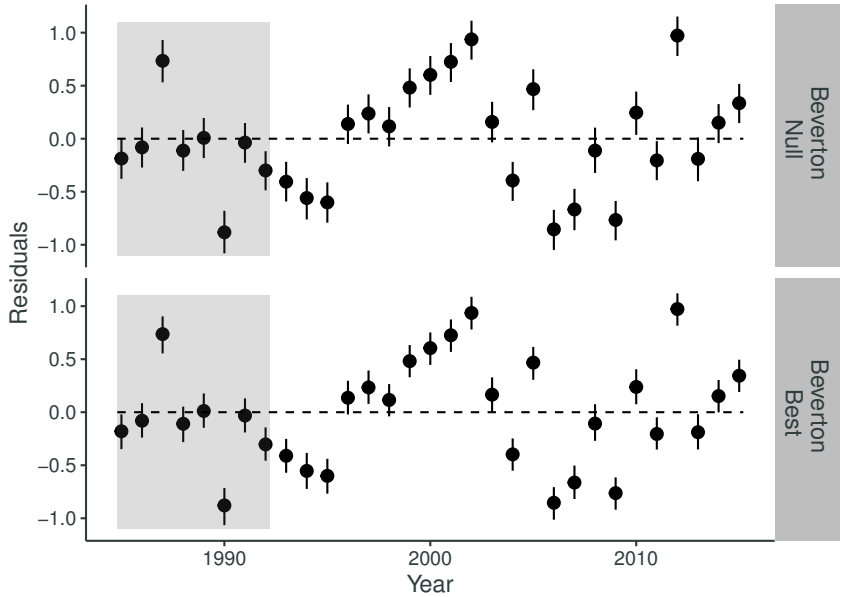

Figure. 2.6: Plot of the residuals of the stock-recruitment relationship (Beverton-Holt model) of the Atlantic salmon population of the Nivelle. The null model was the model $\mathcal{BH}_{\mu}$, a Beverton-Holt model without aggregation (patchiness). The best model was the model $\mathcal{BH}_{\tau}$, a Beverton-Holt model with the aggregation of nests acting on the recruitment variance. Recruitment was the juvenile density in the river while the stock was the estimated density of deposited eggs. Bars indicate the corresponding credibility interval at 95 percent.

sites before 1992. This is consistent with the stronger proportion of used patches found before than after 1992. In addition, the increase of available breeding sites resulting from the dam opening did not seem to modify stock-recruitment relationship. This was supported by the absence of a particular pattern of stock-recruitment residuals, as well as the non-significant difference in the yearly average residuals before and after 1992. Altogether, this indicates that females loosened the potential negative pressure of the dam, by spreading their nests on all sites available near the dam and not necessarily the best ones (Tentelier & Piou 2011).

The upstream part of the Nivelle is probably the zone supporting the major part of the population recruitment after the dam opening. Indeed, in years of strong aggregation, nests tended to be found mostly in the upstream part of the Nivelle (Figure. 2.1), probably more suitable for salmon (Dumas & Haury 1995), with cooler water, less pollution and larger areas of habitat suitable for juveniles (Brun 2011), enhancing survival of juveniles. Therefore, females probably preferentially settle in this zone of the Nivelle. Another impassable dam corresponding to the upper limit of the available zone for salmon in the Nivelle may constrain the distribution of anadromous breeders (Tentelier *et al.* 2016). This additional constraint is probably another explanation for the lack of difference between recruitment before and after the opening of Olha, the breeders being still constrained.

2.4.2 ORIGINALITY OF THE METHOD AND NECESSITY TO ACCOUNT FOR STOCK

The originality of this work lies in the temporal and spatial scales of analysis. By linking spatial aggregation of nests to the whole population recruitment over a 31-year period, our results indicate that local aggregation does not seem to directly affect the average population recruitment. These results may challenge the transfer of local mechanisms such as density-dependence to higher operating scales (Einum & Nislow 2005, Einum *et al.* 2008; 2006, Foldvik *et al.* 2010). Indeed, generalizing such local results to the whole population may lead to erroneous conclusions or misinterpretations when density or habitat quality varies along a river (Einum & Nislow 2005, Gauthey *et al.* 2017). In addition, although stock-recruitment models are commonly used (Govoni 2005), integration of co-variables assessing local distribution is rarely done (Iles 1994, Jonsson *et al.* 1998, Michielsens & McAllister 2004, Rivot *et al.* 2004, Subbey *et al.* 2014.)

Although the population recruitment is firstly dependent on the stock (Prévost & Chaput 2001), we tested the necessity for accounting for the stock or not when testing aggregation effect on the recruitment. Linear models with direct effects of aggregation on recruitment were poorer than stock-recruitment models indicating the necessity to take the population stock into account. However, both methods assessing the aggregation effects on the whole population recruitment provided consistent results.

2.4.3 EFFECTS OF AGGREGATION ON DEMOGRAPHIC PROCESSES AND LINK WITH BREEDING SITES SELECTION

A major result of this study is that increasing local aggregation did not decrease the population recruitment. The first explanation of this result is that aggregation occurs in the best-breeding sites in terms of habitat quality. In this way, even if the density-dependent competition is strong, the quality of the sites may still sustain an average recruitment. This explanation is consistent with previous results found by Tentelier *et al.* (2016), where breeders had a better reproductive success in term of produced off-springs when settled in best-breeding habitats. Indeed, breeding in best quality sites enables sustaining a good survival by compensating for density-dependent competition when individuals are able to evaluate habitat quality and this quality matches with cues (Fretwell & Lucas 1969, Hendry *et al.* 2001, Schlaepfer *et al.* 2002). The recruitment is then sustained by this choice of the best-breeding sites, which is in accordance with the ideal distribution already found for salmon (Falcy 2015, Hendry *et al.* 2001).

Alternatively, the lack of decrease in average recruitment with increasing aggregation might also be due to the already high average juvenile density. In this case, aggregation does not likely matter because the population is already at carrying capacity, a situation in which each individual undergoes a maximum density of neighbors, whatever its location. Estimated parameters of the Beverton-Holt model gave a carrying capacity (0.1082 juveniles/m^2) much lower than the density observed for 14 years of the time series. In addition, the median of the threshold biomass, $\frac{1}{K}$, was estimated at 11.24 eggs/m^2 suggesting that density-dependent mortality was exacerbated at stocks exceeding this value. Then, local competition between juveniles was very intense for most years. In addition, the asymptotic shape of the stock-recruitment relationship clearly advocates for this hypothesis. At low stock levels, lower than the thresold biomass, density-compensation is low. Therefore at stock levels exceeding the threshold biomass, the effects of spatial aggregation through local competition could reduce whole population recruitment at the

margin, making this effect undetectable or hardly detectable.

Aggregation of nests increased at low adult density, something expected under ideal distributions. The negative trend between the number of breeders and the aggregation of nests is consistent with the negative effect of aggregation on the number of effective breeders at low aggregation found by Bacles *et al.* (2018) in the same population. Our results indicate that when few individuals are present they all fit in the best patches, whereas they have to spill out to lower quality patches when density increases. In this way, first arrival breeders can aggregate and secure best sites (Falcy 2015).

Besides the selection of breeding sites on habitat quality, we found that the recruitment variability was reduced by nest aggregation indicating that aggregation buffers the effect of environmental stochasticity on recruitment. Recruitment variability results from density-independent factors such as environmental stochasticity leading to local perturbations such as scouring or emersion (Gauthey *et al.* 2017, Malcolm *et al.* 2004). Thus, our results suggest Atlantic salmon females assess environmental risk when selecting breeding sites like other salmonids (Gauthey *et al.* 2017). Indeed, the effects of these perturbations may be reduced by females selecting temporally stable breeding sites or sites where effects should be dampened such as sites with low temporal flow variability (Moir *et al.* 2006, Soulsby *et al.* 2012), high shear stress (Gauthey *et al.* 2017, Moir *et al.* 2004), or with high intra-gravel flow (Geist & Dauble 1998). Unfortunately, no data are available to predict perturbation occurrence along the Nivelle river, and there is no clear longitudinal gradient of flow predictability in rivers in general (Larned *et al.* 2011). Although aggregation cannot be linked with such perturbations, this highlights a lack of knowledge on the role and selection of breeding sites by females; a topic that deserves attention.

In addition to the effects of aggregation on demographic processes, aggregation of nests may also modify genetic diversity within populations (Bacles *et al.* 2018, Falcy 2015, (Lara-Romero *et al.* 2016, Tentelier *et al.* 2016, Winandy *et al.* 2017)). Indeed, some individuals could have most of their nests destroyed within aggregates due to scouring or nest superimposition, future offsprings of conspecifics being able to colonize empty habitats (Gharrett *et al.* 2013). Finally, strong aggregation should intensify local competition, thereby steepening selection gradients, a corollary of which is skewed re-

productive success and a low effective number of breeders (Chesson & Neuhauser 2002, Ives 1988, Murrell *et al.* 2002, Rejmánek 2002, Tilman 1994). Such effects are ripe areas for future investigation and would require a time series of both genetic and spatial data, which might be available in model populations (Pemberton 2008).

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HIGHLIGHTS OF CHAPTER 2

- Spatial aggregation of salmon females leads to spatial aggregation of their nests.
- Spatial aggregation of nests may diminish the recruitment by exacerbating the density-dependent mortality, but may also enhance the stability of the recruitment if females are aggregated in best-spawning sites.
- Spatial aggregation of nests was implemented within stock-recruitment models and improved their estimations.
- The average recruitment was not impacted by the spatial aggregation of nests but its variability decreased as aggregation increased.
- Effect on the recruitment variability suggests that early arriving or dominant females select the best-spawning sites and forced other females to aggregate in other sites.

SUPPLEMENTARY---S1

DATA COLLECTION OF EGGS AND JUVENILES

Eggs deposition is routinely estimated by the Environmental Research Observatory (ERO) on Diadromous Fish in Coastal rivers (DiaPFC, ERO DiaPFC: https://www6.inra.fr/diapfc) from the number of anadromous females in the Nivelle and their number of sea winters affecting their fecundities. Anadromous females are caught at two dams equipped with fish passes (Uxondoa dam and Olha dam, at 12 km and 16.7

km from the river mouth). Probability of capture taking into account the number of sea winters, was assessed at 0.88 for one sea winter, and 0.82 for multiple sea winters (Servanty & Prevost 2016).

Young of the year (0+) are caught by standardized procedure of electrofishing (Marchand *et al.* 2017). Until 2005, the data collection procedure consisted of the successive removal sampling method. This method consists of multiple passages (2 or 3 in most cases) on each sampling site ($N_{site} = 12$), catch probability being estimated at 0.52, 0.38, and 0.26 for the first, second, and third passage (Servanty & Prevost 2016). Since 2003, another method has been used, based on the number of juveniles fished during 5 min of effective fishing on favorable habitats for them, i.e. abundance index (Prévost & Baglinière 1995). This method consists of a single pass in favorable habitats for juveniles ($N_{site} = 22$, Table. 2.5) for 5 min of effective fishing (i.e. of electric field application in the water) with a portable electrofishing device, and was assessed by Dauphin *et al.* (2009). Approximately 2 km of suitable habitat for juveniles (25 km available for salmon) were sampled along the river (Table. 2.5), the entire width of the river being sampled at each sampling sites. In this way, the total suitable area which was sampled corresponded to more than 12 000 m^2 over the 56 575 m^2 (more than 21 %) available for the salmon. A relationship was built to estimate the juvenile density over the river from the abundance index determined among sampling sites (Brun *et al.* 2011, Dauphin *et al.* 2009, Servanty & Prevost 2016). The relation between the abundance index and the estimated juvenile density does not vary as the length of sample sites changes (Servanty & Prevost 2016). In 2003 and 2004, the two methods were carried out, allowing the building of an abacus based on the correspondence between the two methods (Brun *et al.* 2011). As indicated by Brun *et al.* (2011), modification of the method did not change the quality of the estimations, and the current used sampling method allows to identify yearly variations of juvenile abundance. Overdispersion of abundance estimations, due to the probability of capture varying between sites and the non-random distribution of fry, was taken into account by modelling the fry density with Negative Binomial distribution (Brun *et al.* 2011, Dauphin *et al.* 2009, Servanty & Prevost 2016).

Table. 2.5: Average sampled length in the 22 sampling sites in the Nivelle. At each site, Atlantic salmon juveniles were caught during 5 min of effective electrofishing over the entire width of the river (around 10 m). For each site, the average sampled length is displayed as well as the sampled area. Area values displayed with a * are approximate values, no juveniles being caught at these sites. At the opposite other values are exact measures, corresponding sites are those where juveniles are caught on the main stream and the main tributary.

Site	River / tributary	Site name	Average sampled length (m)	Sampled area (m^2)
01	Main stream	Pont romain Ascain	50	500*
02	Main stream	Ascain	40	449
03	Main stream	Zumabia	50	341
04	Main stream	INRA	140	462
05	Main stream	Olha	130	1 462
06	Main stream	Ile d'Amotz	110	629
07	Main stream	Pont romain Amotz	90	777
08	Main stream	Ustagabea	100	858
09	Main stream	Le couillut	120	479
10	Main stream	Betriena	80	523
11	Main stream	Grand chêne	100	68
12	Main stream	Confluence Sorrimenta	140	1 138
13	Main stream	Petit chêne	100	458
14	Main stream	Moulin Zahara	110	1 542
15	Main stream	Aval Darguy	80	660
16	Tributary - Sorrimenta	Sorrimenta	170	510*
17	Tributary - Opalazio	Opalazio	200	400*
18	Main tributary - Lurgorrieta	Lyonnaise	90	230
19	Main tributary - Lurgorrieta	Ohaldea	100	325
20	Main tributary - Lurgorrieta	Conserverie	130	931
21	Zone not accessible	Amont Darguy	190	1 330*
22	Zone not accessible	Amont Harrieta	200	1 400*
		Total	2 520	15 471
		Total in accessible zone	2 130	12 741

DIMINISHING NUMBER OF STRETCHES

For each of the 624 river stretches (k), the number of years from 1984 to 2015 when at least one nest was found in this stretch was computed (Y_{θ_k}). The probability θ_k that no nest has been found was independently estimated for each initial stretch from a Binomial distribution: $Y_{\theta_k} \sim \mathcal{B}(\theta_k, 32)$. If the θ_k was lower than 0.05, the stretch k was considered as a "*blank stretch*". Each blank stretch, or each succession of blank stretches was defined as a blank zone if this zone was longer than a threshold length (Figure. 2.7). Five threshold lengths were tested: 20, 50, 100, 200, or 500 m. Stretches not included

in blank zones and not separated from each other by blank zones are grouped together. For each threshold length, the final number of new zones was respectively equal to: 164, 93, 43, 11, and 5 (Table. 2.6). Initial stretch definition with 624 stretches was noted as threshold length "00". Logically, when the threshold length increases, the number of new zones decreases and the average length of zone increases (Table. 2.6).

Table. 2.6: Average, minimum, and maximum length of new patches for each threshold length.

Threshold (m)	Average Length (m)	Min Length (m)	Max Length (m)	Number of new patches
00	100.19	6.00	1 854.50	624
20	144.79	7.00	1 922.00	164
50	255.33	7.00	2 929.60	93
100	552.22	24.00	3 980.70	43
200	2 158.69	242.00	5 014.00	11
500	4 749.12	1 315.50	12 640.10	5

SHEPHERD'S STOCK-RECRUITMENT MODEL

As a preliminary approach, Shepherd (1982) stock-recrutment model was used (Eq. 2.8). This model is versatile and can reproduce stock-recruitment curves of Beverton-Holt, Cushing, or Ricker through the parameter β. Advantage of this model is thus the no-choice *a priori* of the curve shape: data drive the curve. But, the model has one additional parameter compared to Beverton-Holt. With the Shepherd model, the density of juveniles (Y_j^*) as a function of egg density (E_j^*) for the year j was:

$$\begin{aligned} \mu_j &= \frac{a \times E_j^*}{1 + \left(\frac{E_j^*}{K}\right)^{\beta}}, \\ Y_j^* &\sim Log\mathcal{N}\left(\log\left(\mu_j\right), \frac{1}{\tau}\right). \end{aligned} \qquad \text{(Eq. 2.8)}$$

Spatial aggregation of year j (patchiness noted P) was added in the same way as

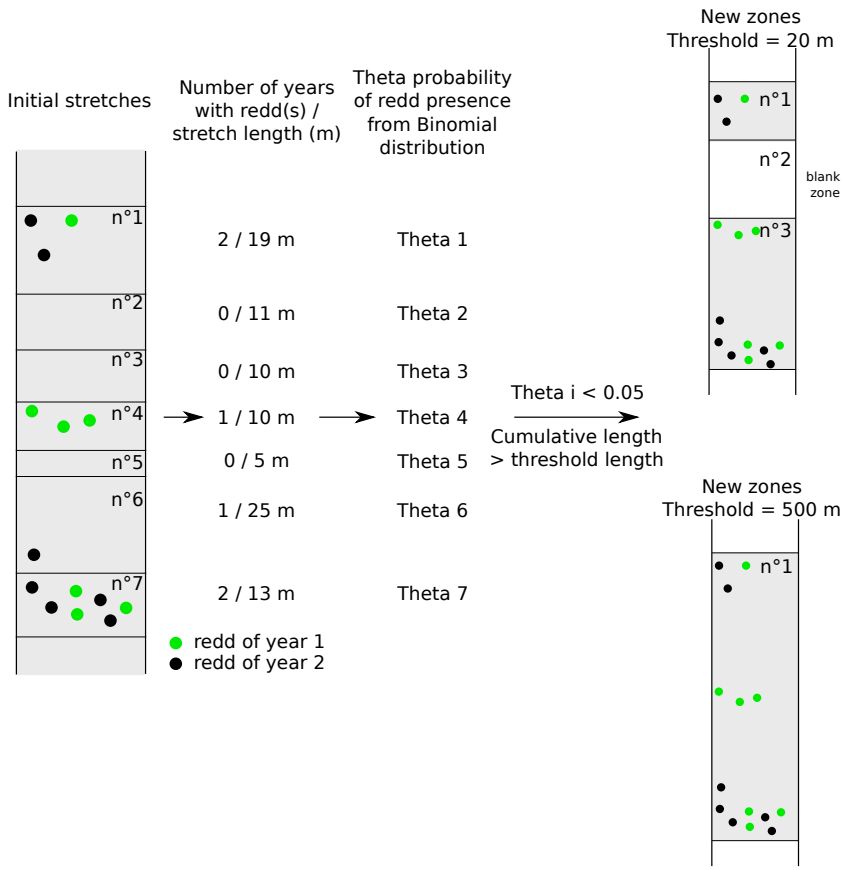

Figure. 2.7: Scheme of the building of new stretches. According to the nests found over the study period, each stretch had a theta probability that at least one nest was found. If this probability was lower 0.05, the strech was defined as "blank" stretch. Each "blank" stretch or row of "blank" stretches longer than a threshold length was considered as "blank" zone. All stretch between "blank" zone were grouped together.

for Berverton:

$$\begin{aligned} \mu_j &= \frac{a \times E_j^*}{1 + \left(\frac{E_j^*}{K}\right)^{\beta} \times P_j^q}, \\ \tau &= \delta \times P_j^{\eta} \\ Y_j^* &\sim Log\mathcal{N}\left(\log\left(\mu_j\right), \frac{1}{\tau}\right) \end{aligned} \qquad \text{(Eq. 2.9)}$$

Prior distributions of Shepherd were the same as those used for Beverton; a Log-Normal distribution was used for $\beta \sim \text{Log}\mathcal{N}\,(0, 5)$.

SUPPLEMENTARY --- S2

NEST COUNTS, AND AGGREGATION VALUE

Aggregation value (patchiness) of nests varied between 2.24 (upper than reference value of 1), in 1984 with threshold lengths of 200 m and 500 m, to 27.46 in 2012 with a threshold length of 50 meters (Figure. 2.8). Increasing of threshold length implied a decrease of aggregation (Figure. 2.8, Anova Type II: $Df = 5,\ F_{value} = 28.41, p_{value} < 0.01$), the number of zones decreasing too. As noted in the main document, aggregation values were higher for a threshold length of 50 m.

The year with lowest nest count (1985), the year with highest nest count (1993), and 2014 (recent year with small residuals with Beverton-Model) were chosen to illustrate the link between spatial distribution of nests, threshold length, and aggregation value (Figure. 2.9). In 1985, aggregation values were similar for lengths of 200 and 500 m (2.37), the number of used zones and total zones was similar between 200 and 500 m (two and four zones - Figure. 2.9). Although number of nests was higher in 1993 (233 against 79 in 2014 - Figure. 2.9), aggregation in 2014 was higher than aggregation in 1993 regardless the threshold lengths. If, aggregation had been assessed by the mean distribution in used stretches (number of nests divided by number of used stretches), the values would have been 1.72 in 2014, and 2.33 in 1993.

STOCK-RECRUITMENT MODELS

Beverton-Holt with all threshold lengths

WAIC of the 48 models with aggregation ranged from - 93.9 to - 88.5 (Figure. 2.10). For complete models (effect on the mean and variability), 19 over 36 were more efficient than the "null model" (with no aggregration) whose WAIC was equal to - 90.4. No semi-model including effect of aggregation on the mean was more efficient than the "null model", while all the six semi-models with effect only on variability were more efficient. Among the 15 best models, 11 were complete models, but the three best were semi-models with aggregation affecting only the variance of recruitment around the stock-based prediction (Table. 2.7).

Seven of fifteen best models were fitted with aggregation effect on τ computed under a threshold length of 50 m ($L_\tau = 50$). The two best models were the semi-models with aggregation under the threshold length of 50 m and 200 m for η ($L_\tau = 50$ and $L_\tau = 200$) and with no effect on the mean.

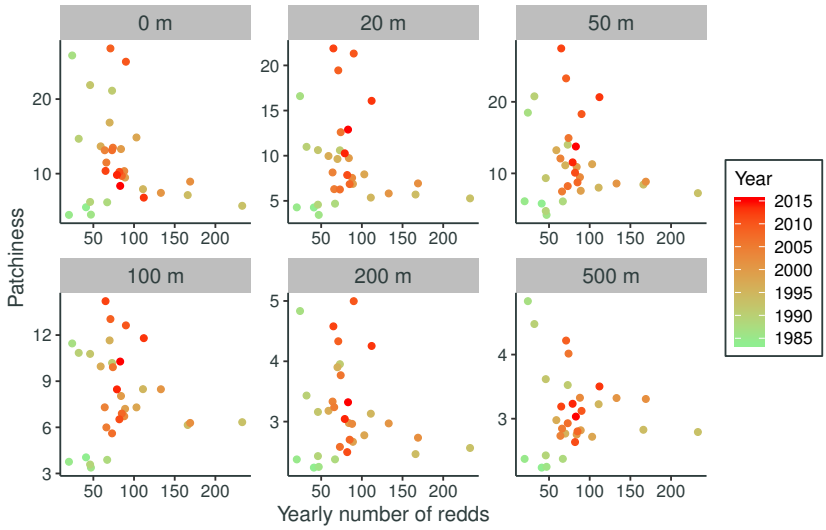

Figure. 2.8: Aggregation value (patchiness) of nests as a function of the yearly nest count, and grouped by threshold length (N = 32 years for each threshold length). Threshold length of "00 m" corresponded to the initial 624 stretches of the Nivelle based on morphodynamical changes along the river.

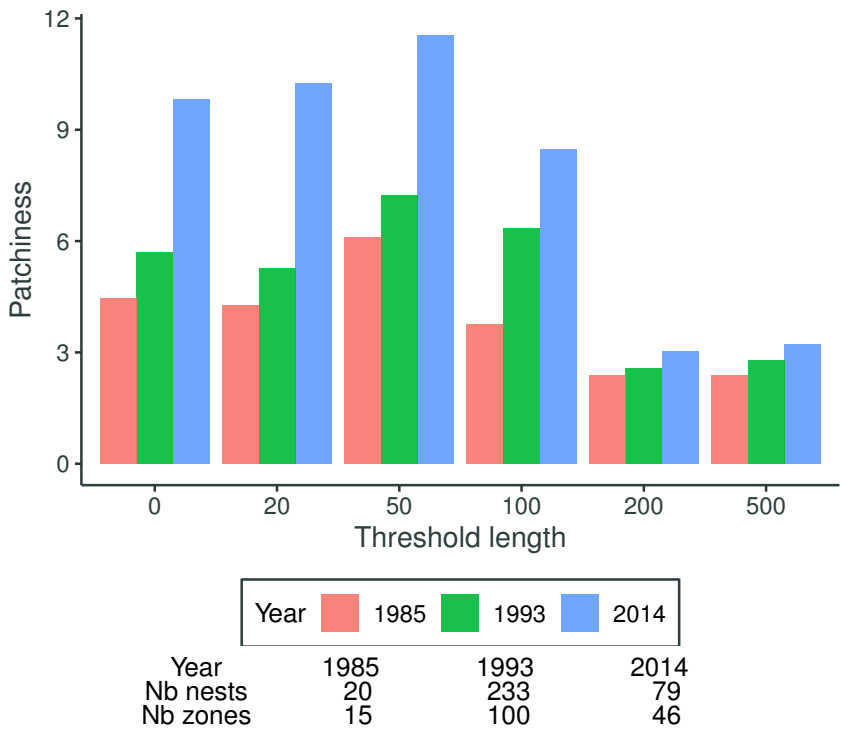

Figure. 2.9: Aggregation value (patchiness) of nests as a function of the threshold length for years 1985 (with the lowest number of nests), 1990 (with the highest number of nests), and 2014 (recent year). For each year, the number of nests found, and the number of stretches (of the 624 initial stretches) where at least one nest was found were displayed below the plot.

Complete models (best was ranked 4) exhibited no significant aggregation effect on the average recruitment (for the model 4: $q = -0.28$ $[-0.96; 0.41]$, Table. 2.7) with between 36 to 79 % of q estimations lower than 0 (over the 6,400 parameter estimations). The 10 best models (complete and semi-models) laid out significant positive effect of aggregation on precision. 2.1 % (model) and 1.9 % (model 4) of the 6,400 η estimations were evaluated lower than 0.

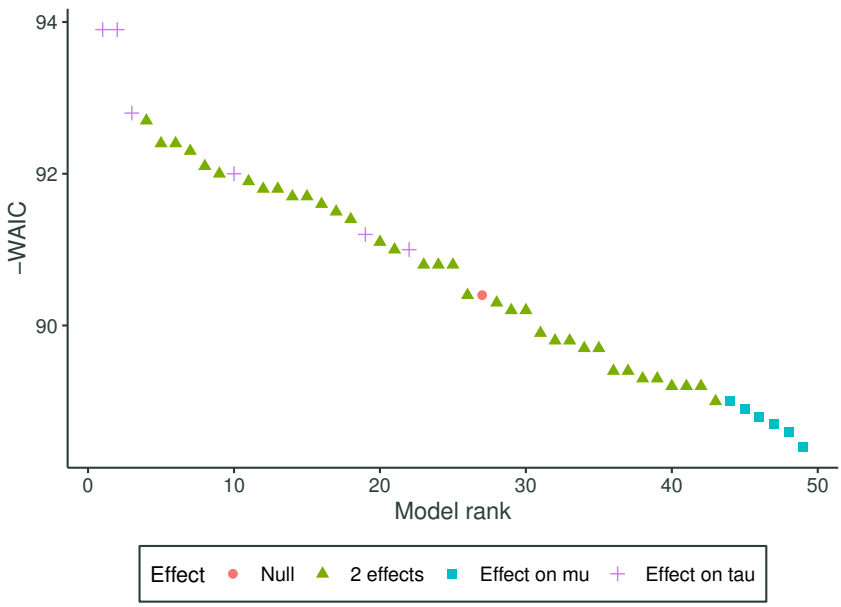

Figure. 2.10: Waic values obtained for the Beverton-Holt models with aggregation effects on μ (parameter q), effects on τ (parameter η), and both effects (parameters q and η).

Table. 2.7: Table of simulations obtained for the Beverton-Holt models with aggregation effects on μ (parameter q), effects on τ (parameter η), and both effects (parameters q and η). L_μ and L_τ were the threshold length used to compute the patchiness applied on parameters μ and τ. The value corresponds to the estimated mean of parameter, and the column test to the percentage of parameter value ≤ 0 in %.

Rank	Length μ	Length τ	WAIC	q		η		δ	a	K
				Value	Test ≤ 0	Value	Test ≤ 0	Value	Value	Value
null	-	-	- 90.4	-	-	-	-	1.95	6.88	0.26
01	-	50	- 93.9	-	-	0.71	02.09	0.54	6.45	0.24
02	-	200	- 93.9	-	-	1.50	01.69	0.51	6.06	0.27
03	-	20	- 92.8	-	-	0.61	02.77	0.70	7.99	0.24
04	200	50	- 92.7	- 0.28	79.66	0.75	01.64	0.49	7.32	0.25
05	500	50	- 92.4	- 0.29	76.36	0.68	02.09	0.56	6.28	0.28
06	200	200	- 92.4	- 0.23	76.50	1.52	02.11	0.51	7.53	0.28
07	500	200	- 92.3	- 0.24	73.39	1.40	02.11	0.56	7.23	0.32
08	20	50	- 92.1	- 0.07	67.22	0.73	01.78	0.51	8.16	0.24
09	00	200	- 92.0	- 0.06	66.56	1.45	02.16	0.54	7.61	0.28
10	-	100	- 92.0	-	-	0.71	04.55	0.68	6.64	0.27
11	100	50	- 91.9	- 0.04	57.56	0.73	02.22	0.52	7.74	0.25
12	20	200	- 91.8	- 0.06	65.81	1.48	02.44	0.53	7.76	0.26
13	00	50	- 91.8	- 0.02	53.55	0.68	02.44	0.56	6.70	0.26
14	50	200	- 91.7	0.00	49.56	1.44	02.73	0.56	7.98	0.26
15	200	20	- 91.6	- 0.27	79.03	0.66	02.77	0.65	7.46	0.26

Shepherd with all threshold lengths

Shepherd models displayed WAIC ranging from -92.3 to -86.1 (Figure. 2.11). The two best models with aggregation were very closed to the WAIC of the null one. Among the fifteen best models, all exhibited a significant positive value of the parameter q (effect on variability) as Beverton models (Table. 2.8). The β parameter of the model distinguishes the type of curve: Cushing ($\beta < 1$), Beverton-Holt ($\beta = 1$), and Ricker ($\beta > 1$). All models displayed parameter β with a mean around 1.1. This value is closed to the reference value distinguishing Beverton-Holt model because 1 was incuded in the confidence interval of the parameter (Figure. 2.12).

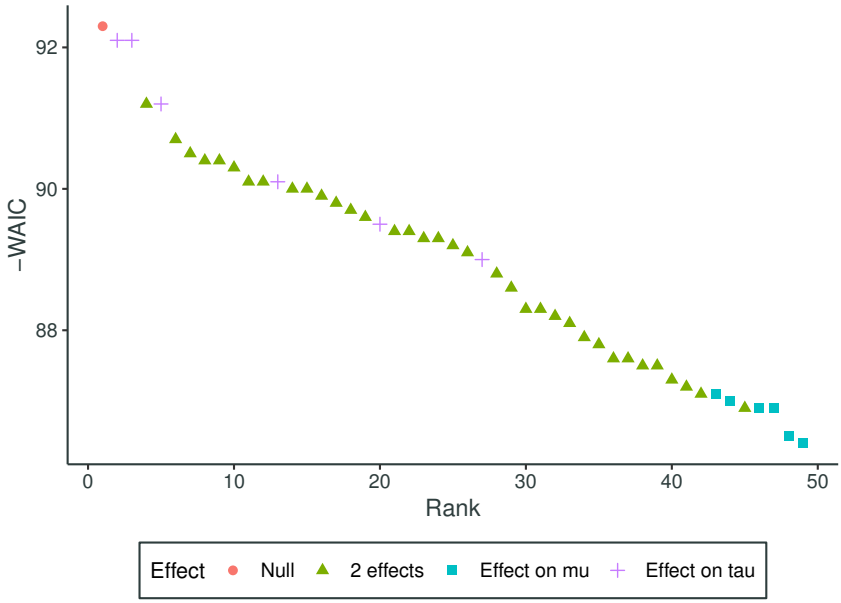

Figure. 2.11: WAIC values obtained for the Shepherd models with aggregation effects on μ (parameter q), effects on τ (parameter η), and both effects (parameters q and η).

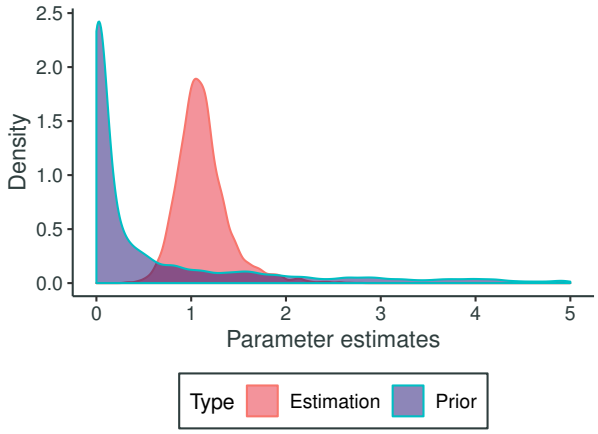

Figure. 2.12: Plot of the prior and estimates of β parameter for the best model of Shepherd with aggregation.

Table. 2.8: Table of simulations obtained for the Shepherd models with aggregation effects on μ (parameter q), effects on τ (parameter η), and both effects (parameters q and η). L_μ and L_τ were the threshold length used to compute the patchiness applied on parameters μ and τ. The value corresponds to the estimated mean of parameter, and the column test to the percentage of parameter value ≤ 0 in %.

Rank	Length μ	Length τ	WAIC	q		η		δ	a	K	β
				Value	Test ≤ 0	Value	Test ≤ 0	Value	Value	Value	Value
null	-	-	- 92.3	-	-	-	-	0.54	4.96	1.10	1.11
01	-	50	- 92.1	-	-	0.68	02.17	0.56	5.17	1.09	1.11
02	-	200	- 92.1	-	-	1.40	02.23	0.56	5.46	0.84	1.06
03	-	20	- 91.2	-	-	0.58	03.59	0.74	5.30	1.05	1.11
04	200	50	- 91.2	- 0.36	84.31	0.72	02.00	0.53	4.76	1.29	1.17
05	200	200	- 90.7	- 0.28	78.67	1.38	02.72	0.58	5.25	1.12	1.11
06	20	50	- 90.5	- 0.12	74.17	0.69	02.63	0.56	5.29	1.19	1.16
07	00	50	- 90.4	- 0.04	60.56	0.64	02.61	0.61	5.27	1.21	1.14
08	500	50	- 90.4	- 0.33	78.56	0.64	02.48	0.60	8.53	1.35	1.14
09	200	20	- 90.3	- 0.36	85.11	0.62	03.19	0.69	5.07	1.28	1.17
10	-	100	- 90.1	-	-	0.69	04.73	0.70	5.20	1.14	1.11
11	500	200	- 90.1	- 0.28	75.16	1.29	03.69	0.64	5.64	1.10	1.08
12	50	50	- 90.1	- 0.06	64.47	0.67	02.88	0.58	4.91	1.19	1.14
13	00	200	- 90.0	- 0.08	69.05	1.33	03.75	0.62	5.26	1.05	1.09
14	100	50	- 90.0	- 0.10	64.52	0.70	02.11	0.54	5.93	1.25	1.15
15	20	200	- 89.9	- 0.08	67.77	1.32	03.70	0.62	5.89	0.94	1.09

CHAPTER 3

A spatially explicit stock-recruitment model to assess the effects of spatial aggregation at a narrower spatial scale

Contents

3.1 CONTEXT

Spatial aggregation may affect recruitment through habitat quality and environmental stability. In salmon, the timing of arrival, as well as the dominance hierarchy, are factors modifying habitat choice. In this way, individuals may not necessarily aggregate in best habitats (Falcy 2015, Hendry *et al.* 2001). Individuals can assess habitats on the number of resources or environmental stability (Doligez *et al.* 2004, Morris 2003). Aggregation of breeders in breeding habitats increases the density-dependent mortality acting on juveniles.

Contrasted results at different scales indicate the importance of spatial scales in population dynamics processes. At the population level, spatial aggregation of nests diminishes the recruitment variability without impacting the average recruitment (chapter 2). These results contradict the findings that highlighted local density-dependent mortality and the resulting negative impact on local recruitment (Einum & Nislow 2005, Einum *et al.* 2008). These different results at different scales suggest that the interplay between recruitment and aggregation results in multiscale effects: from nests to the population. Variability of environment may also exacerbate such effects. For example,

in the upstream main tributary of the Nivelle, egg survival is lower than in the Nivelle River because nests are more clogged (Dumas & Marty 2006) which may lead to a higher negative effect of aggregation.

Rivers are not uniform continuum from their spring to their estuary. Habitat quality is usually better upstream than downstream (An *et al.* 2002, Dumas & Haury 1995, Harding *et al.* 1999) due to the influence of land use on rivers (Allan 2004). Urbanisation and farming activities diminish water quality downstream Figure. 3.1. The relationship between the stock (the number of eggs) and the recruitment (the number of juveniles) may, thus, vary along river or between river zones (Brun 2011, chapter VI). Some migratory species such as salmon tend to migrate upstream to find suitable breeding sites which are patchily distributed along rivers (Finstad *et al.* 2005). Density of individuals tends, thus, to increase upstream. Yet, dams or weirs diminish accessibility to upstream breeding sites to migratory species (Meixler *et al.* 2009) leading to spatial aggregation of breeders to vary along a river (Tentelier & Piou 2011).

Aggregation effect on recruitment may vary along a river. In the Nivelle, one explanation of results at the population level is a possible aggregation in the upstream zone of the Nivelle which may be of better quality (chapter 2). Dumas & Haury (1995) found a better water quality in the upstream zone of the Nivelle than in the downstream zone. A better quality of breeding sites in the Upper Nivelle may lead potential breeders to spawn in this zone rather than in another zone. Distribution of potential breeders and their nests within each zone may be different according to the number of potential breeders within each zone and the quality of available breeding sites. Spatial aggregation of nests can, thus, be computed separately for each river zone. In addition, by applying a stock-recruitment model to different zones of the Nivelle, Brun (2011, chapter VI) found that the upstream one exhibited the highest carrying capacity, whereas the stock of eggs was the lowest. The results of Brun (2011, chapter VI) suggest a low density-dependent mortality in the upstream zone of the Nivelle (Upper Nivelle, Figure. I.viii page 26).

The current chapter aims to compare aggregation and the effects of spatial aggregation on stock-recruitment relationships between river zones. Water quality, carrying capacity, and spatial aggregation can vary among zones, then I hypothesised that effects of spatial aggregation on recruitment vary among Nivelle network zones. In addition, the

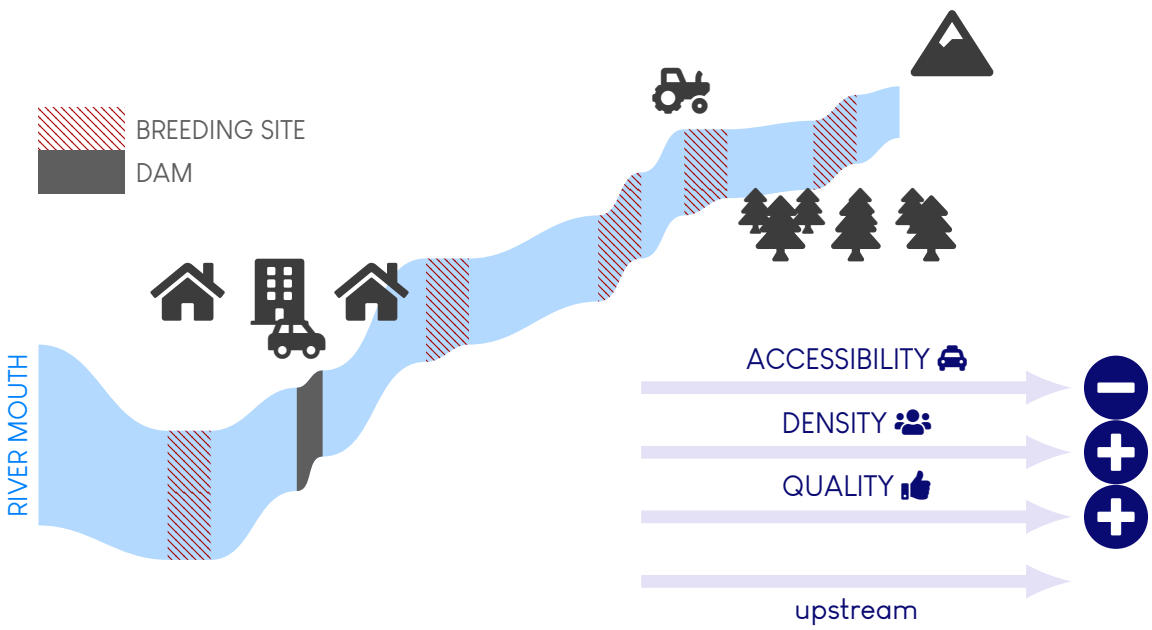

Figure. 3.1: Scheme of factors varying along a river denoting the heterogeneity that can exist between river zones.

time-series allow me testing if these effects of spatial aggregation are affected by a dam opening resulting in the opening of new habitats. I used time-series of stock (number of deposited eggs), recruitment (number of produced juveniles), and redd mapping to build a stock-recruitment model accounting for aggregation of nests for each of the three Nivelle zones.

3.2 METHODS

3.2.1 PARTITIONING OF THE NIVELLE, STOCK-RECRUITMENT DATA AND SPATIAL AGGREGATION

The Nivelle can be partitioned in three zones as done by Brun (2011, chapter VI): i) the "Lower Nivelle" — LN — from the river mouth to the Olha dam; ii) the "Upper Nivelle" — UN — from the Olha dam to the upstream impassable dam on the main stream; iii) the "Lurgorrieta", the main tributary (Figure. I.viii). A unique surface, noted h_{zone}, of available and suitable area for juvenile productivity characterises each Nivelle zone. The surface for the LN corresponds to the total surface available before the opening of Olha: $h_{LN} = 15,011$ m^2 (chapter 2, page 65). The Lurgorrieta exhibits the lowest surface, $h_{Lurgorrieta} = 8,190$ m^2. Finally, the UN is the best river zone when considering the suitable and available area: $h_{UN} = 33,374$ m^2. The total of these three surfaces corresponds to the total surface of suitable area available after the opening of

Olha ($h_{total} = 56,576$ m^2, chapter 2, page 65).

Stock-recruitment data corresponded to the yearly number of deposited eggs and the yearly number of juveniles. Both are routinely estimated by the ORE DiaPFC (see section 2.2.1, page 70) for the entire river[1]. Juveniles are estimated from juveniles caught at 22 sampling sites distributed in the three river zones. These 22 sites associated to the surface of available and suitable habitats for spawning in each river zone enable ORE DiaPFC estimating the number of juveniles produced in each river zone. Number of deposited eggs are estimated from the number of females migrating into the Nivelle network. Fish passages at the Uxondoa dam and the Olha dam are associated with the number of redds found in each river zone to estimate the part of females spawning in each river zone. The latter estimation allows to estimate the number of eggs deposited in each river zone. These number of estimated deposited eggs and produced juveniles for each zone of the Nivelle allowed me to fit a stock-recruitment curve with parameters varying among river zones. Following the same process that in the previous chapter, the stock was computed as the yearly number of eggs divided by h_{zone} and the recruitment as the yearly number of juveniles divided by h_{zone}. The time-series for the LN concerned 31 years (1984 to 2014), while 25 years were available for the UN (1990 to 2014) and 21 years for the Lurgorrieta (1993 to 2014 without 2006). The Upper Nivelle and the Lurgorrieta were accessible since 1992 but anadromous were released in the Upper Nivelle in 1990 and 1991.

3.2.2 SPATIAL AGGREGATION

The spatial aggregation of redds was computed with the patchiness index from the redd mapping data like in the previous chapter (see page 73). Here, the aggregation was independently computed for each river zone by dividing the mean density (the average number of nests in the considered zone) over the number of zone's patches. The initial stretches were grouped following the same process that for the previous chapter within each Nivelle zone. (see section 2.2.2, page 73). However, only the threshold length of 50 m was used here.

I compared the spatial aggregation of nests between each river zone (z) by accounting for a zone effect (α), a year random effect (δ), and an interaction between zone and

[1]More details about collection of juveniles and ORE estimations are displayed in the previous chapter: section 2.2.1, page 70.

year (β). The spatial aggregation of the zone z for the year j was:

$$\begin{aligned} \text{aggregation}_{z,j} &= \mathcal{N} \sim \left(\mu_{z,j}, \sigma_z\right) \\ \mu_{z,j} &= intercept + \alpha_z + \beta_j + \delta_z \times j \end{aligned} \qquad \text{(Eq. 3.1)}$$

The model was fitted under a Bayesian framework by calling `Stan` in `R`. A total of 5,700 iterations was saved after a burn-in of 1,000 iterations and with a thinning interval of 10. The total number of iterations were cumulated from four chains. Chain convergence was graphically checked and also assess through the scale reduction factor: $\hat{r}$ (Gelman & Rubin 1992).

3.2.3 STOCK-RECRUITMENT MODELS

I firstly considered the model of Shepherd because the shape of the stock-recruitment curve characterising each zone may be different. This versatile model allows data to drive the shape of the curve through the parameter β (box Tools II.i). In this way, the curve may tend to be similar to either a Cushing curve ($\beta < 1$), a Ricker curve ($\beta > 1$), or a Beverton-Holt one ($\beta = 1$). The models of Beverton & Holt (1957), Cushing (1973), Ricker (1954), and Shepherd (1982) were also tested. The yearly recruitment in each zone was modelled from a log-normal distribution:

$$Y^*_{z,j} \sim Log\mathcal{N}\left(\log\left(\mu_{z,j}\right), \frac{1}{\tau_z}\right), \qquad \text{(Eq. 3.2)}$$

with $Y^*_{z,j}$ the recruitment corrected by h for the zone z and the year j. The variance, i.e. the inverse of τ_z was estimated for each zone z. Formula of the average recruitment ($\mu_{z,j}$) in Eq. 3.2 without aggregation effect was for each model:

Model	$\mu_{z,j} =$	
Beverton & Holt (1957)	$\dfrac{a_z \times E^*_{z,j}}{1 + \left(\frac{E^*_{z,j}}{K_z}\right)}$	(Eq. 3.3)
Cushing (1973)	$a_z \times E^*_{z,j} \times \left(\dfrac{E^*_{z,j}}{K_z}\right)^{-\beta_z}$	(Eq. 3.4)
Ricker (1954)	$a_z \times E^*_{z,j} \times \exp -\dfrac{E^*_{z,j}}{K_z}$	(Eq. 3.5)
Shepherd (1982)	$\dfrac{a_z \times E^*_{z,j}}{1 + \left(\frac{E^*_{z,j}}{K_z}\right)^{\beta_z}}$	(Eq. 3.6)

K indicates the threshold biomass from which density-dependent compensation occurs. The values of K for the Upper Nivelle and the Lurgorrieta was estimated from the value for the Lower Nivelle as:

$$K_z = v_{\text{Upper Nivelle or Lurgorrieta}} \times k \qquad \text{(Eq. 3.7)}$$

with k being the threshold biomass for the Lower Nivelle. The same process was used to estimate a_z, the slope at origin, for each zone. Null models ($\mathcal{M}odels_{\text{null}}$) without aggregation effect were fitted by replacing $\mu_{z,j}$ in Eq. 3.2 by the Eq. 3.6.

Complete models ($\mathcal{M}odels_{\text{complete}}$) accounted for an effect of the spatial aggregation on $\mu_{z,j}$ and τ_z were fitted like for the $\mathcal{BH}_{\text{complete}}$ in the previous chapter. The equations of $\mu_{z,j}$ was then:

Model	$\mu_{z,j} =$	
Beverton & Holt (1957)	$\dfrac{a_z \times E^*_{z,j}}{1 + \left(\frac{E^*_{z,j}}{K_z}\right)} \times P_j^{q_z}$	(Eq. 3.8)
Cushing (1973)	$a_z \times E^*_{z,j} \times \left(\dfrac{E^*_{z,j}}{K_z}\right)^{-\beta_z} \times P_j^{q_z}$	(Eq. 3.9)
Ricker (1954)	$a_z \times E^*_{z,j} \times \exp -\dfrac{E^*_{z,j}}{K_z} \times P_j^{q_z}$	(Eq. 3.10)
Shepherd (1982)	$\dfrac{a_z \times E^*_{z,j}}{1 + \left(\frac{E^*_{z,j}}{K_z}\right)^{\beta_z}} \times P_j^{q_z}$	(Eq. 3.11)

with a value of q, the parameter estimating the effect of spatial aggregation on the average recruitment, estimated for each zone z. The effect of aggregation on τ_z was assessed for each zone through the parameter η:

$$\tau_z = \delta_z \times P_j^{\eta_z} \qquad \text{(Eq. 3.12)}$$

Semi-models with just an effect on $\mu_{z,j}$ ($\mathcal{M}odels_\mu$) or τ ($\mathcal{M}odels_\tau$) were also fitted like in the previous chapter. All models were fitted under a Bayesian framework by calling `Stan` in `R`. A total of 6,400 iterations was saved after a burn-in of 2,000 iterations and with a thinning interval of 5. The total number of iterations were cumulated from four chains. Chain convergence was graphically checked and also assess through the scale reduction factor: $\hat{r}$ (Gelman & Rubin 1992). Assessment of models was done with the Widely Applicable Information Criterion (WAIC, Vehtari *et al.* 2017).

3.3 RESULTS

3.3.1 SPATIAL AGGREGATION IN EACH NIVELLE ZONE

The spatial aggregation in the Upper Nivelle (UN) was more variable than other zones (σ in Figure. 3.3 — $\sigma_{UN} = 7.89$ [5.86; 8.66], $\sigma_{LN} = 4.14$ [3.04; 5.71], and $\sigma_{LUR} = 1.06$ 0.44; 1.78). The Upper Nivelle also exhibited higher values than other zones, raising up to around 40 (Figure. 3.2) but no difference was found in average (α in Figure. 3.3). Surprisingly, the Lower Nivelle displayed values not much higher than the Lurgorrieta.

Table. 3.1: Summary of the prior distributions of parameters of the stock-recruitment models $\mathcal{B}everton_{\text{null}}$, $\mathcal{B}everton_{\mu}$, $\mathcal{B}everton_{\tau}$, and $\mathcal{B}everton_{\text{complete}}$. Parameter K corresponds to the threshold biomass which indicates the carrying capacity when K is multiplied by a, the slope at origin. Parameters τ and δ are involved in the modelisation of the recruitment variability. Parameters q_z and η_z correspond to the effect of aggregation on the mean and the variability of the Shepherd models for the Nivelle zone z. β_z is the parameter driving the stock-recruitment curve. Models of Cushing, Ricker, and Shepherd used the same priors.

Parameter	Definition	Prior distribution
a	Eq. 3.3 and Eq. 3.8	$Log\mathcal{N}(0,2)$
K—k	Eq. 3.3 and Eq. 3.8	$Log\mathcal{N}(0,10)$
β_z	Eq. 3.3 and Eq. 3.8	$Log\mathcal{N}(0,5)$
v	Eq. 3.7	$\mathcal{C}(1,2.5)$
τ	Eq. 3.3	$\Gamma(0.01,100)$
δ	Eq. 2.6	$\Gamma(0.01,100)$
q_z	Eq. 3.8	$\mathcal{N}(0,20)$
η_z	Eq. 3.8	$\mathcal{N}(0,20)$

The recent years displayed the higher values of aggregation in the Upper Nivelle; the positive interaction found for the Upper Nivelle verified this effect: $\beta_{UN} = 0.95[0.45; 1.44]$[2] ($\beta$ in Figure. 3.3). The interaction effects (β) for the LN and the Lurgorrieta were not significant (Figure. 3.3). No significant year effect was found (Figure. 3.3). In the Lower Nivelle and the Upper Nivelle, the higher values of aggregation were not found at a high number of redds.

[2] 95% Highest Posterior Density

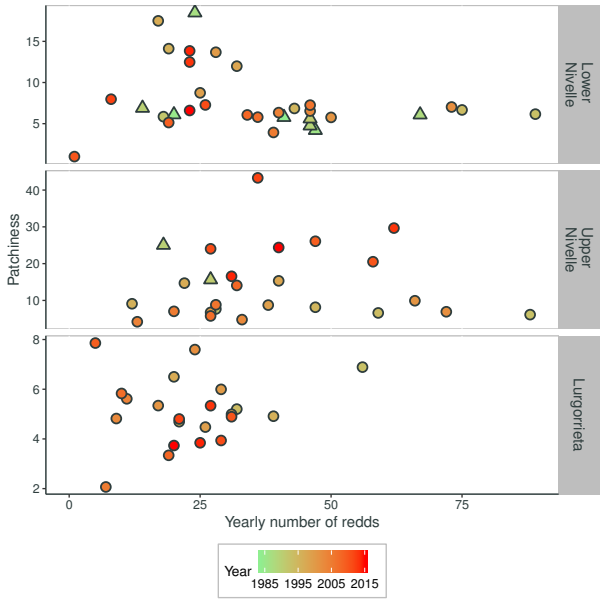

Figure. 3.2: Spatial aggregation of nests (patchiness) computed for the three zones in the Nivelle: Lower Nivelle (31 years), Upper Nivelle (25 years), and Lurgorrieta (21 years) which is the main tributary. The Upper Nivelle and the Lurgorrieta were accessible since 1992 (dots), but anadromous were released in the Upper Nivelle in 1990 and 1991. Triangles correspond to years before 1992.

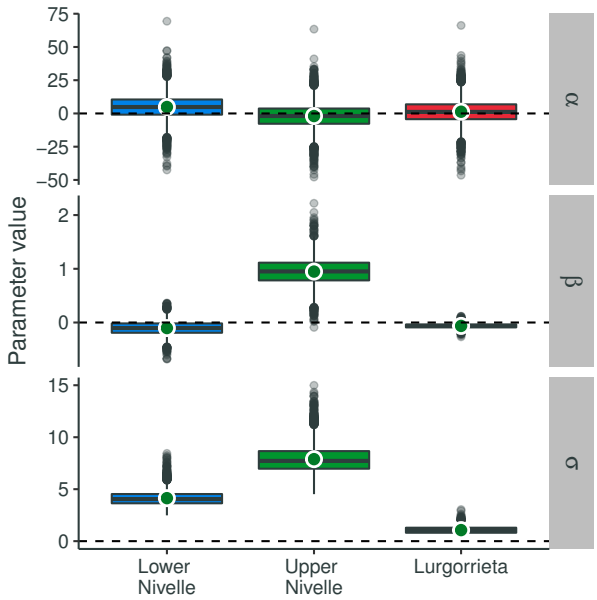

Figure. 3.3: Estimates of the model Eq. 3.1 testing the differences in spatial aggregation between the three zones in the Nivelle. The model accounted for a zone effect (α), a year random effect (δ), and an interaction (β) on μ : $\mu_{z,j} = intercept + \alpha_z + \beta_j + \delta_z \times j$. The model also accounted for an effect of zone on the variability (σ). Data correspond to the spatial aggregation within each zone since 1993, the first year during which nests were found in all zones.

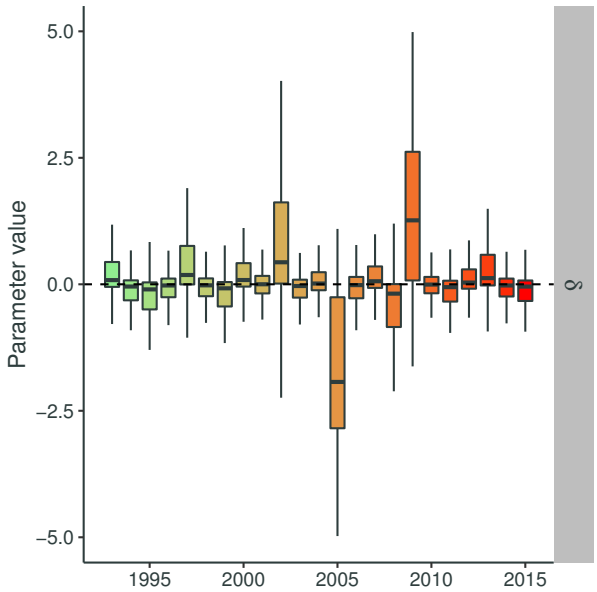

Figure. 3.4: Estimates of the model Eq. 3.1 testing the differences in spatial aggregation between the three zones in the Nivelle. The model accounted for a zone effect (α), a year random effect (δ), and an interaction (β) on μ : $\mu_{z,j} = intercept + \alpha_z + \beta_j + \delta_z \times j$. The model also accounted for an effect of zone on the variability (σ). Data correspond to the spatial aggregation within each zone since 1993, the first year during which nests were found in all zones.

3.3.2 STOCK AND RECRUITMENT

The Lurgorrieta exhibited the highest stock (around 60 eggs.m^{-2}, Figure. 3.5), whereas the Upper Nivelle displayed the lowest one (around 25 eggs.m^{-2}) when standardizing the stock and the recruitment by h. Recruitment was globally similar between zones apart during one year for the Lurgorrieta (Figure. 3.5). In addition, before the 2000s the recruitment seems synchronous between the three zones whereas the stock varied. After the 2000s, the Lurgorrieta seems more variable in regards to the two other zones.

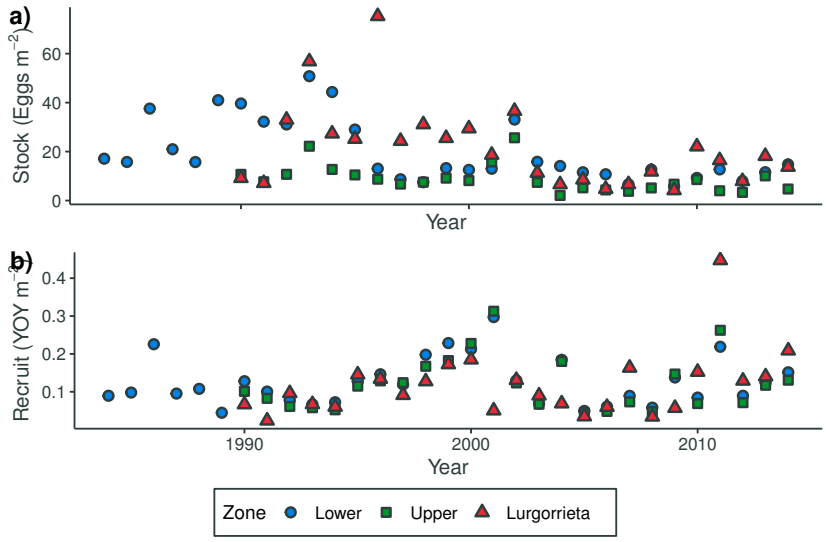

Figure. 3.5: Stock and recruitment values in the three zones in the Nivelle: Lower Nivelle (31 years), Upper Nivelle (25 years), and the Lurgorrieta (21 years). The Upper Nivelle and the Lurgorrieta were accessible since 1992 (dots), but anadromous were released in the Upper Nivelle in 1990 and 1991. Triangles correspond to years before 1992.

3.3.3 EFFECTS OF ACCOUNTING FOR AGGREGATION ON MODELS OF STOCK RECRUITMENT

Beverton-Holt models were the best models (lowest WAIC). The WAIC of the stock-recruitment models was higher when considering spatial aggregation of nests (WAIC $_{\mathcal{B}everton_{\text{null}}} = -223$, WAIC $_{\mathcal{B}everton_{\mu}} = -206$, WAIC $_{\mathcal{B}everton_{\tau}} = -211$), and WAIC $_{\mathcal{B}everton_{\text{complete}}} = -210$. Although the model $\mathcal{B}everton_{\tau}$ exhibited the lowest WAIC, I only present the results of the complete model ($\mathcal{B}everton_{\text{complete}}$) because it has a WAIC very closed to the best one and allows me discussing all effects of aggregation. The model was compared to the null model ($\mathcal{B}everton_{\text{null}}$).

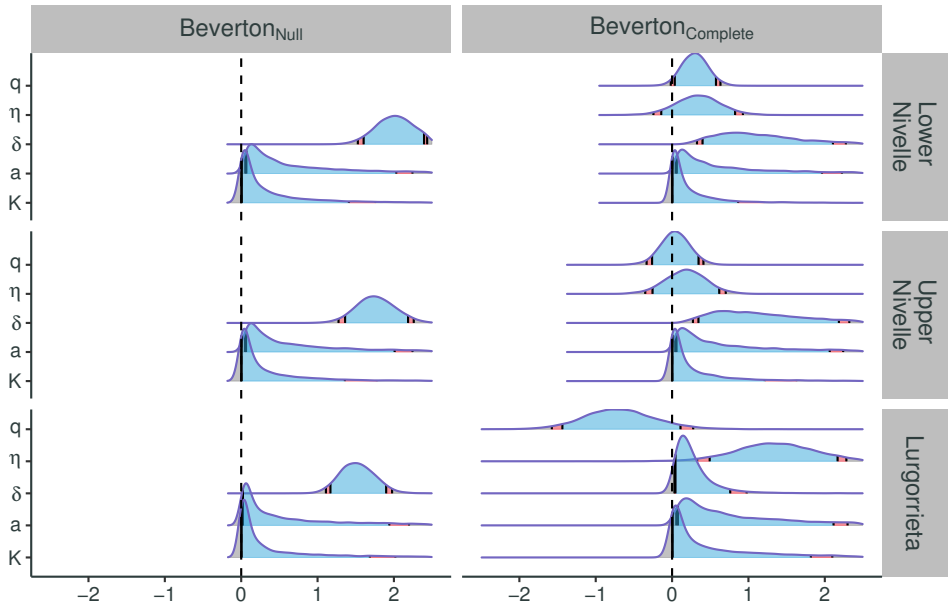

Figure. 3.6: Density plot of the parameter estimates involved in the stock-recruitment models in the three zones in the Nivelle: LN (31 years), UN (25 years), and the Lurgorrieta (21 years). Only parameters varying between the three zones are displayed. The model $\mathcal{B}everton_{\text{null}}$ is a simple Shepherd model, while the model $\mathcal{B}everton_{\text{complete}}$ tested the effect of aggregation of nests on its variability (η parameter). Blue areas represent the values between the quantiles 5 % and 95%. Red areas represent the values between the quantiles 0 and 2.5 % and the values between the quantiles 97.5 % and 1. Green areas represent the values between the quantiles 2.5 and 5 % and the values between the quantiles 95 % and 97.5 %.

Table. 3.2: Parameter estimates for the stock-recruitment models $\mathcal{B}everton_{\text{null}}$ and $\mathcal{B}everton_{\text{complete}}$ fitted to the three zones of the Nivelle: Lower Nivelle (LN), Upper Nivelle (UN), and Lurgorrieta. The model $\mathcal{B}everton_{\text{null}}$ was a simple Beverton-Holt model, while the model $\mathcal{B}everton_{\text{complete}}$ was a Beverton-Holt model including an effect of aggregation of nests on the average recruitment (parameter q) and its variability (parameter η). Each parameter estimate was displayed with its mean and the Highest Posterior Density interval at 95% from 6, 400 iterations. "*" denotes parameters significantly different from zero. Similar letters indicate no significant differences between zones for a parameter.

	Model	Nivelle zone		
		LN	UN	Lurgorrieta
a	$\mathcal{B}everton_{\text{null}}$	$4.65^{*,a}$ $[0.06; 35.74]$	$8.76^{*,a}$ $[0.06; 60.05]$	$6.75^{*,a}$ $[0.02; 51.99]$
	$\mathcal{B}everton_{\text{complete}}$	$5.86^{*,a}$ $[0.05; 36.71]$	$11.34^{*,a}$ $[0.05; 72.78]$	$19.96^{*,a}$ $[0.07; 135.84]$
K	$\mathcal{B}everton_{\text{null}}$	$0.38^{*,a}$ $[0.0030; 2.1033]$	$0.41^{*,a}$ $[0.0017; 2.5024]$	$1.02^{*,a}$ $[0.0019; 7.2855]$
	$\mathcal{B}everton_{\text{complete}}$	$0.22^{*,a}$ $[0.0016; 1.2592]$	$0.35^{*,a}$ $[0.0014; 2.1899]$	$0.73^{*,a}$ $[0.0026; 4.0211]$
q	$\mathcal{B}everton_{\text{null}}$	/		
	$\mathcal{B}everton_{\text{complete}}$	$0.2991^{*,a}$ $[-0.0175; 0.6331]$	0.0401^{a} $[-0.3342; 0.4100]$	-0.6867^{a} $[-1.5753; 0.2762]$
η	$\mathcal{B}everton_{\text{null}}$	/		
	$\mathcal{B}everton_{\text{complete}}$	0.3407^{a} $[-0.2450; 0.9275]$	0.1801^{a} $[-0.3520; 0.7028]$	$1.3686^{*,a}$ $[0.3317; 2.4554]$
δ	$\mathcal{B}everton_{\text{null}}$	$2.03^{*,a}$ $[1.53; 2.56]$	$1.76^{*,a}$ $[1.27; 2.27]$	$1.52^{*,a}$ $[1.11; 1.98]$
	$\mathcal{B}everton_{\text{complete}}$	$1.2731^{*,a}$ $[0.3323; 3.2720]$	$1.3589^{*,a}$ $[0.2824; 3.8713]$	$0.2799^{*,a}$ $[0.0311; 1.0068]$

Table. 3.3: Carrying capacity estimated for the stock-recruitment models $\mathcal{B}everton_{\text{null}}$ and $\mathcal{B}everton_{\text{complete}}$ fitted to the three zones of the Nivelle: LN, UN, and Lurgorrieta. The carrying capacity in juvenile.m^{-2} was computed as: $Cc_z = a_z \times K_z$. The model $\mathcal{B}everton_{\text{null}}$ was a simple model of Beverton-Holt, while the model $\mathcal{B}everton_{\text{complete}}$ was a model of Beverton-Holt accounting for an affect of aggregation of nests on the average recruitment and its variability. Each value was computed from 6, 400 iterations of the parameters a and K, mean being displayed with the Highest Posterior Density interval at 95%. Similar letters indicate no significant differences between zones for a parameter. $^{b.}$ indicates that the difference was quasi significant (0.06).

Model	Nivelle zone		
	LN	UN	Lurgorrieta
$\mathcal{B}everton_{\text{null}}$	$0.1140^{*,a}$ $[0.0938; 0.1396]$	$0.1113^{*,a}$ $[0.0852; 0.1523]$	$0.1054^{*,a}$ $[0.0760; 0.1601]$
$\mathcal{B}everton_{\text{complete}}$	$0.0672^{*,a,c}$ $[0.0305; 0.1248]$	$0.1139^{*,a,b.}$ $[0.0379; 0.2744]$	$0.5143^{*,b.,c}$ $[0.0663; 1.7886]$

When not accounting for aggregation, in the model $\mathcal{B}everton_{\text{null}}$, the parameter a and K did not vary between river zones (Table. 3.2, Figure. 3.6). River zones displayed, thus, similar stock-recruitment curves (Figure. 3.7). Yet, the Upper Nivelle displayed the highest value of a and the Lower Nivelle the lowest (Table. 3.2, Figure. 3.6). The Lurgorrieta exhibited the highest value of K, but the model seemed to have difficulties estimating it (Figure. 3.6). The Lower Nivelle was the zone with the highest value of δ and the Lurgorrieta displayed the lowest value of δ, the inverse of variance. The carrying capacity — computed by multiplying the 6, 400 iterations of the parameters of a by K — estimated for the Lurgorrieta was the lowest one at around 0.1054 juvenile.m^{-2} (mean), whereas the Lower Nivelle exhibited the highest one at around 0.1140 juvenile.m^{-2} (Table. 3.3). The three zones were characterised by closed values of carrying capacity.

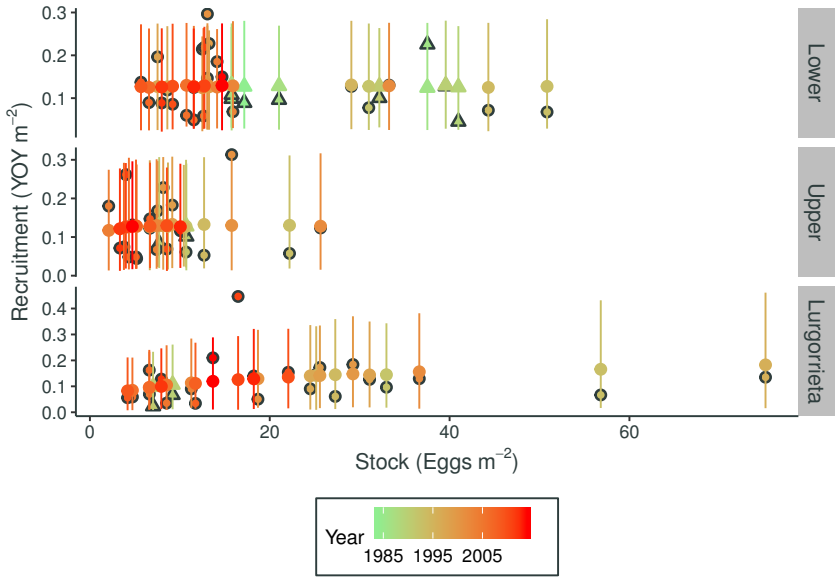

Figure. 3.7: Stock-recruitment curves in the three zones in the Nivelle: LN (31 years), UN (25 years), and the Lurgorrieta (21 years). The Upper Nivelle and the Lurgorrieta were accessible since 1992 (dots), but anadromous were released in the Upper Nivelle in 1990 and 1991. Triangles correspond to years before 1992. Points without range correspond to the observed values, while points with range correspond to the estimated recruitment values with the Credible Interval at 95% from 6, 400 iterations of the model $\mathcal{B}everton_{\text{null}}$.

Considering aggregation did not significantly modify the parameters a and K (Table. 3.2). These two parameters did not vary between river zones as when not accounting for aggregation (Figure. 3.6). The difference in average values are due to difficulties in estimating the parameters as clearly visible on the Figure. 3.6. For the Upper Nivelle,

the carrying capacity was similar when considering spatial aggregation than when not accounting for it (Table. 3.3). The Lower Nivelle exhibited the lowest carrying capacity, half as much as when not considering spatial aggregation (changing from 0.1140 to 0.0672 juvenile.m^{-2}).

The Lower Nivelle exhibited a significantly positive value of q measuring the effect of aggregation on the average recruitment, whereas the two other zones did not exhibit a significant parameter value. Concerning the effect of aggregation on the recruitment variability, the parameter η tended to be positive for the LN and the UN and was significantly positive for the Lurgorrieta (Table. 3.2). The Upper Nivelle was the zone with the highest value of δ at 1.36, whereas the Lurgorrieta exhibited the lowest value at 0.30 (Table. 3.2).

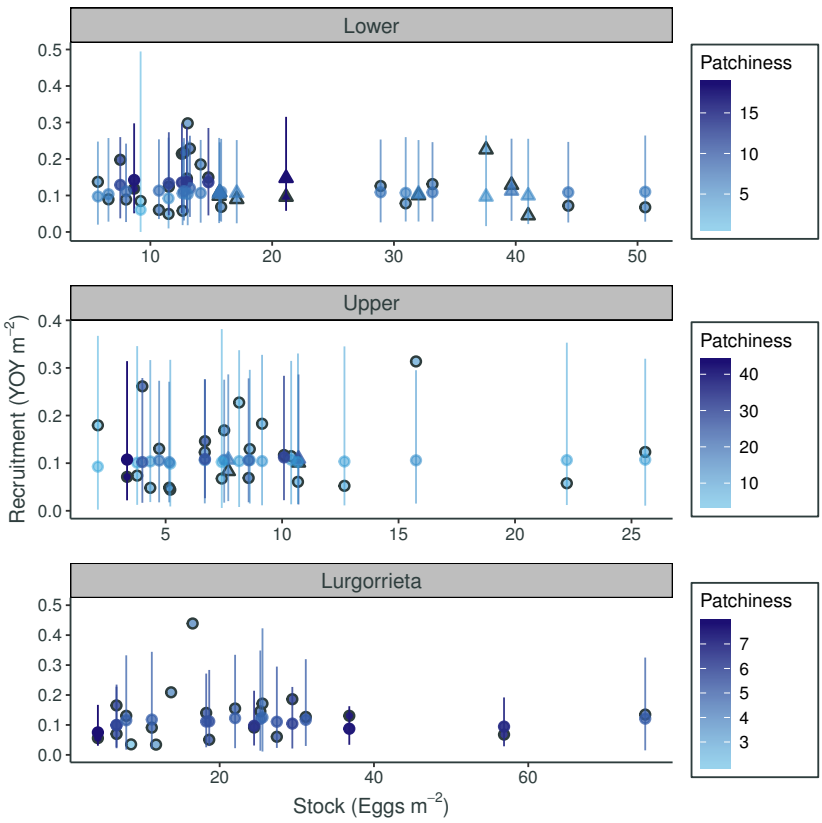

Figure. 3.8: Stock-recruitment curves in the three zones in the Nivelle: LN (31 years), UN (25 years), and the Lurgorrieta (21 years) when accounting for aggregation effects. The Upper Nivelle and the Lurgorrieta were accessible since 1992 (dots), but anadromous were released in the Upper Nivelle in 1990 and 1991. Triangles correspond to years before 1992. Effects of the spatial aggregation of nests on the average recruitment, as well as on the recruitment variability were accounted. Points without range correspond to the observed values, while points with range correspond to the estimated recruitment values with the Credible Interval at 95% from 6, 400 iterations.

3.4 DISCUSSION

The current chapter aimed to test how the spatial aggregation of nests affected the recruitment within each Nivelle zone. The spatial aggregation of nests significantly raised the average recruitment in the Lower Nivelle but not in other zones. Spatial aggregation also diminished recruitment variability for a given level of stock in the Lurgorrieta, whereas a trend transpired in other zones. A model of Beverton-Holt was the best model among all tested models allowing me to compare parameters to those estimated by Brun (2011, chapter VI) who used a Beverton-Holt model. I first discuss differences between zones in stock-recruitment relationships and aggregation, and then the aggregation impacts on stock-recruitment relationships.

Spatial aggregation within each zone varies between river zones. The spatial aggregation of nests was computed for each zone, thus, I focused on how nests were distributed in each zone independently to the other zones. Spatial aggregation was stronger in the Upper Nivelle (UN) than in the Lower Nivelle (LN) for which values were similar to those of the Lurgorrieta. The higher aggregation of nests found for the Upper Nivelle compared to the values found for the other zones may, thus, be due either to a most heterogeneous quality of breeding sites in the UN than in other zones, or to constraints in nest distribution (dams or environmental factors). More interesting is the recent increase in aggregation within the Upper Nivelle, while the number of redds is not increasing. Quality $^{\text{and}}/_{\text{or}}$ availability of breeding sites could, then, diminish year after years.

The upstream migration behaviour (Finstad *et al.* 2005) leads to a higher number of potential breeders in the Upper Nivelle and Lurgorrieta. Yet, the stock was higher in the Lurgorrieta than in the Upper Nivelle, whereas the Upper Nivelle has the higher area suitable for breeding (h). Breeders are also constrained by an upstream dam in the Lurgorrieta. Breeders seem, thus, to distribute their nests between all suitable habitats in the Lurgorrieta leading to a weak aggregation in this zone. In the Upper Nivelle, the dam constraint could interplay with a more heterogeneous quality of habitats. In their study, Tentelier & Piou (2011) found that the upstream dam in the Nivelle constrained nest location. In the Upper Nivelle, dominant potential breeders could use the best breeding sites, whereas subordinate should aggregate their nests in other sites.

Carrying capacity tended to vary among river zones when accounting for aggregation. In the null model the carrying capacity of the three zones were similar at around 0.11 juvenile.m^{-2}. Carrying capacity changed to 0.51 juvenile.m^{-2} for the Lurgorrieta when accounting for aggregation. The highest carrying capacity for the Lurgorrieta was surprising because Dumas & Marty (2006) found that redds were more clogged in the Lurgorrieta than in other river zones and redd clogging diminishes egg survival. In addition, Brun (2011, chapter VI) found a similar carrying capacity between the Lurgorrieta and the Lower Nivelle, whereas Dumas & Haury (1995) highlighted the lowest water quality in these zones compared to the Upper Nivelle. The high value for the Lurgorrieta may be explained by the negative trend between aggregation and average recruitment found for this zone. In addition, the density plot indicates that the parameter estimation was more difficult for the Lurgorrieta. Carrying capacity of the UN and

the LN were must lower than the values estimated by Brun (2011, chapter VI). I estimated it at 0.11 juvenile.m^{-2} compared to the 0.28 juvenile.m^{-2} of Brun (2011, chapter VI) for the Upper Nivelle. For the Lower Nivelle, I estimated it at 0.06 juvenile.m^{-2} compared to the 0.14 juvenile.m^{-2} of Brun (2011, chapter VI). The differences between the values estimated by Brun (2011, chapter VI) and my values may be explained by the different models used, the number of new years accounted in my work, but also the accounting for aggregation. Nonetheless, my values appeared as relevant when looking the stock-recruitment curves (Figure. 3.7 and Figure. 3.8).

A strong density-dependent mortality characterises the Nivelle. The low values of carrying capacity when accounting or not aggregation indicate a low survival of juveniles and an already strong density-dependent mortality, especially since survival of salmon decreases at high densities (Einum & Nislow 2005). The slopes at origin were steeper than the values estimated by Brun (2011, chapter VI) indicating a better survival at low stocks. Yet, I estimated lower threshold biomasses meaning a density-mortality occurring at lowest densities. My work accounted for more years than the work of Brun (2011, chapter VI) and recent years exhibited low stocks what can explain the difference between Brun's results and mine. In addition, threshold biomasses (K) were below the lowest stock observed for each zone with or without accounting for aggregation.

Spatial aggregation may compensate the density-dependent mortality. In the Lower Nivelle, spatial aggregation increases the average recruitment. Same effect was not found for the two other zones. In the Lower Nivelle, high values of aggregation was found for low numbers of redds (Figure. 3.2), a pattern less pronounced in the two other zones. Aggregation of a few numbers of redds in best spawning sites without affecting the density-dependent mortality may explain the positive impact of aggregation on the average recruitment. Accounting for aggregation tended to increase the survival at low densities (a), agreeing with a potential aggregation in best habitats. In this case, the observed high aggregation for low numbers of redds can be explained either by the dominance of some females to secure the best sites (Hendry *et al.* 2001), the availability of sites which are not available during other years, or because some sites were available only for large females (Gauthey *et al.* 2017). Atlantic salmon demonstrate ability to discriminate their kin (Brown & Brown 1992, Moore *et al.* 1994), and preferences for kin related (Brown & Brown 1992), something diminishing their aggressiveness and

increasing their weight gain (Brown & Brown 1996). Yet, Griffiths & Armstrong (2001) found an advantage to avoid kin in winter and an advantage to increase genetic diversity. Aggregate in the Lower Nivelle could increase the number of potential mates searching for females in the Lower Nivelle that raises the genetic diversity within each egg batch through multiple paternity. It could be more difficult for females to have partners in the Lower Nivelle because less potential breeders remain in the Lower Nivelle since the Upper Nivelle and the Lurgorrieta are available.

Spatial aggregation decreased recruitment variability. Recruitment variability for a considered level of stock may arise from redd scouring, overdigging, or redd emerging for example which impact egg survival (Gauthey *et al.* 2017, Lapointe *et al.* 2000). Although only trends existed for the Lower Nivelle and the Upper Nivelle, the Lurgorrieta exhibited a significant effect. Aggregate in safer breeding habitats should be advantageous for salmon, especially in Lurgorrieta which is an upstream tributary. Perturbations, occurring after fry emergence and until recruitment assessment in September, may also play an influential role. For example, Jensen & Johnsen (1999) found that floods increased the mortality of salmon alevins. The effect of spatial aggregation on recruitment variability was less pronounced in the UN indicating either that this zone seems the less impacted by environmental perturbations, or that all salmon in the UN spawn in safe sites.

Spatial aggregation of nests varied in the three zones of the Nivelle potentially through variations in habitat quality. The temporal effect in habitat quality seems also coming into play to explain yearly increase in aggregation within the Upper Nivelle. Considering spatial aggregation did not improve models, but the expanding number of parameters is not negligible. Nonetheless, spatial aggregation diminished recruitment variability within the Lurgorrieta and improved recruitment in the Lower Nivelle. The Upper Nivelle seemed less subject to effects of spatial aggregation and exhibited steadier recruitment. The Upper Nivelle also displayed the highest stocks but not the highest recruitments. The Upper Nivelle also displayed the highest spatial aggregation while the suitable area to breed is the highest one. The Upper Nivelle also exhibited low carrying capacity. The Upper Nivelle is probably the zone where management actions should be favoured such as the enhancement of habitat quality or the opening of the upstream dam. Finally, the current chapter highlights differences between river zones

and stresses the need to deeply investigate the spatial aggregation of nests, its effects on local recruitment. Processes acting on females' choices of breeding habitats should also be deeply investigated to explain differences of spatial aggregation of nests between river zones.

HIGHLIGHTS OF CHAPTER 3

- Spatial aggregation of nests varies between the three zones of the Nivelle: Lower Nivelle (LN), Upper Nivelle (UN), and Lurgorrieta (main tributary).
- Spatial aggregation decreased recruitment variability in the Lurgorrieta, while trends were found in the LN and the UN.
- The Lurgorrieta exhibited the highest carrying capacity despite the potential lowest habitat quality...
- ...and the Upper Nivelle exhibited a low carrying whereas the available suitable are was the highest one in this zone.
- The higher spatial aggregation of nests in the UN and its low carrying capacity stress the need to improve habitat quality in the UN...
- ...and to identify mechanisms leading to spatial aggregation.

Discussion of Part II

The current part aimed to assess the spatial aggregation of nests and to test its potential effect on the population recruitment. Chapter 1 (page 57) highlighted that spatial aggregation provides valuable information about the spatial distribution of nests. Chapter 1 emphasized that patchiness was the most appropriate measure of aggregation to test the effect of spatial distribution of nests on population regulation. Chapter 2 (page 65) showed that at the population scale, average recruitment was not linked to spatial aggregation but it was less variable as aggregation increased. In addition, this chapter highlighted the improvement of stock-recruitment models when accounting for aggregation. The last chapter (chapter 3, page 101) applied the same analysis at a more local scale: the river zone. Consequences of spatial aggregation on the recruitment varied in intensity between zones and differences in spatial aggregation exist between river zones. Finally, the three chapters indicated that i) spatial aggregation of nests is an important population characteristic which ii) affects population and river zones' recruitment, and iii) interplays with habitat quality, environmental perturbations, and constraints of dams.

SPATIAL AGGREGATION AS AN INDICATOR OF SPATIAL DISTRIBUTION

Spatial aggregation and not density. Chapter 1 (page 57) showed the inability of the mean and the variance of density to discriminate well spatial distribution of nests. The mean or the variance of density is, by definition, affected by the number of nests. At the opposite, chapter 2 (page 65) provided new insight by indicating that patchiness is more independent on the number of nests and therefore on the number of breeders (i.e. a negative trend was found). Using spatial aggregation prevented a skew of spatial distribution measure caused by an increase in the number of breeders. Like the work of Lloyd (1967), the current part advocated emphasising the mean number of neighbours

through an index of spatial aggregation rather than mean density when looking to spatial distribution effects.

Aggregation of nests arises from the habitat choice of salmon females. Chapter 2 (page 65) suggested that females tend to preferentially aggregate in best breeding sites and to repel other females into low-quality sites (Falcy 2015). Chapter 3 (page 101) supported such assumptions but also gone further by suggesting that such interactions between females may vary between river zones. For instance, spatial aggregation within each river zone was stronger in the Upper Nivelle, the Nivelle zone with the highest number of available sites and the highest habitat quality (Dumas & Haury 1995, Dumas & Marty 2006). It appears that females have to face other factors that the unique presence of other females and the availability of breeding sites when choosing them.

Environmental factors cause spatial aggregation to be variable. Spatial aggregation varied between years either at population scale (chapter 2, page 65) or at the river zone scale (chapter 3, page 101). Yearly variations in nest placements have already been observed in salmon (Parry *et al.* 2018, Soulsby *et al.* 2012). Environmental factors such as floods, water levels, or available suitable breeding habitats likely constrain females' choices generating variations in spatial aggregation. For example, Parry *et al.* (2018) found that flow levels condition the accessibility to some breeding habitats. The high flow levels during the last breeding season in the Nivelle (2017-2018) forced some females to spawn in unsuitable sites (Figure. II.iii). Causes of nest spatial aggregation should be studied especially in the context of habitat fragmentation or climate change since spatial aggregation of nests affects population dynamics. Climate change could increase the magnitude of floods in autumn and winter and diminish dry weather flows for such latitudes (IPCC 2014). Environmental perturbations could thus more influence the availability of breeding sites leading to a variable competition for breeding sites and aggregation of nests. In this way, females abilities to assess environmental stability could be a factor promoting spatial aggregation in safest and more stable sites (Doligez *et al.* 2003).

(a) A de-watered redd where only the depression is still under water.

(b) A redd in the Nivelle where the dome is beginning to emerge. Eggs are buried under this dome.

Figure. II.iii: Photo of a de-watered redd (a) and a redd (b) in the Nivelle during the breeding season 2017-2018. These two redds were dug during a flood forcing females to spawn near the river banks. ©C.Bouchard

AGGREGATION MODULATES POPULATION REGULATION THROUGH ENVIRONMENTAL PREDICTABILITY

The best fit of a Beverton-Holt model rather than a Ricker one (chapter2 page 65 and chapter 3 page 101) meant that density-compensation (i.e. density-dependent mortality at high stocks) is strong but not variable whatever the spatial scales (population or river zones). Ricker's curve images a high survival at low stock, something less marked for a Beverton-Holt's curve (box Tools II.i). Stock levels exceeded the carrying capacity in all models fitted to the population or to each zone. These findings agree with those of previous stock-recruitment models fitted to the Nivelle population (Brun 2011). Altogether, results indicate that density-compensation was seemingly not the predominant cause of recruitment variations at the juveniles stages in the Nivelle. Variations in habitat quality (quantity of resources **and** environmental stability), availability of suitable breeding sites, and distribution of nests within them seem important reasons causing fluctuations in recruitment. Raise the availability of breeding sites and enhance their environmental stability in order to diminish spatial aggregation between the best habitats could be a suitable management action.

Environmental stochasticity as a major regulation for the Nivelle population. In their study, Honkanen *et al.* (2018) suggested that environmental stochasticity overrides density-dependence in Atlantic salmon recruitment. Here, environmental stochasticity pooled together impacts of environmental perturbations against eggs such as nest scouring (Gau-

they *et al.* 2017, Lapointe *et al.* 2000, Steen & Quinn 1999), and against juveniles such as variability in habitat quality due to floods, for instance (Gauthey *et al.* 2017, Jensen & Johnsen 1999). The period after emergence is critical for salmon juveniles (Einum & Fleming 2000, Nislow *et al.* 2004) because they tend to stay near their nests (Close & Anderson 1992, Garcia de Leaniz *et al.* 2000, Gustafson-Greenwood & Moring 1990) and are unable to hold station during high flows (Aas *et al.* 2011). Hence, environmental stochasticity may considerably alter the population recruitment.

Spatial aggregation of nests interplays with environmental stochasticity. Although generating density-dependent mortality, spatial aggregation of nests cannot exacerbate density-compensation because stocks overwhelmed the carrying capacity in all years. Spatial aggregation of nests diminished recruitment variability at the population scale. The Lurgorrieta displayed the latter effect, whereas the Lower and the Upper Nivelle exhibited only a trend. The recruitment in the Upper Nivelle was also the least variable. The river zones seem, thus, interplay as a metapopulation stabilising recruitment in the Upper Nivelle and at the population level (Carlson & Satterthwaite 2011, Schindler *et al.* 2015). The Upper Nivelle exhibits the highest habitat quality (Dumas & Haury 1995, Dumas & Marty 2006), and the Lurgorrieta flows into it (Figure. I.viii, page 26). At the population level, redds aggregating within the Upper Nivelle as aggregation increased is beneficial for the population recruitment. When a perturbation affects nests aggregated in the Upper Nivelle, the recruitment of the UN can be compensated by juveniles of the Lurgorrieta. Terui *et al.* (2018) observed that branching complexity has a stabilising effect (i.e. here the Lurgorrieta is branched to the Nivelle River in the Upper Nivelle). The Nivelle population seems thus to cope with environmental perturbations occurring at the river zone scale depending on where nests are aggregated. Hence, spatial aggregation of nests seems to interplay with environmental stochasticity when influencing recruitment (Figure. II.iv).

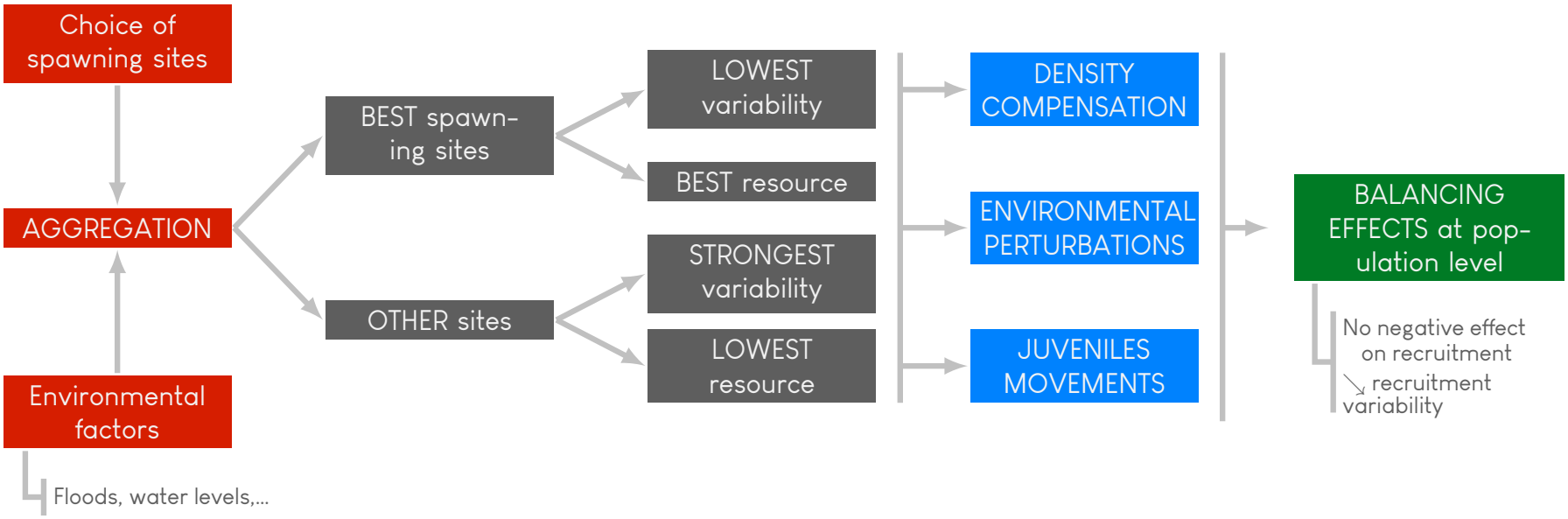

Figure. II.iv: Effects of spatial aggregation of nests on recruitment at the population level. Spatial aggregation is caused by the habitat selection of females interplaying with environmental factors. Spatial aggregation of nests involves density-compensation, but also differences in occurrence probability of environmental perturbations depending where nests are aggregated. Yet, spatial aggregation in different zones enables dispersal of juveniles which may mitigate losses due to environmental perturbations or density compensation. Altogether this suggests potential balancing effects stabilising the recruitment at the population level.

CONCLUSION

Implications for the Nivelle population. Results of the current part vindicate to better account for spatial aggregation of nests when investigating population recruitment at the population level, but also at the river zone one. Indeed, spatial aggregation seemed to interplay with density-dependent processes (e.g. density-compensation) and density-independent ones (e.g. environmental perturbations) to stabilise the population recruitment. The latter impact depended on the level of aggregation, as well as, the location of aggregates (Figure. II.iv). The presence of impassable dams constrains anadromous movements (Tentelier *et al.* 2016), and nest placement (Tentelier & Piou 2011), favouring spatial aggregation of nests. Equipping dams with fish pass could enhance the habitat available for females and, *in fine* the populations dynamic. For example, Forget *et al.* (2018) predicted a threefold extension of the breeding area after dam removal in the Sélune River (France) leading to a possible expansion of the salmon population. The positive impact of aggregation on the recruitment stability was less pronounced in the Upper Nivelle than in the Lurgorrieta. A management action could create new suitable breeding sites in the Upper Nivelle to reduce aggregation in the Upper Nivelle which appeared less beneficial.

Opening. The concept of mean crowding and the impact of neighbours should be prioritised when investigating density-dependent processes as proved in the actual part (Wade *et al.* 2018). More generally, my work raises the question of the mechanisms linking spatial aggregation of nests and recruitment at multiple scales: from nests to populations. Processes driving breeding habitat choices by females could also be studied to identify why females aggregate. The assessment of environmental stability by females could be a potential workstream. How females abilities to assess environmental stability drive their reproductive success and therefore recruitment could be investigated. For example, Gauthey *et al.* (2017) suggested that tactics enabling to reduce shear stress and nest scouring should be favoured in brown trout, *Salmo trutta*. Finally, how aggregation of several females in best sites which forces others to aggregate in lower suitable sites affects the reproductive success of females could be investigated. Tentelier *et al.* (2016) found that the reproductive success of females increased with habitat quality in their home range which itself decreased with their arrival order. It could be interesting to investigate how neighbourhood affects the reproductive success of individuals because spatial aggregation also involved neighbours.

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Bibliography

Aas, O., Balshine, S., Klemesten & Skurdal (eds.) (2011) *Atlantic salmon ecology*. Blackwell Pub, Chichester ; Ames, Iowa.

Adkison, M.D., Ward, M.B. & Quinn, T.P. (2014) Nest site preference and intrasexual competition in female sockeye salmon, *Oncorhynchus nerka*. *Environmental Biology of Fishes* **97**, 385–399.

Allan, J.D. (2004) Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annual Review of Ecology, Evolution, and Systematics* **35**, 257–284.

Almada, V.C., Gonçlalves, E.J., Santos, A.J. & Baptista, C. (1994) Breeding ecology and nest aggregations in a population of *Salaria pavo* (Pisces: Blenniidae) in an area where nest sites are very scarce. *Journal of Fish Biology* **45**, 819–830.

An, K.G., Park, S.S. & Shin, J.Y. (2002) An evaluation of a river health using the index of biological integrity along with relations to chemical and habitat conditions. *Environment International* **28**, 411–420.

Armstrong, J.D. & Nislow, K.H. (2006) Critical habitat during the transition from maternal provisioning in freshwater fish, with emphasis on Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Journal of Zoology* **269**, 403–413.

Bacles, C.F.E., Bouchard, C., Lange, F., Manicki, A., Tentelier, C. & Lepais, O. (2018) Estimating the effective number of breeders from single parr samples for conservation monitoring of wild populations of Atlantic salmon *Salmo salar*. *Journal of Fish Biology* **92**, 699–726.

Beall, E. (1994) Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. *ICES Journal of Marine Science* **51**, 1–9.

Beverton, R.J.H. & Holt, S.J. (1957) *On the dynamics of exploited fish populations*, vol. 19 of *2*. Springer Netherlands, Dordrecht.

Boulinier, T. & Danchin, E. (1997) The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology* **11**, 505–517.

Broly, P., Mullier, R., Deneubourg, J.L. & Devigne, C. (2012) Aggregation in woodlice: social interaction and density effects. *ZooKeys* **176**, 133–144.

Brown, G.E. & Brown, J.A. (1992) Do rainbow trout and Atlantic salmon discriminate kin? *Canadian Journal of Zoology* **70**, 1636–1640.

Brown, G.E. & Brown, J.A. (1996) Does kin-biased territorial behavior increase kin-biased foraging in juvenile salmonids? *Behavioral Ecology* **7**, 24–29.

Brun, M. (2011) *Aide à la décision pour la conservation des populations de saumon atlantique (Salmo salar L.)*. Ph.D. thesis, Pau.

Brun, M., Abraham, C., Jarry, M., Dumas, J., Lange, F. & Prévost, E. (2011) Estimating an homogeneous series of a population abundance indicator despite changes in data collection procedure: A hierarchical Bayesian modelling approach. *Ecological Modelling* **222**, 1069–1079.

Carlson, S.M. & Satterthwaite, W.H. (2011) Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 1579–1589.

Carpenter, B., Gelman, A., Hoffman, M., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M.A., Guo, J., Li, P. & Riddell, A. (2016) Stan: A probabilistic programming language. *Journal of statistical software* .

Chesson, P. & Neuhauser, C. (2002) Intraspecific aggregation and species coexistence. *Trends in ecology & evolution* **17**, 210–211.

Clark, P.J. & Evans, F.C. (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* **35**, 445–453.

Close, T.L. & Anderson, C.S. (1992) Dispersal, density-dependent growth, and survival of stocked steelhead Fry in lake superior tributaries. *North American Journal of Fisheries Management* **12**, 728–735.

Clotfelter, E.D. & Yasukawa, K. (1999) The effect of aggregated nesting on red-winged blackbird nest success and brood parasitism by brown-headed cowbirds. *The Condor* **101**, 729–736.

Crisp, D.T. (1995) Dispersal and growth rate of O-group salmon (*Salmo salar* L.) from point-stocking together with some information from scatter-stocking. *Ecology of Freshwater Fish* **4**, 1–8.

Cushing, D.H. (1973) Dependence of recruitment on parent stock. *Journal of the Fisheries Research Board of Canada* **30**, 1965–1976.

Danchin, E. & Wagner, R.H. (1997) The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution* **12**, 342–347.

Dauphin, G., Prevost, E., Adams, C.E. & Boylan, P. (2009) A Bayesian approach to estimating Atlantic salmon fry densities using a rapid sampling technique. *Fisheries Management and Ecology* **16**, 399–408.

de Gaudemar, B., Schroder, S.L. & Beall, E.P. (2000) Nest placement and egg distribution in Atlantic salmon redds. *Environmental Biology of Fishes* **57**, 37–47.

Dobson, A.P. & Lees, A.M. (1989) The population dynamics and conservation of primate populations. *Conservation Biology* **3**, 362–380.

Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* **66**, 973–988.

Doligez, B., Pärt, T., Danchin, E., Clobert, J. & Gustafsson, L. (2004) Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. *Journal of Animal Ecology* **73**, 75–87.

Du, W.g. & Ji, X. (2006) Effects of constant and fluctuating temperatures on egg survival and hatchling traits in the northern grass lizard (*Takydromus septentrionalis*, Lacertidae). *Journal of Experimental Zoology Part A: Comparative Experimental Biology* **305A**, 47–54.

Dumas, J. & Haury, J. (1995) Une rivière du Piémont pyrénéen: la Nivelle (Pays basque). *Acta Biologica Montana* **11**, 113–146.

Dumas, J. & Marty, S. (2006) A new method to evaluate egg-to-fry survival in salmonids, trials with Atlantic salmon. *Journal of Fish Biology* **68**, 284–304.

Dumas, J. & Prouzet, P. (2003) Variability of demographic parameters and population dynamics of Atlantic salmon (*Salmo salar* L.) in a south-west French river. *ICES Journal of Marine Science* **60**, 356–370.

Dunham, J., Rieman, B. & Davis, K. (2001) Sources and magnitude of sampling error in redd counts for bull trout. *North American Journal of Fisheries Management* **21**, 343–352.

Durant, J., Hjermann, D., Ottersen, G. & Stenseth, N. (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* **33**, 271–283.

Einum, S. & Fleming, I.A. (2000) Selection against late emergence and small offspring in atlantic salmon (*Salmo salar*). *Evolution* **54**, 628–639.

Einum, S. & Nislow, K.H. (2005) Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. *Oecologia* **143**, 203–210.

Einum, S., Nislow, K.H., Mckelvey, S. & Armstrong, J.D. (2008) Nest distribution shaping within-stream variation in Atlantic salmon juvenile abundance and competition over small spatial scales. *Journal of Animal Ecology* **77**, 167–172.

Einum, S., Nislow, K.H., Reynolds, J.D. & Sutherland, W.J. (2007) Predicting population responses to restoration of breeding habitat in Atlantic salmon: Effects of breeding habitat restoration. *Journal of Applied Ecology* **45**, 930–938.

Einum, S., Sundt-Hansen, L. & H Nislow, K. (2006) The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos* **113**, 489–496.

Elliott, K.H., Elliott, J.E., Wilson, L.K., Jones, I. & Stenerson, K. (2011) Density-dependence in the survival and reproduction of Bald Eagles: Linkages to Chum Salmon. *The Journal of Wildlife Management* **75**, 1688–1699.

Engen, S., Bakke, O. & Islam, A. (1998) Demographic and environmental stochasticity-concepts and definitions. *Biometrics* **54**, 840.

Evans, J.C., Votier, S.C. & Dall, S.R.X. (2016) Information use in colonial living: Information use in colonial living. *Biological Reviews* **91**, 658–672.

Falcy, M.R. (2015) Density-dependent habitat selection of spawning Chinook salmon: broad-scale evidence and implications. *Journal of Animal Ecology* **84**, 545–553.

Finstad, A.G., Einum, S., Ugedal, O. & Forseth, T. (2009) Spatial distribution of limited resources and local density regulation in juvenile Atlantic salmon. *Journal of Animal Ecology* **78**, 226–235.

Finstad, A.G., Okland, F., Thorstad, E.B. & Heggberget, T.G. (2005) Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology* **67**, 919–930.

Foldvik, A., Finstad, A.G. & Einum, S. (2010) Relating juvenile spatial distribution to breeding patterns in anadromous salmonid populations. *Journal of Animal Ecology* **79**, 501–509.

Forget, G., Baglinière, J.L., Marchand, F., Richard, A. & Nevoux, M. (2018) A new method to estimate habitat potential for Atlantic salmon (*Salmo salar*): predicting the influence of dam removal on the Sélune River (France) as a case study. *ICES Journal of Marine Science* .

Forster, C.A. (1990) Evidence for juvenile groups in the ornithopod dinosaur *Tenontosaurus tilletti* Ostrom. *Journal of Paleontology* **64**, 164–165.

Fretwell, S.D. & Lucas, H.L.J. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16–36.

Garcia de Leaniz, C., Fraser, N. & Huntingford, F.A. (2000) Variability in performance in wild Atlantic salmon, *Salmo salar* L., fry from a single redd. *Fisheries Management and Ecology* **7**, 489–502.

Gauthey, Z., Lang, M., Elosegi, A., Tentelier, C., Rives, J. & Labonne, J. (2017) Brown trout spawning habitat selection and its effects on egg survival. *Ecology of Freshwater Fish* **26**, 133–140.

Geist, D.R. & Dauble, D.D. (1998) Redd site selection and spawning habitat use by fall chinook salmon: the importance of geomorphic features in large rivers. *Environmental Management* **22**, 655–669.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A. & Rubin, D.B. (eds.) (2014) *Bayesian data analysis*. Texts in Statistical Science Series, CRC Press/Chapman & Hall, Boca Raton, Florida, USA., 3. ed edn.

Gelman, A., Jakulin, A., Pittau, M.G. & Su, Y.S. (2008) A weakly informative default prior distribution for logistic and other regression models. *The Annals of Applied Statistics* **2**, 1360–1383.

Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science* **7**, 457–472.

Gharrett, A.J., Joyce, J. & Smoker, W.W. (2013) Fine-scale temporal adaptation within a salmonid population: mechanism and consequences. *Molecular Ecology* **22**, 4457–4469.

Gokhale, D.V. (1975) Indices and models for aggregation in spatial patterns. *A modern course on statistical distributions in scientific work*, NATO Advanced Study Institutes Series, pp. 343–353, Springer, Dordrecht.

Govoni, J.J. (2005) Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years. *Scientia Marina* **69**, 125–137.

Griffiths, S.W. & Armstrong, J.D. (2001) The benefits of genetic diversity outweigh those of kin association in a territorial animal. *Proceedings of the Royal Society of London B: Biological Sciences* **268**, 1293–1296.

Griffiths, S.W., Armstrong, J.D. & Metcalfe, N.B. (2003) The cost of aggregation: juvenile salmon avoid sharing winter refuges with siblings. *Behavioral Ecology* **14**, 602–606.

Gustafson-Greenwood, K.I. & Moring, J.R. (1990) Territory size and distribution of newly-emerged Atlantic salmon (*Salmo salar*). *Hydrobiologia* **206**, 125–131.

Harding, J.S., Young, R.G., Hayes, J.W., Shearer, K.A. & Stark, J.D. (1999) Changes in agricultural intensity and river health along a river continuum. *Freshwater Biology* **42**, 345–357.

Hendry, A.P., Berg, O.K. & Quinn, T.P. (2001) Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores). *Oikos* **93**, 407–418.

Herrando-Pérez, S., Delean, S., Brook, B.W. & Bradshaw, C.J.A. (2012) Density dependence: an ecological Tower of Babel. *Oecologia* **170**, 585–603.

Hoare, D., Couzin, I., Godin, J.G. & Krause, J. (2004) Context-dependent group size choice in fish. *Animal Behaviour* **67**, 155–164.

Honkanen, H.M., Boylan, P., Dodd, J.A. & Adams, C.E. (2018) Life stage-specific, stochastic environmental effects overlay density dependence in an Atlantic salmon population. *Ecology of Freshwater Fish* .

Iles, T.C. (1994) A review of stock-recruitment relationships with reference to flatfish populations. *Netherlands Journal of Sea Research* **32**, 399–420.

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Tech. rep., IPCC, Geneva, Switzerland.

Ives, A.R. (1988) Aggregation and the coexistence of competitors. *Annales Zoologici Fennici* **25**, 75–88.

Jensen, A.J. & Johnsen, B.O. (1999) The functional relationship between peak spring floods and survival and growth of juvenile Atlantic Salmon (*Salmo salar*) and Brown Trout (*Salmo trutta*). *Functional Ecology* **13**, 778–785.

Jonsson, N., Jonsson, B. & Hansen, L.P. (1998) The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon (*Salmo salar*). *Journal of Animal Ecology* **67**, 751–762.

Kallimanis, A.S., Kunin, W.E., Halley, J.M. & Sgardelis, S.P. (2005) Metapopulation extinction risk under spatially autocorrelated disturbance. *Conservation Biology* **19**, 534–546.

Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* pp. 911–927.

Lapointe, M., Eaton, B., Driscoll, S. & Latulippe, C. (2000) Modelling the probability of salmonid egg pocket scour due to floods. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 1120–1130.

Lara-Romero, C., García-Fernández, A., Robledo-Arnuncio, J.J., Roumet, M., Morente-López, J., López-Gil, A. & Iriondo, J.M. (2016) Individual spatial aggregation correlates with between-population variation in fine-scale genetic structure of *Silene ciliata* (Caryophyllaceae). *Heredity* **116**, 417.

Larned, S.T., Schmidt, J., Datry, T., Konrad, C.P., Dumas, J.K. & Diettrich, J.C. (2011) Longitudinal river ecohydrology: flow variation down the lengths of alluvial rivers. *Ecohydrology* **4**, 532–548.

Lindenmayer, D.B., Cunningham, R.B. & Donnelly, C.F. (1997) Decay and collapse of trees with hollows in eastern Australian forests: impacts on arboreal marsupials. *Ecological Applications* **7**, 625–641.

Lloyd, M. (1967) Mean crowding. *Journal of Animal Ecology* **36**, 1–30.

López-Sepulcre, A., Kokko, H. & Norris, K. (2010) Evolutionary conservation advice for despotic populations: habitat heterogeneity favours conflict and reduces productivity in Seychelles magpie robins. *Proceedings of the Royal Society of London B: Biological Sciences* **277**, 3477–3482.

Louhi, P., Mäki-Petäys, A. & Erkinaro, J. (2008) Spawning habitat of Atlantic salmon and brown trout: general criteria and intragravel factors. *River Research and Applications* **24**, 330–339.

Macpherson, E. (1998) Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. *Journal of Experimental Marine Biology and Ecology* **220**, 127–150.

Malcolm, I.A., Soulsby, C., Youngson, A.F., Hannah, D.M., McLaren, I.S. & Thorne, A. (2004) Hydrological influences on hyporheic water quality: implications for salmon egg survival. *Hydrological Processes* **18**, 1543–1560.

Marchand, F., Beaulaton, L., Prévost, E. & Azam, D. (2017) Abundance indices and biological traits of juvenile salmon (*Salmo salar*) sampled in three rivers on the Atlantic and Channel coasts (France). *Biodiversity Data Journal* **5**, e15125.

Mathéron, G. (1981) La sélectivité des distributions. Tech. Rep. N-686, Ecole des mines de Paris, Centre de géostatistique, Fontainebleau.

McPeek, M.A., Rodenhouse, N.L., Holmes, R.T. & Sherry, T.W. (2001) A general model of site-dependent population regulation: population-level regulation without individual-level interactions. *Oikos* **94**, 417–424.

Meixler, M.S., Bain, M.B. & Todd Walter, M. (2009) Predicting barrier passage and habitat suitability for migratory fish species. *Ecological Modelling* **220**, 2782–2791.

Michielsens, C.G. & McAllister, M.K. (2004) A Bayesian hierarchical analysis of stock recruit data: quantifying structural and parameter uncertainties. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 1032–1047.

Milner-Gulland, E.J., Bukreeva, O.M., Coulson, T., Lushchekina, A.A., Kholodova, M.V., Bekenov, A.B. & Grachev, I.A. (2003) Conservation: Reproductive collapse in saiga antelope harems. *Nature* **422**, 135.

Moir, H., Gibbins, C., Soulsby, C. & Webb, J. (2004) Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (*Salmo salar* L.). *Geomorphology* **60**, 21–35.

Moir, H.J., Gibbins, C.N., Soulsby, C. & Webb, J.H. (2006) Discharge and hydraulic interactions in contrasting channel morphologies and their influence on site utilization by spawning Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2567–2585.

Moir, H.J., Soulsby, C. & Youngson, A. (1998) Hydraulic and sedimentary characteristics of habitat utilized by Atlantic salmon for spawning in the Girnock Burn, Scotland. *Fisheries Management and Ecology* **5**, 241–254.

Moll, R.J., Killion, A.K., Montgomery, R.A., Tambling, C.J. & Hayward, M.W. (2016) Spatial patterns of African ungulate aggregation reveal complex but limited risk effects from reintroduced carnivores. *Ecology* **97**, 1123–1134.

Moore, A., Ives, M.J. & Kell, L.T. (1994) The role of urine in sibling recognition in Atlantic salmon *Salmo salar* (L.) parr. *Proc. R. Soc. Lond. B* **255**, 173–180.

Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia* **136**, 1–13.

Morris, W.F., Bloch, P.L., Hudgens, B.R., Moyle, L.C. & Stinchcombe, J.R. (2002) Population viability analysis in endangered species recovery plans: past use and future improvements. *Ecological Applications* **12**, 708–712.

Murdoch, W.W., Briggs, C.J., Nisbet, R.M., Gurney, W.S.C. & Stewart-Oaten, A. (1992) Aggregation and stability in metapopulation models. *The American Naturalist* **140**, 41–58.

Murrell, D., Purves, D. & Law, R. (2002) Intraspecific aggregation and species coexistence. *Trends in Ecology & Evolution* **17**, 211.

Neave, F. (1953) Principles affecting the size of pink and chum salmon populations in British Columbia. *Journal of the Fisheries Research Board of Canada* **9a**, 450–491.

Nislow, K.H., Einum, S. & Folt, C.L. (2004) Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon. *Journal of Fish Biology* **65**, 188–200.

Norris, K. (2004) Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology* **41**, 413–426.

Palm, D., Lindberg, M., Brännäs, E., Lundqvist, H., Östergren, J. & Carlsson, U. (2009) Influence of European sculpin, *Cottus gobio*, on Atlantic salmon *Salmo salar*, recruitment

and the effect of gravel size on egg predation – implications for spawning habitat restoration. *Fisheries Management and Ecology* **16**, 501–507.

Parry, E.S., Gregory, S.D., Lauridsen, R.B. & Griffiths, S.W. (2018) The effects of flow on Atlantic salmon (*Salmo salar*) redd distribution in a UK chalk stream between 1980 and 2015. *Ecology of Freshwater Fish* **27**, 128–137.

Pemberton, J.M. (2008) Wild pedigrees: the way forward. *Proceedings of the Royal Society of London B: Biological Sciences* **275**, 613–621.

Petitgas, P. (1998) Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves. *ICES Journal of Marine Science: Journal du Conseil* **55**, 443–453.

Prevost, E. (2003) Setting biological reference points for Atlantic salmon stocks: transfer of information from data-rich to sparse-data situations by Bayesian hierarchical modelling. *ICES Journal of Marine Science* **60**, 1177–1193.

Prévost, E. & Baglinière, J.L. (1995) Présentation et premiers éléments de mise au point d'une méthode simple d'évaluation du recrutement en juvéniles de Saumon Atlantique (*Salmo salar* L.) de l'année en eau courante. *Les recherches francaises en évaluation quantitative et modélisation des ressources et des systèmes halieutiques.*, vol. Actes du colloque, Rennes, du 29 juin au 1er juillet. ORSTOM, COLLOQUES et SEMINAIRES,, pp. 39–48, Gascuel, D., Durand, J.L., Fonteneau, A. (Eds.), Paris.

Prévost, E., Baglinière, J.L., Maisse, G. & Nihouarn, A. (1996) First elements of an Atlantic salmon (*Salmo salar*) stock/recruitment relationship in France. *Cybium* **20**, 7–26.

Prévost, E. & Chaput, G. (2001) *Stock, recruitment and reference points: assessment and management of Atlantic salmon.* INRA Editions, Paris, France.

Rejmánek, M. (2002) Intraspecific aggregation and species coexistence. *Trends in Ecology & Evolution* **17**, 209–210.

Ricker, W.E. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada* **11**, 559–623.

Rivot, E., Prévost, E., Parent, E. & Baglinière, J. (2004) A Bayesian state-space modelling framework for fitting a salmon stage-structured population dynamic model to multiple time series of field data. *Ecological Modelling* **179**, 463–485.

Sæther, B.E. (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology & Evolution* **12**, 143–149.

Schindler, D.E., Armstrong, J.B. & Reed, T.E. (2015) The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment* **13**, 257–263.

Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. (2002) Ecological and evolutionary traps. *Trends in Ecology & Evolution* **17**, 474–480.

Sergio, F., Pedrini, P. & Marchesi, L. (2003) Adaptive selection of foraging and nesting habitat by black kites (*Milvus migrans*) and its implications for conservation: a multi-scale approach. *Biological Conservation* **112**, 351–362.

Servanty, S. & Prevost, E. (2016) Mise à jour et standardisation des séries chronologiques d'abondance du saumon atlantique sur les cours d'eau de l'ORE DiaPFC et la Bresle. Rapport final Fiche action ONEMA – INRA 2013-2015 (action num 35), INRA - Pôle Gest'Aqua, Saint-Pée sur Nivelle, Pyrénées Atlantique, France.

Shepherd, J.G. (1982) A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *Journal du Conseil* **40**, 67–75.

Simon, C., Karban, R. & Lloyd, M. (1981) Patchiness, Density, and Aggregative Behavior in Sympatric Allochronic Populations of 17-Year Cicadas. *Ecology* **62**, 1525–1535.

Soulsby, C., Grant, J., Gibbins, C. & Malcolm, I.A. (2012) Spatial and temporal variability of Atlantic salmon (*Salmo salar* L.) spawning activity in braided river channels: a preliminary assessment. *Aquatic Sciences* **74**, 571–586.

Stan Development Team (2017) RStan: the R interface to Stan .

Steen, R.P. & Quinn, T.P. (1999) Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. *Canadian Journal of Zoology* **77**, 836–841.

Steingrimsson, S.O. & Grant, J.W.A. (1999) Allometry of territory size and metabolic rate as predictors of self-thinning in young-of-the-year Atlantic salmon. *Journal of Animal Ecology* **68**, 17–26.

Subbey, S., Devine, J.A., Schaarschmidt, U. & Nash, R.D.M. (2014) Modelling and forecasting stock-recruitment: current and future perspectives. *ICES Journal of Marine Science* **71**, 2307–2322.

Sydeman, W.J. & Allen, S.G. (1999) Pinniped population dynamics in central California : correlations with sea surface temperature and upwelling indices. *Marine Mammal Science* **15**, 446–461.

Tentelier, C., Larranaga, N., Lepais, O., Manicki, A., Rives, J. & Lange, F. (2016) Space use and its effects on reproductive success of anadromous Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 1461–1471.

Tentelier, C. & Piou, C. (2011) Obstacles to migration constrain nest distribution of Atlantic salmon. *Ecology of Freshwater Fish* **20**, 400–408.

Terui, A., Ishiyama, N., Urabe, H., Ono, S., Finlay, J.C. & Nakamura, F. (2018) Metapopulation stability in branching river networks. *Proceedings of the National Academy of Sciences* p. 201800060.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology* **75**, 2–16.

Tregenza, T. (1995) Building on the Ideal Free Distribution. *Advances in Ecological Research* **26**, 253–307.

Vehtari, A., Gelman, A. & Gabry, J. (2017) Practical bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* **27**, 1413–1432.

Wade, M.J., Fitzpatrick, C.L. & Lively, C.M. (2018) 50-year anniversary of Lloyd's "mean crowding": Ideas on patchy distributions. *Journal of Animal Ecology* **87**, 1221–1226.

Wagner, R.H. & Danchin, E. (2003) Conspecific copying: a general mechanism of social aggregation. *Animal Behaviour* **65**, 405–408.

Wang, Y. & Liu, Q. (2006) Comparison of Akaike information criterion (AIC) and Bayesian information criterion (BIC) in selection of stock–recruitment relationships. *Fisheries Research* **77**, 220–225.

Ward, A.J.W. & Hart, P.J.B. (2003) The effects of kin and familiarity on interactions between fish. *Fish and Fisheries* **4**, 348–358.

Weldon, A.J. & Haddad, N.M. (2005) The effects of patch shape on indigo buntings: evidence for an ecological trap. *Ecology* **86**, 1422–1431.

Winandy, L., Legrand, P. & Denoël, M. (2017) Habitat selection and reproduction of newts in networks of fish and fishless aquatic patches. *Animal Behaviour* **123**, 107–115.

Wong, M.Y.L., Munday, P.L., Buston, P.M. & Jones, G.P. (2007) Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish. *Behavioral Ecology* **19**, 353–361.

Young, L.J. & Young, J.H. (1998) Aggregation and spatial correlation. *Statistical Ecology*, pp. 215–271, Springer, Boston, MA.

PART III

Consequences of the spatial use of potential breeders on sexual selection and mating system

Introduction of Part III

Breeding in specific environmental conditions leads to habitat choices. Individuals select their breeding habitats according to the availability and quality of habitats. The main theories about the distribution of individuals among breeding sites remain the Ideal Free Distribution of Fretwell & Lucas (1969) expressed in a breeding context (Parker 1970; 1974), and the Ideal Despotic Distribution (Andren 1990, Calsbeek & Sinervo 2002). Individuals usually chose the best breeding site that they can select, generating costs of aggregation (Doligez *et al.* 2003). The preceding part examined the effects of the spatial distribution of potential breeders on population dynamics. More specifically, Part II (page 49) emphasised that the spatial aggregation of nests, resulting from the spatial distribution of females and their habitat choices, reduces the variability of recruitment. The spatial distribution of potential breeders also shapes encounters between potential breeders (see Box Glossary III.i).

Spatial distribution and movements of potential breeders may influence their possibility to mate. In systems where sexual reproduction occurs, the fertilisation of gametes with low mobility (e.g. internal fertilisation, immobile eggs, or eggs settling to the bottom) requires i) an encounter between potential sexual partners and that ii) these two partners access each other (Jones 2009, Kokko & Rankin 2006, Kuijper *et al.* 2012). Sexual selection arises when the reproductive success varies among phenotypes or the phenotypic trait value, which is inheritable (Kuijper *et al.* 2012). Such selection acts, thus, on the processes influencing the encounters and accesses potential mates (see Box Glossary III.i), namely the pre-copulatory competition. For instance, several males may compete to have access to the same female as in Birds-of-paradise (Kirkpatrick & Ryan 1991). The pre-copulatory competition involves either direct interactions (Hunt *et al.* 2009, Jones 2009, Kokko & Rankin 2006, Kuijper *et al.* 2012) or indirect ones through

the mate choice of individuals of the other sex (Andersson & Simmons 2006, Hunt *et al.* 2009, Kokko & Rankin 2006). In polygynous species, sexual selection may also realise through post-copulatory competition which happened when several individuals mate with the same individual (Kuijper *et al.* 2012). All of these processes — mate choice, direct interactions, post-copulatory competition — have usually a **density-dependent** component and, above all, are **relative** (Gasparini *et al.* 2013, Kokko & Rankin 2006).

SPATIAL DISTRIBUTION OF POTENTIAL BREEDERS, MATING SYSTEM, AND EFFECTIVE BREEDERS

The spatial distribution of potential breeders shapes the mating system. The spatial distribution of potential breeders is one among factors affecting the Operational Sex Ratio (Figure. III.i, Shuster & Wade 2003), the sex ratio of individuals participating in the reproduction (i.e. potential breeders). Intuitively, a local skewed OSR experienced by individuals can modify the competition that they suffer to access potential mates (Chuard *et al.* 2016, Weir *et al.* 2011). The Operational Sex Ratio is one of the factors shaping sexual selection occurring on the sex competing for potential mates (Janicke & Morrow 2018, Wacker *et al.* 2013). The Operational Sex Ratio and the spatial distribution of potential breeders influence the Environmental Potential for Polygamy (EPP, Emlen & Oring 1977) that is the opportunity of individuals to access multiple sexual partners (e.g. individuals near several potential mates). The Environmental Potential for Polygamy associated with individuals ability to access several potential mates (e.g. tall individuals may have an advantage in competitive interactions) drives the mating system (Figure. III.ii, Emlen & Oring 1977).

GLOSSARY III.i: Who are concerned by mating?

Potential breeders — All mature individuals in the population who can participate in reproduction.

Potential mates — Among potential breeders, individuals of the opposite sex.

Potential competitors — Among potential breeders, individuals of the same sex.

Breeders — Individuals who actively participate in repro-

	duction. Because no information were available on behavioural matings, individuals are considered as breeders when they produced juveniles. Thus effective breeders and breeders define the same individuals.
Mates	— Individuals with whom a focal individual shared juveniles.
Sexual competitors	— Individuals of the same sex who had at least one mate in common with a focal individual.

The spatial distribution of potential breeders affects the number of effective breeders by modifying the mating system. Typically, OSR and the resulting EPP were conceptualised to explain mate monopolisation in harems and leks (Emlen & Oring 1977).

> « The OSR provides an empirical measure of the degree of monopolizability of mates. The greater the degree of imbalance in the OSR, the greater the expected variance in reproductive success among members of the limited sex... » — Emlen & Oring 1977

According to the work of Emlen & Oring (1977), spatial aggregation of females should influence the capacity of males to monopolise them. Variability in such abilities should impact the variance in mating success among individuals of the monopolising sex. A moderate spatial aggregation could support mate monopolisation and polygyny. For instance, Pérez-González & Carranza (2011) observed that the spatial aggregation of females raises the mean harem size in red deer (*Cervus elaphus*). However, a high level of aggregation may lead to a costly monopolisation of potential mates due to a high number of competitors or satellite males attempting to access these potential mates (Kokko & Rankin 2006, Shuster & Wade 2003). At the opposite, a weak spatial aggregation of potential mates should favour monogamy because individuals can not monopolise potential mates that are too far (Shuster & Wade 2003). Spatial aggregation of potential breeders can, thus, influence mating behaviour and ultimately the reproductive success at an individual level, while it can affect the number of effective breeders (i.e. individuals

contributing to the recruitment) at the population level.

SPATIAL DISTRIBUTION OF POTENTIAL MATES AFFECTS THE INDIVIDUAL SOCIAL ENVIRONMENT AND SEXUAL SELECTION

At the individual level, spatial distribution influences mate choice. Encounters of individuals, i.e. number and sex, depend on individual locations and individual movements in space and time (i.e. temporal dimension in movements/location[3]). For example, Robert *et al.* (2012) linked home-range overlaps and contact rates in raccoons (*Procyon lotor*). Mate choice is fundamentally dependent on encounters, spiritual matings not existing. When mate choice implies preferences, variations in characters between individuals reveal their performance. For example, the handicap principle precepts that females' preferences evolve because these preferences allow females to mate with males exhibiting high fitness (Zahavi 1975). Either choice or preference is relative (i.e. individual chooses an individual and not another, and individual prefers one trait value to another) and necessarily involved simultaneous or sequential encounters. Spatial distribution of potential mates shapes encounters between them, and, may ultimately affect their mate choice.

Spatial distribution drives sexual selection by shaping encounters. During the breeding season, social encounters with mature individuals involve either potential mates or potential competitors and define the social environment of individuals. The social environment may affect the individual number of mates and the mating success of individuals (i.e number of matings producing juveniles) by influencing mate choices, OSR, and mate monopolisation. In this way, the social environment may change the intrasexual competition (Procter *et al.* 2012). The social environment may also affect how males share their mates with competitors (Shuster & Wade 2003). When social selection or multilevel selection occurs, the reproductive success of a focal individual is affected by its phenotype but also by the phenotype of its social competitors (McDonald *et al.* 2013, Muniz *et al.* 2015). For example, in forked fungus beetles (*Bolitotherus cornutus*), Formica *et al.* (2011) found disruptive selection acting on body size between a focal male and its social competitors. Formica *et al.* (2011) found a positive selection on the size of focal males and a negative one on the size of social competitors. Social environment may,

[3]you can go to the best French bakery to buy a delicious "chocolatine" — and not "bread with chocolate" — , but if you go in front of this bakery during night your hands will be your best friends to cry

thus, affect sexual selection through pre-copulatory competition (mate choice, direct antagonist interactions) and post-copulatory (cryptic mate choice, sperm competition due to mate sharing).

A females' point of view: must individuals aggregate or isolate? Ordinarily, females do not compete to access potential mates due to their high parental investments. Nevertheless, their social environment and especially the presence of other females may affect their reproductive success. First, the breeding habitat choices may favour the spatial aggregation of females (Doligez *et al.* 2003, Fretwell & Lucas 1969) but females may also aggregate to diminish sexual harassment (Cassini 2000, Trillmich & Trillmich 1984), favour genetic diversity through promiscuity (e.g. when several males fertilise eggs in a laying event, Moran & Garcia-Vazquez 1998), and decrease kinship. Second, spatial isolation of females, the opposite of their aggregation, may lead to an Allee effect when no males find them. Then, spatially isolated females may encounter few males what modifies their mate preferences and mate choices (Tinghitella *et al.* 2013). Hence, the spatial distribution of females may ultimately influence their reproductive success, their mating success, and their number of sexual partners by changing their social environment and their spatial isolation.

The current part aims to examine the consequences of the spatial distribution of potential breeders on the mating system and the reproductive success of individuals. The choice of breeding sites in Atlantic salmon generates spatial aggregation of nests, a proxy of the spatial aggregation of females, as viewed in the previous part (Part II, page 49). In chapter 4 (page 153) I aim to test the relationship between the spatial aggregation and the number of effective breeders according to the idea that the spatial aggregation of females drives their potential monopolisation by males. The next chapter (chapter 5, page 161) concentrates on the local social structure produced by the spatial distribution of potential breeders, as well as on the consequences of such a structure on sexual selection faced by anadromous males. Many studies in Atlantic salmon have investigated the genetic structure of populations, while sometimes highlighting a subpopulation structure in a salmon population (Garant *et al.* 2000). Nevertheless, the social structure at a fine scale has been less studied. Moreover, the links found between the OSR and intrasexual competition in salmon (Weir *et al.* 2011) justify making the hypothesis that social environment may influence sexual selection operating in salmon.

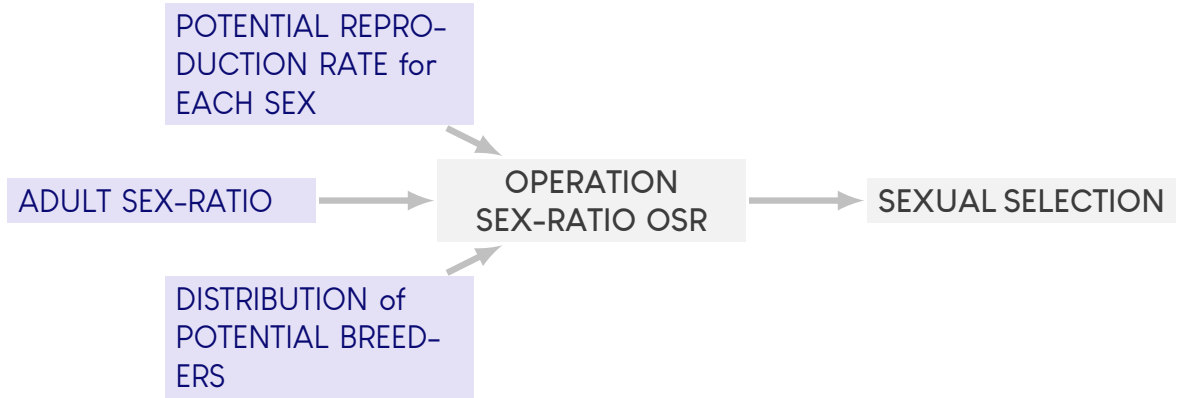

Figure. III.i: Scheme of factors influencing the Operational Sex Ratio, from Emlen & Oring 1977.

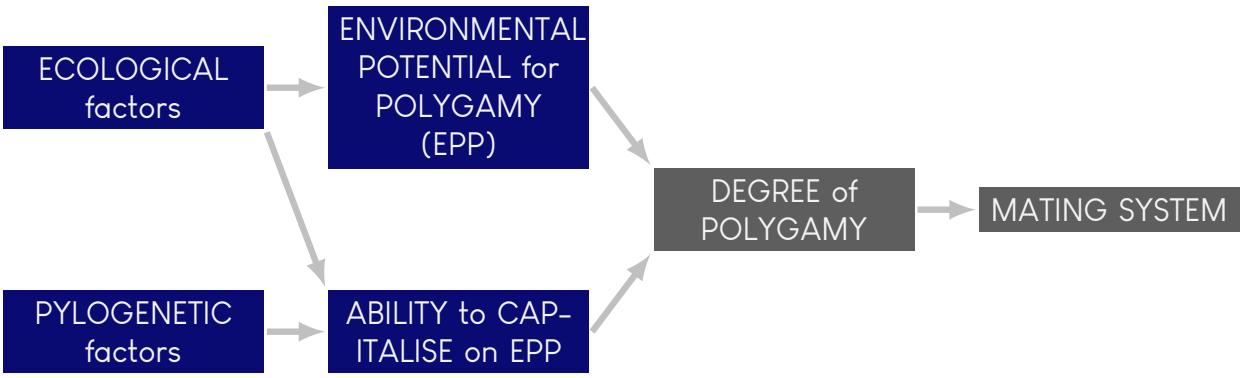

Figure. III.ii: Scheme of factors influencing the Environmental Potential for Polygamy and the mating system, from Emlen & Oring 1977.

Finally, the last chapter (chapter 6, page 199) adopts a females' view investigating how their spatial isolation influence their reproductive success, as well as their number of anadromous mates.

CHAPTER 4

Spatial aggregation of females modifies the environmental potential for polygyny in salmon

Contents

The present chapter corresponds to a collaboration with C. Bacles and O. Lepais published in the Journal of Fish Biology. *The article evaluated whether estimating the number of effective breeders — N_{b_t} — from the Young Of the Year sampled during the yearly surveys of juveniles abundance in the Nivelle is possible. The reason for the study was to reduce the costs associated with analysis usually required to estimate N_{b_t}. My work was to link N_{b_t} to the spatial aggregation of nests calculated in the previous part (Part II, page 49), a proxy of the spatial aggregation of salmon females. Because the major part of the paper is the work of C. Bacles and O. Lepais, I only present here the only parts corresponding to my work.*
Nevertheless, the full paper is accessible either by scanning the following QR-code with your smartphone or by directly clicking on the QR-code in the pdf file. I modified the layout of the text and figures to better incorporation in the thesis. All the text added to improve the understanding and facilitate the incorporation in the thesis is displayed in italic and in grey, like these few lines.

Citation: Bacles, C. F., Bouchard, C. , Lange, F. , Manicki, A. , Tentelier, C. and Lepais, O. (2018), Estimating the effective number of breeders from single parr samples for conservation monitoring of wild populations of Atlantic salmon *Salmo salar*. J Fish Biol, 92: 699-726. doi:10.1111/jfb.13537

4.1 CONTEXT

Effective breeders define individuals who participate in the production of offsprings. Individuals of the dominant sex (i.e. in number) have to compete to access potential mates in species with sex-biases in parental investment and exhibiting biases of sex-ratio. Nevertheless, the spatial distribution of potential breeders may influence the capacity of individuals to access mates (Emlen & Oring 1977, Shuster & Wade 2003). According to Emlen & Oring (1977), the spatial distribution of potential breeders modifies their Environmental Potential for Polygamy because the local spatial aggregation of potential mates enables monopolisation of them by an individual of the other sex. Such monopolisation is typically exacerbated in harems, where an individual secure numerous potential mates from competitors. However, a too large harem (i.e. a too high aggregation), or the proximity to other harems, raises the competition caused by sneaky males (Muniz et al. *2015).*

In salmon, anadromous males compete to access polyandrous females who select their breeding sites on environmental characteristics (Hendry et al. *2001, Louhi* et al. *2008). The spatial distribution and the size of breeding sites cause aggregation of females which varies among years (chapter 2, page 65). Hence, we assessed whether spatial aggregation of females determined the number of effective breeders. We hypothesised spatial aggregation influence the intensity of the competition among males leading to variations in the number of effective breeders. Weak spatial aggregation should promote monogamy, whereas strong spatial aggregation should favour polygamy and participation of sneaky males. A moderate spatial aggregation should lead to mate monopolisation by dominant males. A positive parabola between the effective number of breeders and the spatial aggregation could, thus, be hypothesised.*

4.2 METHODS

The workgroup ORE DiaFC (`https://www6.inra.fr/ore-pfc/`) carried redd monitoring since 1984. The zone accessible for Atlantic salmon was entirely covered by walking directly in the water, two or three times per breeding season. A same duo of observers carried out the survey during the study period, their experience and training diminishing redd survey errors (Dunham et al. *2001). Observers visually detect nests as a typical depression-dome sequence where algae and silt were removed by females when digging.*

Spatial aggregation of redds was also quantified, in order to test its effect on N_b,

through competition for mates between adults and competition for feeding territories for YOY. Redd aggregation was computed following the patchiness index (I_P; Lloyd 1967) as:

$$I_P = \frac{\bar{m} + \left(\frac{\sigma^2}{\bar{m}} - 1\right)}{\bar{m}} \qquad \text{(Eq. 4.1)}$$

with $\bar{m}$ and σ^2 the mean and variance of number of redds in each of the 93 known spawning patches. Then, for each year t, the mean of the estimated number of effective breeders N_{b_t} was regressed against the yearly redd aggregation (patchiness, I_{P_t}). Because N_{b_t} is a discrete variable, a Poisson distribution was used. Aggregation may not have a monotonic effect on N_b and thus a quadratic term was included in the model:

$$\begin{aligned} N_{b_t} &\sim Poisson(\lambda) \\ \lambda &= \exp(lp) \\ lp &= intercept + \alpha \times I_{P_t} + \beta \times I_{P_t}^2 \end{aligned} \qquad \text{(Eq. 4.2)}$$

The Poisson regression was fitted using a Bayesian framework to improve the robustness of parameter estimates. Posterior distributions of parameters were obtained by hybrid Monte-Carlo sampling using the package `rstan` for `R` (Stan Development Team 2016). Weakly informative priors were applied to each parameter: $intercept, \alpha, \beta \sim Cauchy\,(0, 2.5)$, as advised by Gelman *et al.* (2008). Four independent chains were runs to save 10, 000 iterations with a thin equal to three and after a warm-up of 2, 000 iterations. Chain convergence was assessed visually and parameter convergence was assessed with the scale reduction factor r̂ (Gelman & Rubin 1992). A sample of 2, 000/10, 000 values of each parameter estimates was extracted to compute 2, 000 estimations of N_{b_t} for each value of I_{P_t} to ensure the quality of the model.

4.3 RESULTS

The relationship between N_{b_t} and redd aggregation displayed a U-shaped pattern (Figure. 4.1) with a significant quadratic term ($\beta = 0.006$ 95% C.I.: 0.003–0.009). Intercept was estimated at 5.30 ($4 \cdot 59$–5.98) and simple effect α at -0.216 (-0.311 to -0.120).

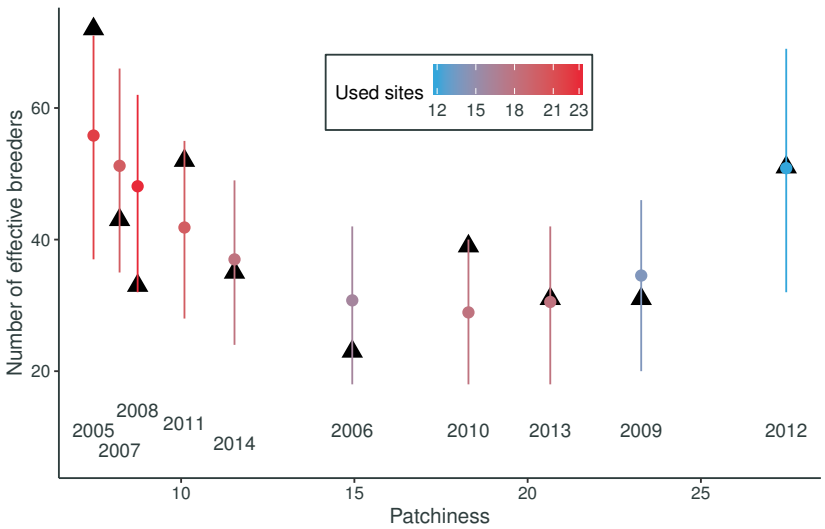

Figure. 4.1: Relationship between nest aggregation (Patchiness) and the number of effective breeders (N_b) across ten years in *S. salar* Nivelle population. Triangles correspond to yearly observed data of N_b, and dots correspond to the estimates with the Credibility Interval at 95%. Color of dots is the yearly number of used breeding sites in the Nivelle.

The model accurately estimated N_b, all the observed data being within the 95% C.I. for each year. High and low levels of redds aggregation correspond to high estimates of N_b, while years with intermediate redds aggregation showed low N_b estimates (Figure. 4.1). For a given effective number of mates, levels of aggregation were negatively linked with the number of used spawning patches. Indeed, a weak aggregation was linked to a high number of used spawning patches (Figure. 4.1).

4.4 DISCUSSION

The *S. salar* mating system is polygynandrous and characterized by high variability in individual reproductive success, which affects the number of effective breeders. Females may dig several redds (up to 7; Taggart *et al.* 2001), on which they can lay several egg batches (up to 11; de Gaudemar *et al.* 2000), each potentially fertilized by several males (up to 16 males per redd; Grimardias *et al.* 2010, Weir *et al.* 2010). Throughout the season, males can sequentially mate with several females (up to 16; Garant *et al.* 2001). Beside these high numbers, one important characteristic of *S. salar* mating success is its individual variability. Accounting for all potential anadromous mates in the River Nivelle upstream of Olha, Tentelier *et al.* (2016b) found that half of the males and one third of the females had no offspring detected in spring, even though sampling was intensive. High mating variance is potentially affected by environmental conditions

which fluctuate among years, explaining the variability of $N_b : N_c$[1]. One example of this environmental variation can be observed in the effect of redd aggregation. The significant U-shaped relationship between N_b and redd aggregation may be interpreted through the environmental potential for polygamy (EPP; Emlen & Oring 1977). When males compete to access females, the capacity of a male to secure mating with multiple females depends on his competitiveness and on the spatial distribution of sexually active females, which depends itself of their breeding sites selectivity (Hendry *et al.* 2001, Louhi *et al.* 2008). At low levels of aggregation, individuals and redds are distributed among many breeding sites, such that males cannot monopolize females, resulting in an even mating success hence a high N_b. As aggregation strengthens, the EPP increases resulting in a stronger male competition to monopolize females, skewing mating success towards more competitive males (Tentelier *et al.* 2016a) and lowering N_b. When females focus on few breeding sites, aggregation of breeders is so strong that competition for mates turns from contest to scramble, resulting in more even mating success and a high N_b. *In the current chapter, we wanted to test the effect of aggregation of females on their monopolisation by males. The potential effect of aggregation (patchiness) on N_b was, thus, tested leading to having patchiness in horizontal-axis in Figure. 4.1. The potential effect of the number of potential breeders (N_c) on aggregation was tested in the chapter 2 (page 65) and no effect was found (Figure. 2.3, page 80).*

HIGHLIGHTS OF CHAPTER 4

- U-shaped relationship linked the spatial distribution of females through their spatial aggregation to the effective number of breeders in the population.
- The Environmental Potential for Polygamy and the Operational Sex Ratio provides a context to explain the relationship.
- Thereby, the spatial aggregation of females allows a male to monopolise several females and expels other males, diminishing the effective number of breeders.
- At low spatial aggregation, a monopolisation is impossible due to the spatial isolation of females. At the opposite, a high aggregation raises the number of competitors what increases the cost of competition and favours the

[1] *N_c corresponds to the yearly estimated number of returning adults*

sneaky behaviour of other males. These two situations raise the effective number of breeders.

CHAPTER 5

Evaluating the local social structure and its effects on the pre-copulatory selection acting on Atlantic salmon males by inferring the population sexual network

Contents

This chapter is based on a collaboration with Tommaso Pizzari and Grant McDonald from the Edward Grey Institute (University of Oxford) with whom I had the chance to exchange for two months at Oxford. The following chapter is an early version of a manuscript in preparation.

Abstract: Space use of individuals may affect their encounters and their sexual networks. In polygynandrous species, males may mate with females for which sperm competition is intense. Moreover, the outcome of intrasexual competition and mate choice depends on an individual's phenotype relative to that of its competitors'. Accounting for the social structure is crucial for a reliable description of sexual selection.
This study aimed to infer encounters and sexual network of a small population of Atlantic salmon during two breeding seasons. Sexual networks enabled testing the potential existence of a local social structure and its effects on the pre-copulatory competition on sperm competition and sexual selection. The effects of the social structure and the social

environment on sexual selection were also tested.
No individual occupied a central position in the network and a local social structure emerged. The local structure varied between years as show by a sexual network more nested during the first season. The mating system of the first season displayed a more negative assortment which increased the Bateman gradient. The correlation between the mating success of individuals and the sperm competition that they suffered was more variable during the first season. Finally, male body length had a positive effect on reproductive success. The arrival date of males in the breeding area also had a positive effect during the first season but not the second. This yearly difference was also found concerning the effect of the group phenotype. Indeed, a positive effect of the body length of local competitors was found during the first season and a negative effect during the second. Opposite signs were found concerning the arrival date.
This study highlights the importance of accounting for the local social structure *in natura* when investigating sexual selection and pre-copulatory competition. Furthermore, the mating system of Atlantic salmon seems to be highly dynamic among years even in a small river. The potential variable participation of males displaying a sneaky behaviour may explain the yearly differences in sperm competition. Finally, the group phenotype may have opposite effects on reproductive success compared to the effects of the individual phenotype. The latter result vindicates the need of new studies about the competitors' phenotype effect on individual reproductive success in salmon.

Keywords: Assortative mating, Bateman gradient, hierarchical bayesian model, multilevel selection, network analysis, probabilistic networks, *Salmo salar*, sneaker males, sperm competition intensity

5.1 INTRODUCTION

Movements of individuals affect their social network when encounters are regarded as interactions between individuals. While networks correspond to edges linking nodes, social networks link individuals according to their interactions depending on social interactions researchers consider (see box Tools III.i). Social networks depict either a present/absent interaction between individuals or weighted interactions. In weighted networks, a weight (e.g. number of antagonist interactions) characterises interactions between individuals. Depending on how much and where it moves, each individual may not encounter all individuals, interacting only with a subset of individuals within the population. Studying

such social networks permit to better understand social organisation (Quevillon *et al.* 2015), group living (Wey *et al.* 2008, Wolf *et al.* 2007), or to explain infectious disease dynamics in humans (De *et al.* 2004) but also in animals (Farine 2017, Perkins *et al.* 2009).

Recently, several authors have focused on how space use shapes sexual networks. Sexual networks are a subclass of social networks focusing on potential breeders and depicting who mated with whom either by visual observations of copulation or genetic parentage analyses. Then, sexual networks link potential breeders by considering either whether they mate together or not, or the number of mating events between them, or the number of sired juveniles between them, for instance. Spatial distribution of potential breeders through their home range affects their access to potential mates and therefore their mating success (Fisher & Lara 1999). A social structure (i.e. the formation of groups via connections among individuals) may appear in sexual networks because all individuals do not encounter all potential mates (Krause *et al.* 2007, Montiglio *et al.* 2018). For instance, Muniz *et al.* (2015) argued that the spatial distribution of *Serracutisoma proximum* affects the males' sexual network. Therefore, such local social structure may have great importance by shaping the spread of sexually transmitted diseases (De *et al.* 2004), modifying genetic diversity (Cunningham *et al.* 2018, Montiglio *et al.* 2018), or impacting the mating system through the Environmental Potential for Polygamy (EPP, Emlen & Oring 1977). Each individual, encountering different subsets of competitors and potential mates may, thus, face different local Operational Sex Ratio (OSR) leading to variation in EPP between individuals (Emlen & Oring 1977, Shuster & Wade 2003).

The local sexual structure may affect sexual competition faced by individuals. Indeed, knowing who interact with whom is the first step of evaluating sexual competition (Kamath & Losos 2018). Sperm competition determines how males share their reproductive success with competitors who mated with the same females (Shuster & Wade 2003). Such sharing with other males diminish their reproductive success affecting the Bateman gradient, namely the slope of the relationship between mating success and reproductive success (McDonald *et al.* 2013, Muniz *et al.* 2015). The structure of sexual networks leads to a positive or negative assortment, i.e. the correlation between an individual's and his mates' mating success, a key parameter to study sexual selection.

Thus, assortative mating can flatten or steepen the Bateman gradient by shaping the relationship between the intensity of sperm competition faced by males and their mating success (McDonald & Pizzari 2016; 2017). By shaping the local OSR and EPP experienced by each individual, the spatial distribution of potential breeders may affect the structure of sexual networks (Muniz *et al.* 2015, Silk *et al.* 2018) and the intensity of sperm competition suffered by individuals (Muniz *et al.* 2015). The spatial distribution of potential breeders may, thereby, drive sexual competition.

Moreover, the spatial distribution of potential breeders shapes phenotypes of competitors faced by males. The local social environment can have strong implications for patterns of sexual selection when populations are structured. The strength of sexual selection on males is not only shaped by the intensity of sperm competition but also by the phenotypes of the competitors that males face. For example, Oh & Badyaev (2010) found that males of wild house finches may adjust their social environment including less attractive males and increasing their reproductive success. Moreover, Formica *et al.* (2011), found antagonist selection on body size on forked fungus beetles (*Bolitotherus cornutus*) favouring larger males with small competitors in their social group. The phenotype of competitors may, thus, affect the reproductive success of a focal individual through sexual competition (West-Eberhard 1983). Phenotypes expressed in a social environment may also modify the reproductive success of a focal individual through Indirect Genetic Effects which are modifications of individual phenotype by the phenotype of other individuals (Wolf *et al.* 1998). The phenotype of mates may also modify the phenotype of a focal individual (Teplitsky *et al.* 2010). Nevertheless, we only focused on the impact of the competitors' phenotype. Analyses that estimate the contribution of the phenotypic composition of a male local socio-competitive environment may be crucial in understanding how social structure shapes sexual selection (McDonald *et al.* 2013, Okasha 2004). Multilevel selection analyses enable accounting for the effect of individual phenotype but also of the social-competitive phenotype (McDonald *et al.* 2013).

Although sexual networks provide useful information to understand mating systems and especially patterns of assortative mating, they only refer to a mating layer. Integrating social information (potential competitors) and spatial information to the mating layer may enhance our understanding of mating behaviour and mating system (Silk *et al.* 2018). For instance, Schlicht *et al.* (2015) used a spatially explicit model to assess the

probability of extra-pair mating in birds and improve understanding of the effects of breeding distance on extra-pair mating. However, applying such multilayer and explicit spatial approach *in natura* requires a large amount of data but also involves different types of data to have different layers (Silk *et al.* 2018). Moreover, another challenge *in natura* remains to obtain information about all possible nodes in the considered network in order to not bias assortativity for example (Kossinets 2003).

TOOLS III.i: Social network analysis

Usually, biologists build social networks by linking individuals — nodes — and either by categorising individuals according to sex for example — bipartite network — or not (Figure. 5.1). Links between individuals — edges — are either directed (e.g. A attacks B) or undirected (e.g. A reproduces with B). A weighted network corresponds to a network where each edge is distinguished by the number or the strength of interactions between nodes (Figure. 5.1). Social networks have been recently used in ecological and behavioural studies resulting in several recent reviews, opinion, or book (Blüthgen 2010, Butts 2009, Croft *et al.* 2011, Farine & Whitehead 2015, Krause *et al.* 2007, Pinter-Wollman *et al.* 2014).

As justified by Farine & Whitehead (2015), networks analysis provides a useful way to describe social systems at the species level (e.g. to describe predator-prey interaction) or at the population level (e.g. which individual interact which whom). In addition, social analyses may be used to link individual behaviour to individual fitness (Formica *et al.* 2010). Networks permit describing interactions between nodes by viewing the presence/absence of interactions (e.g. whether a pair has copulated or not, McDonald *et al.* 2013). However, a weighted network permits to fully capture the richness of the information contained in data (Opsahl & Panzarasa 2009).

Network analyses permit highlighting that individual heterogeneity and connections between individuals may modify group and individuals outcomes (Sih *et al.* 2009). Considerations of a spatial dimension is notably a potential way of improvements of network analyses (Sih *et al.* 2009, Silk *et al.* 2018). Accounting for connections between individuals may be enhanced by accounting for other layers of information (temporal, spatial,

..., Silk *et al.* 2018). However, incorporated different data types and incomplete data can be damageable in such analysis (James *et al.* 2009). Bayesian Hierarchical models can be a solution to estimate probabilities of encountering and mating from different data types. Working with probabilities also permits estimating interactions between individuals for whom some data are not available. Bayesian Hierarchical models can also link different networks (e.g. encounter network and mating network in my thesis).

Ellis *et al.* (2017) found that male's sociality in killer whales, *Orcinus orca*, enhanced their survival in years of low salmon abundance. In humans, De *et al.* (2004) highlighted that the position in networks of individuals was more important in infectious transmission than the number of interactions. Network analyses could give valuable information about effects of the social structure, especially in colonial species where dominance, or rank, for example, may affect the survival or recruitment such as in kittiwake (*Rissa tridactyla*, Cam *et al.* 2003).

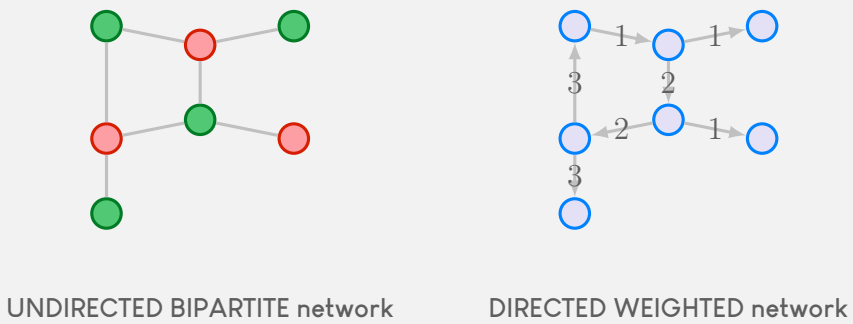

Figure. 5.1: Two examples of social networks.

Atlantic salmon (*Salmo salar*) is a relevant species to investigate the influence of breeders' spatial distribution on local structure and the resultant effects on sexual selection. After growth at sea, salmon migrate to freshwater to reproduce. After a "migration phase" to go up the river, individuals exhibit a "search phase" during which they research a breeding site, as well as potential mates (Finstad *et al.* 2005, Økland *et al.* 2001). The "search phase" may favour the appearance of a structure in encounters. Moreover, spatial aggregation of nests and thus of females varies among years

(Bouchard *et al.* 2018), suggesting a potentially fluctuating social network. Although salmon is a model of sexual selection and notoriously polygynandrous species (Garant *et al.* 2001), sexual selection has never been looked through the prism of networks, only at the scale of the spawning act (behavioural observations of male-male and male-female interactions, Järvi 1990, Mjølnerød *et al.* 1998, Myers & Hutchings 1987) or the whole population pooled in parentage analyses (Bacles *et al.* 2018, Taggart *et al.* 2001). In addition, some studies have investigated the spatial dimension but either on the location of breeding sites (Hendry *et al.* 2001), the habitat quality in their home range (Tentelier *et al.* 2016a), or on the resultant density of offspring (Einum *et al.* 2008, Foldvik *et al.* 2010). Finally, previous studies have suggested a within-population local structure when studying population dynamics at the juvenile level in salmon (Finstad *et al.* 2009).

We used data of individual movements and parentage analyses from Tentelier *et al.* (2016a) and Tentelier *et al.* (2016b) to infer a spatially explicit sexual network in a small population of Atlantic salmon (*Salmo salar*) during two breeding seasons. The present study aimed to evaluate the effects of the spatial distribution and movements of potential breeders affect the strength of sexual selection. We tested whether spatial distribution and movements of potential breeders i) shape mating assortativity and the subsequent sperm competition, and ii) affect sexual selection through the effects of social-competitive phenotypes on reproductive success in Atlantic salmon. The approach developed here bridges the gap between behavioural studies at the spawning act scale and genetic studies at the population scale, looking at the individual sexual environment and accounting for who encounters whom. We firstly inferred the encounters and sexual networks linking potential mates according to their encounter probability and to their mating probability. Then, we assessed mating assortativity and the subsequent sperm competition. The phenotypes of mated males were compared to those of encountered males and to those of all males in the population to test the importance of accounting for encounters when investigating sexual selection. Finally, previous studies observed the influences of body size and arrival date on salmon's reproductive success (Seamons *et al.* 2004, Tentelier *et al.* 2016a). We, thereby, evaluated the impacts of the local socio-competitive environment on the individual reproductive success through a multilevel selection analysis, no studies have tested for it in salmon.

5.2 METHODS

5.2.1 DATA

Data came from the studies of Tentelier *et al.* (2016a) and Tentelier *et al.* (2016b). Authors monitored *in natura* the daily movements of anadromous salmon within the upstream part of the Nivelle River (France) during two breeding seasons (Figure. 5.2). The upstream limit of the studied area was an impassable dam (Figure. 5.2), while the downstream limit was a dam equipped with a fish trap ("Olha" dam in Figure. 5.2). The fish trap provides a passage for fish and allows researchers to tag all individual entering in the studied are. The number of tracked individuals changed between the two years: 15 females and 17 males the first year (2009) and 45 females and 46 males the second one (2010). The observed difference is due to a yearly variation in returning adults in the Nivelle (Bacles *et al.* 2018). Authors monitored the daily positions of all tagged individuals within the study area and throughout the breeding season (Tentelier *et al.* 2016a).

Beside the described monitoring, authors also mapped all redds, which are the nests of Atlantic salmon. After each breeding season, juvenile sampling along the study area permitted to perform genetic parentage analysis giving a male-female matrix filled with the number of common offspring (Tentelier *et al.* 2016b). Parentage analyses provided the necessary data to compute the individual reproductive success corresponding to the number of sired juveniles (effective breeders: 10 fathers and 13 mothers in 2009 — 22 fathers and 27 mothers in 2010). Parentage analyses also permitted to compute the mating success of individuals as the number of different mates. The high number of caught juveniles (1677 juveniles in 2009 and 1350 in 2010) diminished the probability to miss an anadromous parent (Bacles *et al.* 2018). However, missing some of anadromous remained possible, especially when their true reproductive success was low. Hence, some matings were unnoticed by the parentage analysis which convinced us to prefer working with the probability of mating which uses information from the encounter process rather than the mating success for some analyses. Likewise, the daily position of all individuals allows building a three-dimension array, male-female-day, filled with the daily distance for each day of the season. The latter array was wrapped to another male-female matrix to have a quantitative appreciation of the fidelity between individuals and an estimate of a true encounter during the season (Eq. 5.2).

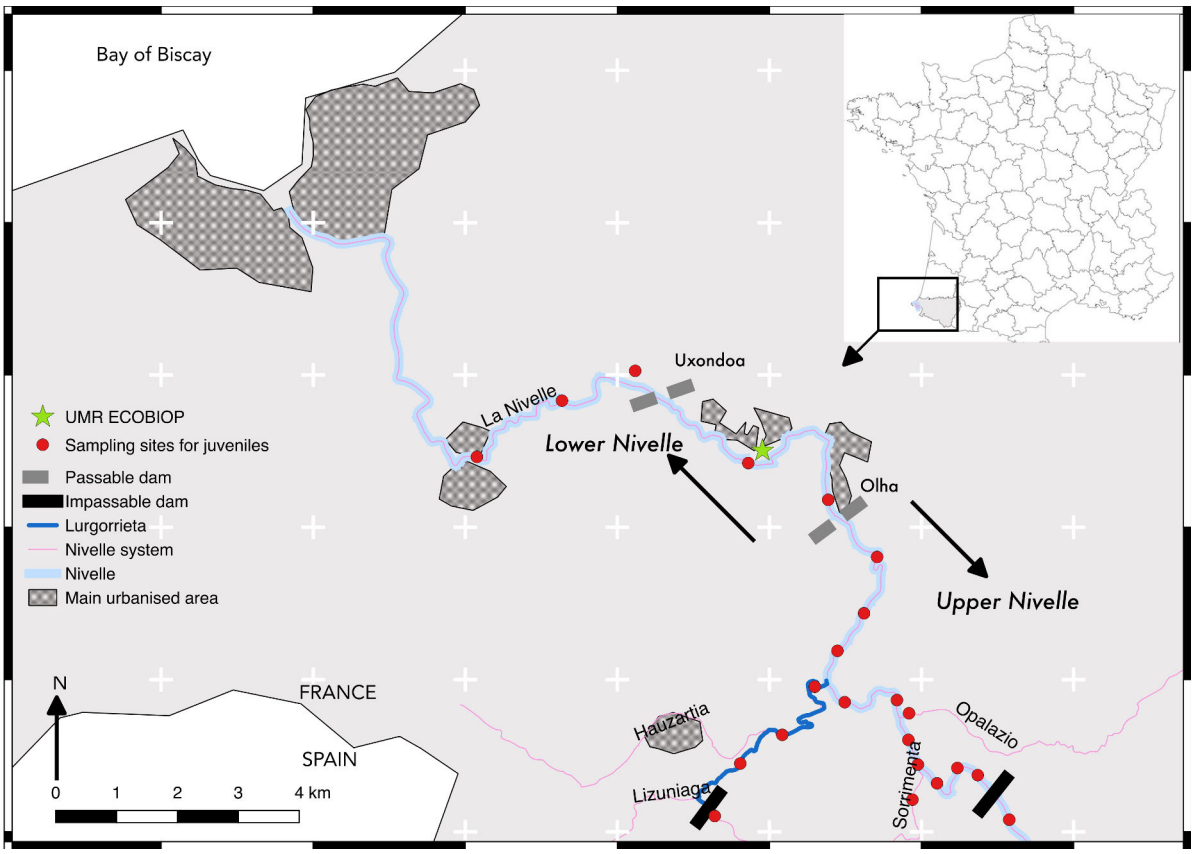

Figure. 5.2: Map of the Nivelle River. The dams "Uxondoa" and "Olha" are now equipped with a fish pass. The Olha dam marked the limit between the Upper Nivelle ("UN") and the Lower Nivelle ("LN"). The red dots correspond to the 22 sites where salmon juveniles are yearly sampled. The Lurgorrieta is the main tributary. Saint-Pée sur Nivelle is the urbanised area between Uxondoa and Olha dams. The yellow star indicates the geographic position of the UMR ECOBIOP.

5.2.2 Inferring the sexual network

The bipartite and undirected sexual network of anadromous salmon in the Nivelle River was based on the mating probability, the probability that a female — f — and a male — m — sired at least one juvenile. Inferring this probability used four types of information: 1) the juveniles sired by each anadromous couple and obtained by the parentage analysis (Tentelier *et al.* 2016b), 2) the encounters obtained from the daily positions (Tentelier *et al.* 2016a), 3) the encounters near a redd obtained from the daily positions and redd mapping (Tentelier *et al.* 2016a), and 4) female body size affecting its fecundity which may affect the number of mating events. The challenge lies in how to combine such different sources of information which are also incomplete. Parentage analysis may miss some parents because electrofishing does not sample all juveniles in the river. Moreover, all encounters cannot be noticed by monitoring the individual positions once a day, and all redds cannot be found (Dunham *et al.* 2001). Bayesian hierarchical models permit to combine different sources of information which can be incomplete (Brun *et al.* 2011). In addition, working with probabilities allowed us estimating encounters or matings between all individuals even if any offspring in common was sampled.

Let M_{f-m} the mating success of the pair formed by the female f and the male m. M_{f-m} is either equal to 0, or to 1 when the pair $f-m$ sired at least one juvenile. The probability to obtain $M_{f-m} = 1$, namely the success probability referred to as the mating probability, is estimated from the encounter probability — E_{f-m} —, the probability that a salmon pair visit the same redd — R_{f-m} —, and a term — ϕ_f — accounting for the female body size.

$$M_{f-m} \sim \mathcal{B}ernoulli\,(p)\,,$$

$$\Pr\left[M_{f-m} = x \mid E_{f-m}, R_{f-m}, \phi_f\right] = \begin{cases} p, & \text{if } x = 1 \\ 1-p, & \text{if } x = 0 \end{cases}$$

$$= \begin{cases} \dfrac{exp\left(base + \alpha_1 \times E_{f-m} + \alpha_2 \times R_{f-m} + \alpha_3 \times \phi_f\right)}{exp\left(base + \alpha_1 \times E_{f-m} + \alpha_2 \times R_{f-m} + \alpha_3 \times \phi_f\right) + 1} \\ 1 - \dfrac{exp\left(base + \alpha_1 \times E_{f-m} + \alpha_2 \times R_{f-m} + \alpha_3 \times \phi_f\right)}{exp\left(base + \alpha_1 \times E_{f-m} + \alpha_2 \times R_{f-m} + \alpha_3 \times \phi_f\right) + 1} \end{cases} \quad \text{(Eq. 5.1)}$$

Probabilities were estimated under a Bayesian framework by calling `Stan` in `R` (Stan

Development Team 2018). The model, like the following ones, was separately fitted for each breeding year. Three chains were fitted, each one containing $52,500$ iterations, and permitted to save $5,000$ iterations with a thinning interval of 10 iterations and after a warm-up of $2,500$ iterations. Graphical examinations, the scale reduction factor: $\hat{r}$, as well as the effective sample size and the autocorrelation of parameter estimates, permitted to assess chain convergence. The model used all tracked individuals during the two breeding seasons: 17 males - 15 females in 2009, and 46 males - 45 females in 2010.

5.2.2.1 Encounter probability --- E_{f-m}

The daily distances between each male — m — and each female — f — permitted the computation of their encounter probability — E_{f-m}. From these daily distances between male — m — and female — f —, we extracted the number of days during which this distance was shorter than 500 m (this day count was noted D_{f-m}). The threshold distance, which is similar to the distance used by Tentelier *et al.* (2016a), corresponds to the distance at which a male may stay from a redd before participating in reproduction at this redd. The number of inverted positions between a male and a female was also accounted to diminish the number of omissions of potential encounters. Then, we count an inverted position if two individuals invert their positions between two days (e.g. a male is upstream from a female one day and downstream from this female the next day) and if the distance between them was longer than 500m during the two days in order to do not count a day two times. An inverted position necessarily tended to a highly probable encounter due to the narrow width and the shallow depth of the Nivelle. Thus, relative positions of individuals allowed us to compute the number of inverted positions for each pair — IP_{f-m} — which was implemented in the estimation of the encounter probability to improve it. Because all individuals did not enter the same day in the study area, D_{f-m} and IP_{f-m} were standardised by the number of days during which a female and a male were both in the study area (noted S_{f-m} to define the Season length of potential encounters between f and m). Hence, the encounter probability — E_{f-m} — between a male — m — and a female — f — corresponded to:

$$E_{f-m} = \begin{cases} \dfrac{D_{f-m} + \beta \times IP_{f-m}}{S_{f-m}}, & \text{if } S_{f-m} \neq 0 \\ 0, & \text{if } S_{f-m} = 0 \end{cases} \qquad \text{(Eq. 5.2)}$$

Because the relative importance of IP_{f-m} in encounter probability is unknown, the effect of IP_{f-m} was modulated through a parameter: β. No constrains were directly applied to β but an indirect because the fraction was constrain to be lower than one and upper than zero.

5.2.2.2 Probability to visit a redd --- R_{f-m}

The redd mapping associated with the daily positions of anadromous permitted computing the daily distances between each redd — r — and each anadromous, male and female. Like for the encounter probability for each anadromous pair, a threshold length of 500 m was chosen. The number of days during which the distance between a redd — r — and an anadromous (male or female) was shorter than this threshold length was thus extracted (noted $D_{r-f \text{ or } m}$). $D_{r-f \text{ or } m}$ was standardised by the number of days during which the focal anadromous was able to visit the redd ($S_{r-f \text{ or } m}$). $S_{r-f \text{ or } m}$ corresponds to the number of days between the previous redd survey and the redd survey during which the redd was found. The average number of days was 5.9 days. The probability that a male and a female visited the same redd (R_{f-m}) was, therefore:

$$\Pr\left[R_{f-m} \mid D_{r-f}, D_{r-m}, S_{r-f}, S_{r-m}\right] = \begin{cases} \dfrac{1}{1+exp\left(-x\right)}, & \text{if } S_{r-f} \;\&\; S_{r-m} \neq 0 \\ 0, & \text{if } S_{r-f} \text{ or } S_{r-m} = 0 \end{cases}$$

$$\text{with } x = \sum_{r=1}^{Nr_j} \frac{D_{r-f}}{S_{r-f}} \times \frac{D_{r-m}}{S_{r-m}}, \text{ if } S_{r-f} \;\&\; S_{r-m} \neq 0$$

(Eq. 5.3)

with Nr_j the number of redds found during the breeding season j.

5.2.2.3 Accounting for female fecundity --- phi_f

In salmon, fecundity is dependent on the body size which affects the number of eggs females can lay (Thorpe *et al.* 1984). Females may adjust the number of eggs that they laid during a mating event in relation to the sperm depletion level of males (Weir *et al.* 2010). Fecundity, which depends on body size, may thus influence the laying probability. The laying probability shapes the number of mating events of females. The fecundity may influence the number of mating events of females, only because if a low number of eggs are spawn, the probability to sample juveniles diminishes. Finally, larger females usually spawn larger eggs and with a burial deeper of nests. These two effects enhance egg survival (Berghe & Gross 1984, Kazakov 1981, Steen & Quinn 1999). However, in other salmonid, eggs of smaller females may exhibit an enhanced survival (Holtby &

Healey 1986). The effect of body size on the mating probability should, consequently, be accounted for.

$$\phi_f = \frac{1}{1 + exp(-FL_f)} \qquad \text{(Eq. 5.4)}$$

with FL_f the fork length of the female f.

5.2.2.4 Formation of binary and weighted networks

The model Eq. 5.1 permits estimating of an encounter probability (E_{f-m}) and a mating probability ($\Pr\left[M_{f-m} = 1\right]$) between each potential pair of breeders ($f - m$). The encounter and sexual networks are bipartite networks linking all individuals to all opposite-sex individuals. The links between individuals are weighted either with the encounter probability (E_{f-m}) in the case of the encounter network or with the mating probability ($\Pr\left[M_{f-m} = 1\right]$) in the case of the sexual network. Closeness centrality measures the position of individuals within a network with the idea that an individual exhibiting short distance to other individuals can productively spread information through the network (Beauchamp 1965). For weighted networks, especially in our cases, the distance between two individuals ($d(i, j)$) corresponds to the encounter or the mating probability between them because all potential mates are connected. The closeness centrality of the individual i is thus computed as (Wei *et al.* 2013):

$$Cc_i = \frac{1}{\sum_x^N d(i, j)} \qquad \text{(Eq. 5.5)}$$

With N the total number of potential mates. A low Cc_i, due to a high denominator ($\sum_x^N d(i, j)$), indicates that the individual i is highly connected to potential mates and occupies a "central position".

Based on these networks and all links, we can isolate links which are "probable". A male was, then, considered as encountered by a female when the encounter probability between the female and the male, E_{f-m}, was upper than 0.05. It means that the weight of the edge linking the female f to the male m was upper than 0.05 to consider the link as likely. Then sexual partners were recognised through the mating probability — higher than 0.05 like for the encounter probability.

5.2.3 MATING ASSORTATIVITY & THE BATEMAN GRADIENT

5.2.3.1 Nestedness

The nestedness, a concept originated from metacommunity study, is a measure of the mating assortativity. Recent studies quantified the pattern of assortativity in sexual networks through the nestedness (McDonald & Pizzari 2016). A nested network arises when males with low mating success, and then a few mating partners, preferentially mate with the most polyandrous females. In this way, males with the highest mating success also mate with less polyandrous females. In terms of assortativity, a nested network corresponds to a negative assortment between the male mating success and the female mating success. Patterns of assortativity are easily visible through matrix representation of sexual networks with males as rows and ranked from top to bottom in order of decreasing mating success, and females as columns ranked from left to right also according to decreasing mating success. The ordered matrices of sexual network permit assessing the nestedness of the population through the NODF, the acronym of nestedness metric based on overlap and decreasing fill, and defined by Almeida-Neto *et al.* (2008). From an ordered matrix, and for each pair of males — i and j rows — we computed the Decreasing Fill (DF) and the Percentage Overlap (PO). DF is calculated by comparing the mating success (M) of the upper ranked male (row i) to the mating success of the other male (row j). If $M_i > M_j$, then $DF_{ij} = 100$ and if $M_i \leq M_j$, then $DF_{ij} = 0$.The Percentage Overlap of the pair of rows $i - j$ was calculated as the percentage of male j's mating partners shared with the male i. Same calculations between column pairs permit assessing DF and PO for females with the female i, the leftmost female. Individual nestedness — N_{ij} — then be calculated as:

$$\begin{aligned} &\text{If } DF_{ij} = 0, \quad \text{then } N_{ij} = 0 \\ &\text{If } DF_{ij} = 100, \quad \text{then } N_{ij} = PO_{ij} \end{aligned} \qquad \text{(Eq. 5.6)}$$

Then, the nestedness characterising the whole network can be calculated as:

$$NODF = \frac{\sum N_{ij}}{\left[\frac{f(f-1)}{2}\right] + \left[\frac{m(m-1)}{2}\right]} \qquad \text{(Eq. 5.7)}$$

f and m correspond to the number of females and males in the network, respectively. NODF may range from 0 to 100, 0 indicating no nestedness and 100 a perfect nestedness (Almeida-Neto *et al.* 2008). Besides the computation of the NODF based on the mating

success (M) and thus the matrices of sired juveniles, NODF was also computed by replacing the mating success by the mating probability estimated in the equation Eq. 5.1. For this second computation, we compared the cumulative mating probability of the male or female i to the cumulative mating probability of the male or female j instead of comparing mating success. In this case, $DF_{ij} = 0$ when the cumulative mating probability of the individual i was lower than that of the individual j. $DF_{ij} = 0$ was then the percentage of male j's partners with which he had an higher mating probability than the male i had. For example, if the male j had just one partner, if the mating probability between this female and j was 0.7 and 0.2 with a male i, therefore $PO = 100$. For the first calculation, we considered just tracked individuals that sired at least one juvenile: 9 males / 8 females in 2009 and 13 males / 13 females in 2010. For the second calculation, the mating probability enabled to consider all individuals: 17 males / 15 females in 2009 and 46 males / 45 females in 2010, which diminishes potential bias in the estimation of the nestedness due to missing nodes (Kossinets 2003).

5.2.3.2 Sperm competition and the Bateman gradient

Salmon females being polyandrous, males compete to access to them and face sperm competition. Indeed, several males may participate in the fertilisation of a laying event of one female. The number of sperm competitors, therefore, diminishes the reproductive success of a focal male. According to Shuster & Wade (2003), the sperm competition intensity (SCI) suffered by a male can be assessed through the harmonic mean of the mating success of male's partners. The sperm competition intensity faced by males informs on patterns in assortative mating at a population level. Let a focal male that mates with three females: 1) one female which does not remate and no competitors are present, 2) one female which does not remate but one competitor also fertilises some eggs, 3) one female which remates with two males. For the first female, the focal male faces no sperm competition. But for the two other females, the focal male must compete with the sperm of other males. Direct competition occurs when a competitor also fertilises some eggs during the same laying event while an indirect sperm competition occurs when the female remate with other males. The average paternity share of this focal male across its three partners is then: $\frac{1}{3} \times \left(\frac{1}{1} + \frac{1}{2} + \frac{1}{3}\right) = 0.611$. Then, this focal male must face $\frac{1}{0.611} = 1.64$ competitors. This computation may be generalised for the mth male as:

$$\mathrm{SCI}_{m,j} = \frac{1}{\frac{1}{M_{m,j}} \times \sum_{f=1}^{M_{m,j}} \frac{1}{k_{f,j}}} \qquad \text{(Eq. 5.8)}$$

with $M_{m,j}$ the mating success of the male m during the breeding season j, and $k_{f,j}$ the mating success of the female f during the same season j.

Strength of selection on mating success is usually assessed through the Bateman gradient (β) measuring the relation between the mating success of an individual and its reproductive success: $T_{m,j} = \beta \times M_{m,j}$. In addition to the pre-copulatory competition, sperm competition may also modulate the reproductive success of an individual. According to McDonald & Pizzari (2016), SCI was incorporated in the equation linking the mating success to the reproductive success of individuals:

$$T_{m,j} \sim \mathcal{N}\left(intercept + \beta_{M \bullet SCI} \times M_{m,j} + \beta_{SCI \bullet M} \times SCI_{m,j},\ \sigma_T\right) \qquad \text{(Eq. 5.9)}$$

with $\beta_{M \bullet SCI}$ the Bateman gradient controlling for variation in SCI and $\beta_{SCI \bullet M}$ measuring the effect of sperm competition on reproductive success. The model accounted for all individuals having a no-null reproductive success ($T_{m,j} > 0$) and all variables ($T_{m,j}$, $M_{m,j}$, $SCI_{m,j}$) were standardised like this: $\frac{T_{m,j} - mean(T_j)}{2 \times sd(T_m)}$. The model (Eq. 5.9) was fitted under Bayesian framework like previous models in the current study. A total of $12,000$ iterations were saved from three chains with a thinning interval of 5 iterations and a warm-up of $2,000$ iterations. Convergence was assessed in the same way those previous models. In this model, we also computed the Sperm Competition Intensity Correlation — SCIC — corresponding to the link between the mating success (M) and the sperm competition intensity (SCI, McDonald & Pizzari 2016; 2017):

$$SCI_{m,j} = \mathcal{N}\left(intercept_{SCIC} + SCIC \times M_{m,j},\ \sigma_{SCIC}\right) \qquad \text{(Eq. 5.10)}$$

A male who mates with polyandrous females, then facing to numerous sperm competitors, will, therefore, have positive SCIC. In this model, the mating success, the reproductive success, and the SCI were standardised like in the previous model.

5.2.4 PHENOTYPIC SELECTION

5.2.4.1 Phenotype of mated males compared to phenotype of potential breeders

Phenotype of mated males is usually compared to the average phenotype in the population to test if females mate with a particular phenotype. However, mate choice, whether direct or indirect, is a relative process. A female may choose a male only in encountered ones and by comparing encountered ones. In order to test the effect of encounters be-

tween potential mates, we suggested to also compare the phenotype of mated males to the phenotype of encountered males. Encounters matter if the two comparisons, namely with the population phenotype and with the encountered phenotypes, provide different results.

Then, one normal distribution was fitted to model the phenotypes (body length and date of arrival) of all males in the population estimating the average phenotype and the corresponding standard deviation:

$$Phenotype_m \sim \mathcal{N}\left(\mu_{\text{population}},\ \sigma_{\text{population}}\right) \qquad \text{(Eq. 5.11)}$$

For each female, a normal distribution was also fitted to model the phenotypes of males this female f encountered and another normal distribution was fitted for the phenotypes of males this female mated:

$$\text{if } E_{f-m} > 0.05 : Phenotype_{m,f} \sim \mathcal{N}\left(\mu_{\text{encountered}-f},\ \sigma_{\text{encountered}-f}\right) \qquad \text{(Eq. 5.12)}$$

$$\text{if } \Pr\left[M_{f-m} > 0.05\right] : Phenotype_{m,f} \sim \mathcal{N}\left(\mu_{\text{mated}-f},\ \sigma_{\text{mated}-f}\right) \qquad \text{(Eq. 5.13)}$$

Then, for each female, the average phenotype of its sexual partners — $\mu_{\text{mated}-f}$ — was compared to the average phenotype of all males in the population — $\mu_{\text{population}}$ — and to the average phenotype of males encountered by each female — $\mu_{\text{encountered}-f}$. The values of $\mu_{\text{population}}$ and $\sigma_{\text{population}}$ estimated in Eq. 5.11 were replaced in the equation of Δ_{pop}, while the values of $\mu_{\text{encountered}-f}$, $\sigma_{\text{encountered}-f}$ and $\mu_{\text{mated}-f}$ estimated in Eq. 5.12 and Eq. 5.13 were replaced in the equation of $\Delta_{\text{encountered}}$.

$$\begin{aligned} \Delta_{\text{pop}-f} &= \frac{\mu_{\text{population}} - \mu_{\text{mated}-f}}{\sigma_{\text{population}}} \\ \Delta_{\text{encountered}-f} &= \frac{\mu_{\text{encountered}-f} - \mu_{\text{mated}-f}}{\sigma_{\text{encountered}-f}} \end{aligned} \qquad \text{(Eq. 5.14)}$$

A positive value of $\Delta_{\text{encountered}-f}$ indicates that the female f mated with the larger males she encountered.

A hierarchical Bayesian model was used to estimate the parameters of the three equations Eq. 5.11, Eq. 5.12, and Eq. 5.13, and thereafter the subsequent comparisons: Δ_{pop}, $\Delta_{\text{encountered}}$. Hence, this hierarchical model enabled to estimate the average phenotype of encountered and mated males for each female. This model also allowed us to compare the average phenotype of mated males to phenotype of encountered males and to the average phenotype in the population. Since we hypothesised that each female may encounter and mate a different subset of males, $\sigma_{\text{encountered}-f}$ was modelled for each female from the $\sigma_{\text{population}}$ as: $\sigma_{\text{encountered}-f} = \eta_f \times \sigma_{\text{population}}$; and $\sigma_{\text{mated}-f}$ was estimated from $\sigma_{\text{encountered}-f}$ as: $\sigma_{\text{mated}-f} = \upsilon_f \times \sigma_{\text{encountered}-f}$. Three chains were fitted enabling to save a total of $4,800$ iterations from $10,000$ iterations per chains after a warm-up of $2,000$ iterations and with a thinning interval of 5 iterations. Convergence was assessed in the same way as for the model Eq. 5.1.

5.2.4.2 Assessing the effect of the social environment on reproductive success

The reproductive success of salmon males is usually explained by their body length (Tentelier *et al.* 2016b). Yet, the local socio-competitive environment may also affect the sexual selection. We performed a multilevel selection analysis accounting for the effect of individual phenotype but also of the social-competitive phenotype on individual reproductive success. The social-competitive phenotype was assessed through a neighbour analysis. In neighbour analysis, the phenotype of a group (g) where is a focal individual (m) is computed as the mean trait value for all neighbours of m belonging in this group including the focal individual (McDonald *et al.* 2013, Okasha 2004). We used a neighbour analysis rather a contextual one — where the phenotype of the group is the mean value of neighbours and focal male — to prevent collinearity between the focal phenotype and the group phenotype in small groups. Then for each focal male (m) we extracted the identity of its competitors to compute the phenotype of its group. Competitors are other males who encountered ($E_{f-m} > 0.05$ in Eq. 5.1) the females with whom the focal male mated. For instance, lets a male who has mated with two females. The first female has encountered a male while the second female has encountered two males. The group phenotype of the focal male is then the mean trait value of its three neighbours. Each male was, thus, characterised by its reproductive success, its phenotype, and the phenotype of its group. The multilevel selection linking individual reproductive success ($T_{m,g}$) to individual phenotype ($z_{m,g}$) and group phenotype ($Z_{m,g}$)

through a Poisson regression was:

$$T_{m,g} \sim \mathcal{P}\left(exp\left(intercept_{social} + \alpha \times z_{m,g} + \beta_{group} \times Z_{m,g}\right)\right) \quad \text{(Eq. 5.15)}$$

We did not use a network based on males encounters because we considered competitors on the basis of encounters between males that have involved females. Such considerations motivated us to used the encounter and sexual networks previously defined. Indeed, encounters between males without involving females have not necessarily lead to competition between males either direct (e.g. on male chasing other males) or indirect (e.g. their own presence). A total of $60,000$ iterations were saved from three chains with a thinning interval of 10 iterations and a warm-up of $1,000$ iterations.

5.3 RESULTS

5.3.1 INFERRING THE SEXUAL NETWORK & THE ENCOUNTER PROBABILITY

Inferring the sexual network from the parentage analysis, redd mapping, and individual tracking enabled to estimate the encounter probability, as well as the mating probability. In 2009, one male displayed an encounter probability and a mating probability lower than 0.05 with all females (Figure. 5.3). Some patterns appear in agencement of encounters and matings within the population. Some males exhibited high encounter probabilities with several females, while some males exhibited low probabilities also with several females. No female or male displayed a high probability to encounter all individuals of the other sex (Figure. 5.3 a). The closeness centrality for males and based on the encounter probability (Cc_i, Eq. 5.5) varied from 0.21 to 0.95, while it varied from 0.29 to 1.12 when accounting for the mating probability. In females, Cc_i varied from 0.21 to 1.26 when accounting for the encounter probability, and from 0.31 to 1.08 when accounting for the mating probability. For the two sexes and the two probabilities the values were not relatively low indicating that no individual occupied a "central position". We simulated 1000 networks with 17 males interacting with 15 females by simulating encounter probabilities from a uniform distribution between 0 and 1, the Cc_i ranged in average from 0.09 to 0.25. The low centrality exhibited by individuals led to have three subgroups emerging from the matrix representation (Figure. 5.3 c). Similar observations can be made from the network and matrix representation of the mating probability: females and males displaying high probabilities with only some individuals. In 2010, the high number of anadromous individuals makes the networks difficult to graphically read (Figures in Supplementary). However, the networks seemed more homogeneous in 2010

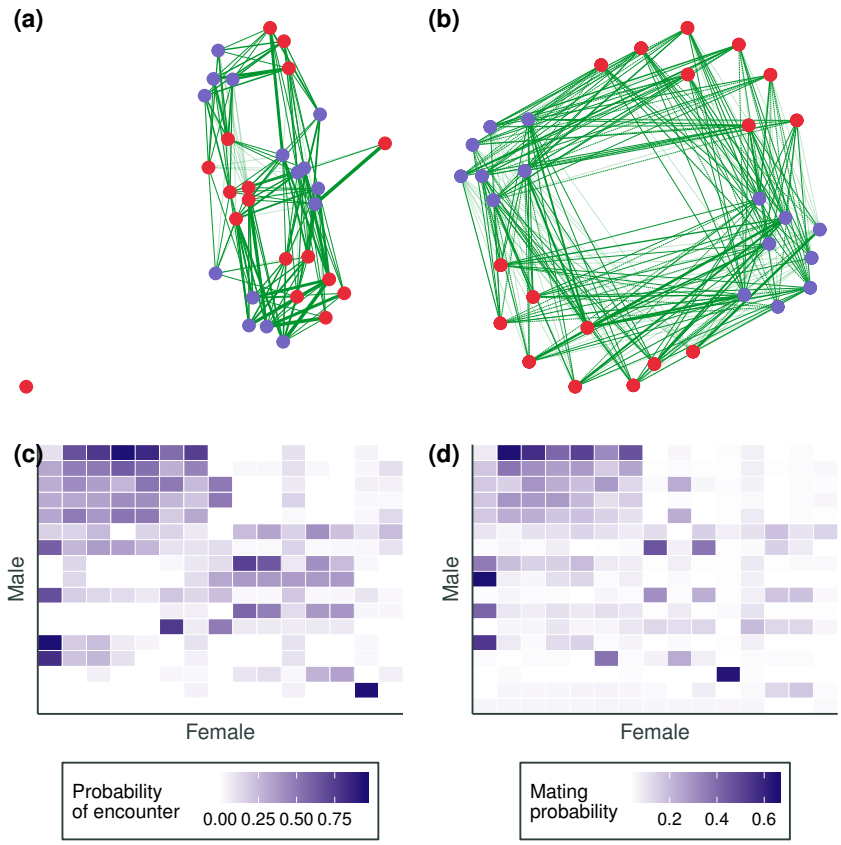

Figure. 5.3: Bipartite networks of males (red) and females (blue) based on their encounter probability (a & c) and their mating probability (b & d) in 2009. In network plots, probabilities lower than 0.05 are not displayed. The width of nondirectional edges increases with the corresponding probability. In matrix plots, males with the highest cumulative sum of encounter probability in c) or of mating probability in d) is displayed at the top. For females, individuals are ordered from left to right with a decreasing cumulative sum of probability. A total of 17 anadromous salmon males and 15 females was tracked during a breeding season which enabled by coupling with parentage analysis and redd mapping to rebuild this sexual network.

than in 2009.

5.3.2 MATING ASSORTATIVITY & THE BATEMAN GRADIENT

5.3.2.1 Nestedness

Matrices of the number of juveniles sired by each anadromous pair enabled to discover a negative assortment pattern during the first breeding season (Figure. 5.4). For this breeding season, the nestedness accounting individuals for whom at least one juvenile was found, was computed at 43.81 which indicates a negative assortment (Table. 5.1). Concerning the second breeding season, a pattern of assortative mating appears in the top left corner of the matrix while the rest of the matrix shows a more homogeneous

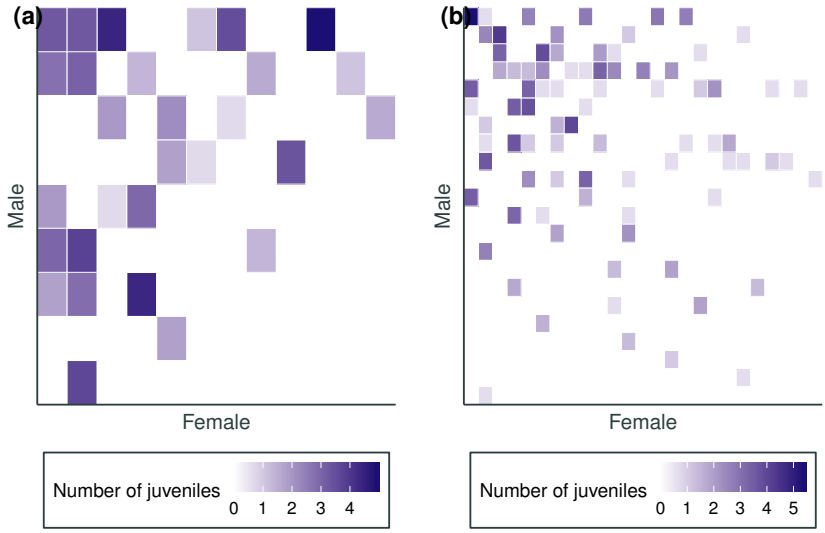

Figure. 5.4: Matrices of the number of juveniles (expressed in $log(\text{NJuvenile} + 1)$) sired by each anadromous pair in the Nivelle during two breeding seasons — 2009 (a) and 2010 (b). Only individuals who have sired at least one juvenile are displayed in matrices. Males are *rows* and females *columns*. To enable the computations of nestedness defined by Almeida-Neto *et al.* (2008), both matrices were ordered of left to right (females) and top to bottom (males) in order of decreasing mating success.

pattern (Figure. 5.4). A value of 28.11 was computed for the second breeding season, almost twice lower than for the first one. Nestedness computed on the basis of juveniles sired by individuals and not the mating probability gave similar results for the second season but a more high value (62.61) during the first season. With both methods, the network of the first season was more nested than the network of the second season.

Table. 5.1: Table of the nestedness (NODF, according to Almeida-Neto *et al.* (2008)) computed for two breeding seasons in an anadromous salmon population. Nestedness was computed as usual through the number of mates (mating success) but also through their probability of mating. For the first calculation, we considered just tracked individuals that sired at least one juvenile: 9 males / 8 females in 2009 and 13 males / 13 females in 2010. For the second calculation, the mating probability enabled to consider more individuals: 17 males / 15 females in 2009 and 46 males / 45 females in 2010.

Year	Type	Nestedness (NODF)
2009	Number of juveniles	43.81
2009	Probability of mating	62.61
2010	Number of juveniles	28.11
2010	Probability of mating	29.14

5.3.2.2 Sperm competition and the Bateman gradient

The sperm competition intensity of males (SCI) was more variable and also higher in 2009 than in 2010 despite the lower number of individuals during the first year (mean $\pm$ standard deviation: 15.2 ± 7.4 and 9.2 ± 6.4 in 2009 and in 2010 respectively). This yearly difference is visible on the Figure. 5.5, but two-times more individuals are plotted in 2010 than in 2009. The relationship between the SCI and the reproductive success seems to be positive in 2009, while in 2010, all individuals having a SCI higher than ten exhibited low reproductive success (Figure. 5.5).

For the two breeding seasons, the Bateman gradient controlling for variation in sperm competition, $\beta_{M \bullet SCI}$, was positive (Figure. 5.7). The gradient was steeper during the first season: 0.84 against 0.55. The SCI (parameter $\beta_{SCI \bullet M}$ in the Eq. 5.9) had a positive but not significant effect in 2009 ($\beta_{SCI \bullet M} = 0.5$, 93% of parameter estimates upper than zero). In 2010, a null effect was found ($\beta_{SCI \bullet M} = -0.04$, "Beta-SCI" in Figure. 5.7). Finally, a negative trend was estimated for the SCIC in 2009 (-0.36, 55% of parameter estimates lower than zero, Figure. 5.7). In 2010, the SCIC was clearly less variable and was significantly negative (-0.49, 2% of parameter estimates upper than zero). The negative trend in 2009 and the negative effect found in 2010 were clearly visible in the Figure. 5.6.

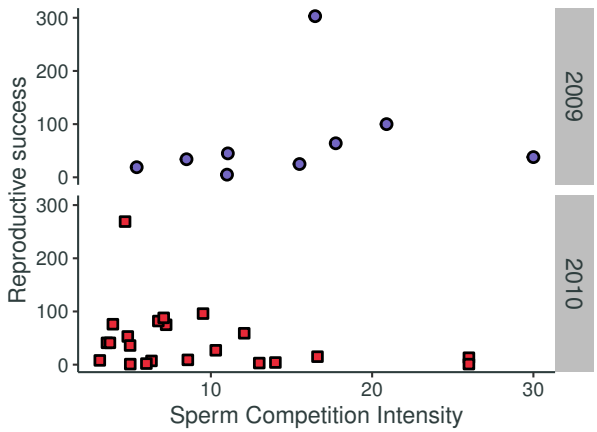

Figure. 5.5: Relationship between the reproductive success and the sperm competition intensity of Atlantic salmon males in a small population during two breeding seasons. Data correspond to 9 anadromous males in 2009 and 22 in 2010 which sired at least one juvenile.

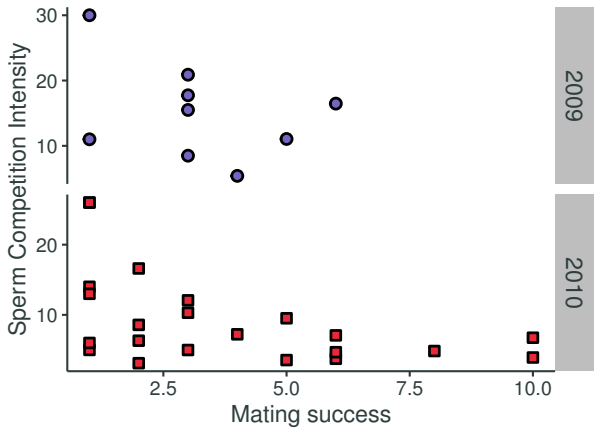

Figure. 5.6: Relationship between the mating success and the sperm competition intensity of Atlantic salmon males in a small population during two breeding seasons. Data correspond to 9 anadromous males in 2009 and 22 in 2010 which sired at least one juvenile.

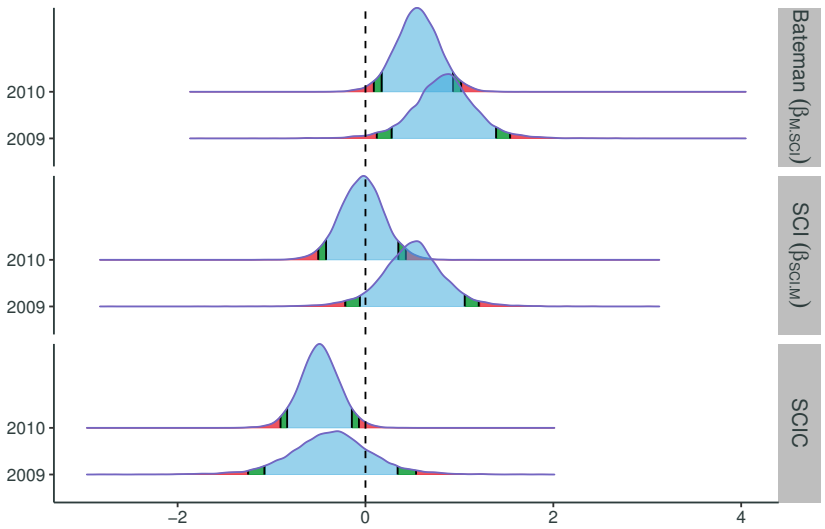

Figure. 5.7: Plot of the estimated Bateman gradient ($\beta-$Bateman), as well as the effect of the sperm competition ($\beta-$SCI) on the reproductive success of Atlantic salmon males in a small population during two breeding seasons. The Sperm Competition Intensity Correlation (SCIC) measures the correlation between the mating success and the SCI of individuals. Each parameter distribution corresponds to $12,000$ iterations. Blue areas represent the values between the quantiles 5 % and 95%. Red areas represent the values between the quantiles 0 and 2.5 % and the values between the quantiles 97.5 % and 1. Green areas represent the values between the quantiles 2.5 and 5 % and the values between the quantiles 95 % and 97.5 %.

5.3.3 PHENOTYPIC SELECTION

5.3.3.1 Phenotype of mated males compared to phenotype of potential breeders

A negative sign indicates that the average body size of mated males was higher than the average body size of the subset (population or encountered males). In 2009 and for each female, with the exception of the female 15, the average body size of mated males was similar to the average body size of encountered ones (Figure. 5.8). Instead, comparisons of mated males to the males in the population was more variable. Indeed, some comparisons tend to be negative (for females 6, 7 or 13 for example) while others tend to be positive (females 11 and 12 for example). In addition, for these females (6, 7, 11, 12, and 13) the two comparisons displayed a different sign. In 2010, differences between the two comparisons were also found (Fig. in Supplementary). For most of the females, the average body size of mated males was closer to the average body size of encountered males than to the average body size in the population. However, in 2010, a majority of females displayed an average body size of mated males different to the average body size in the population or in the subset of encountered males.

5.3.3.2 Assessing the effect of the social environment on reproductive success

First, the individual body length had a positive effect on the individual reproductive success during the two breeding seasons (Figure. 5.9), but a stronger effect was highlighted in 2009. Concerning the group selection, the average body length of the competitors increased the reproductive success of a focal males in 2009, whereas the opposite effect was found in 2010. Second, the date of arrival of individuals did not impact their reproductive success in 2009 but diminished it in 2010. A negative effect signifies that a late arrival male displayed a lower reproductive success. Opposite effects were found for the effect of the group phenotype, a negative effect being estimated in 2009 and a positive one in 2010. Regarding the date of arrival, the group effect was stronger than the individual effect which was not the case for the body length (Figure. 5.9).

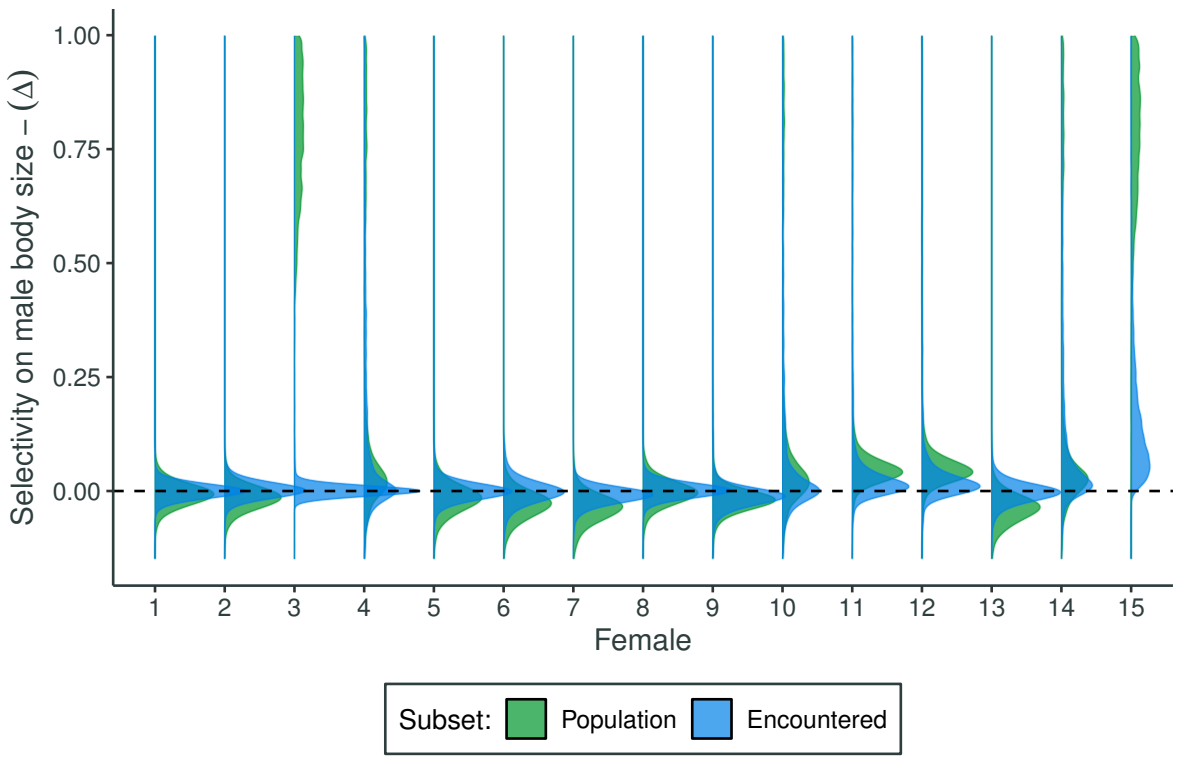

Figure. 5.8: Plot of the salmon female selectivity in male body size during the first breeding season. The average body size of males with whom a female mated has been compared to the average body size of males in the population (subset "Population") or to encountered males (subset "Encountered") for two breeding seasons: $\Delta = \frac{\mu_{\text{subset}} - \mu_{\text{mated}}}{\sigma_{\text{subset}}}$.

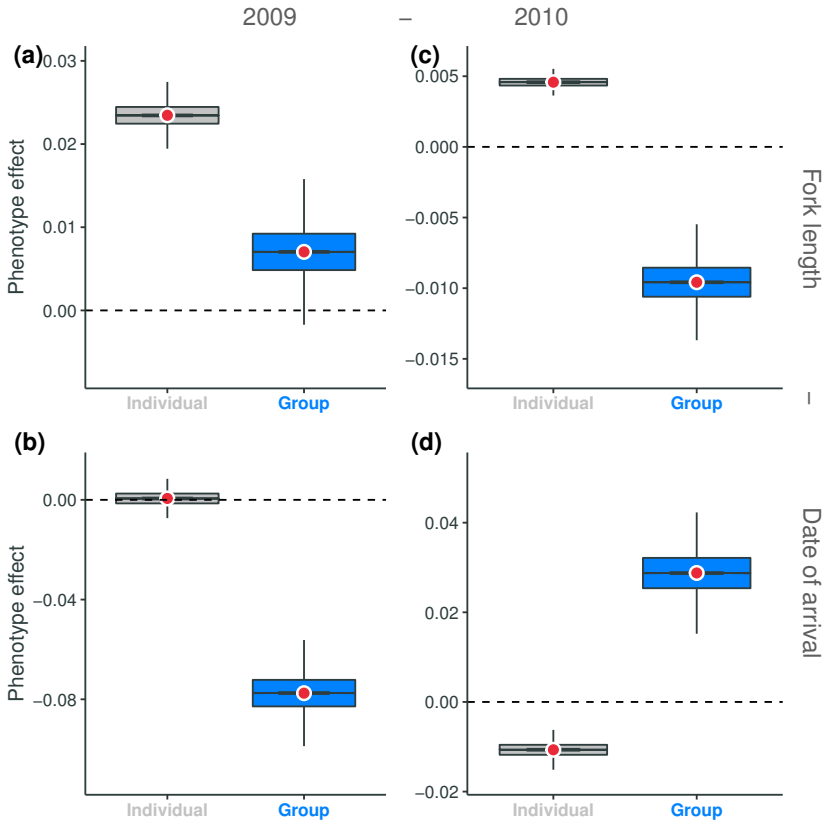

Figure. 5.9: Boxplot of the results of a neighbour analysis concerning the reproductive success of male anadromous salmon. Like classical analyses, the effects of male phenotype (fork length or date of arrival at breeding sites) on its reproductive success was tested (individual). The effects of the phenotype of its group (neighbour competitors of the focal male) on its reproductive success was also tested to assess a potential group selection. Each box represents the distribution of 60, 000 iterations, red dots highlighting the mean values.

5.4 DISCUSSION

Differences in spatial behaviours involve the potential emergence of a local social structure. The network representation, as well as the matrix one, highlighted the existence of such a local social structure in groups of Atlantic salmon potential breeders. Indeed, no individual seemed to occupy a central position in the encounter network and no individual encountered all potential mates. In addition, the network seems more homogeneous during the second season indicating a less marked local social structure. The year difference in social structure may be explained by a yearly difference in home ranges exhibited by anadromous males. Indeed, using the same data set, Tentelier *et al.* (2016a) found that salmon males tended to exhibit broader home ranges during the second breeding season, which favours encounters between individuals. In their studies on racoons, Robert *et al.* (2012) also found a positive correlation between home range overlap and encounter rates.

Mating of males with females depends on the subset of encountered males by females. The comparisons of females mates to encountered males and to all males do not suggest that large males always have increased access to females. It seems that it was particularly true during the first breeding season when males exhibited smaller home ranges (Tentelier *et al.* 2016a), the selectivity ($\Delta_{\text{encounter}} = \frac{\mu_{\text{encounter}} - \mu_{\text{mated}}}{\sigma_{\text{encounter}-f}}$) being near zero for all females. This was clearly not the case in the second season, the average phenotype of mated males being smaller than the phenotype of encountered ones for a lot of females. Our results agree with the results of Taggart *et al.* (2001) who found that larger females mated with larger males for one season over three. For the two other years, the maximum distance between redds of the same parent was more variable suggesting that some individuals exhibited broader home ranges. Our results can also explain why Jones & Hutchings (2002) did not find a positive effect of anadromous size on individual reproductive success.

The local social structure may obscure local patterns of sexual selection on phenotypic traits if not accounted for. Sexual selection acts on a phenotypic trait when this trait plays a role in access to mates. In salmon, the body size may play such a role when anadromous males compete to access to females (Järvi 1990). However, our results about the size of encountered and mated males, as well as the various findings of other studies Jones & Hutchings (2002), Taggart *et al.* (2001) suggest that the sexual

selection on body size is probably less pronounced than supposed and highly dependent of the subset of encountered males, hence, dependent to the social environment. In any case, this vindicates in accounting for local social structure when assessing the effect of sexual selection on phenotypic traits.

The assortative mating of sexual network informs on the participation of anadromous sneaker males. Salmon population in the Nivelle exhibited a higher nestedness in 2009 than in 2010 indicating a more nested network and a more negative assortment in 2009 (Almeida-Neto *et al.* 2008, McDonald & Pizzari 2016). The more negative assortment pattern found in 2009 was highlighted with the two methods including the one accounting all individuals which reduces bias in calculations of network metrics (Kossinets 2003). Biologically, this result means that males with low mating success mated with females with high mating success. Here, the more negative assortment found in 2009 compared with 2010 may be due to higher participation of anadromous sneaker males that have to compete with guarder males to access to females. Indeed, spatial aggregation of redds and therefore of females was higher in 2009 than in 2010 (Bouchard *et al.* 2018), stronger aggregation enabling an easier monopolization of females by guarder males (Emlen & Oring 1977, Shuster & Wade 2003). However, when aggregation is too high, anadromous sneaker males may be concentrated around aggregated females allowing them to fertilise more eggs (Bacles *et al.* 2018). Such participation of anadromous sneaker males was previously suggested by Weir *et al.* (2011) in salmon when the OSR was strongly skewed towards males but also in other fishes (Chuard *et al.* 2016). In addition, using the same data set, (Tentelier *et al.* 2016a) found that males move less during the first season resulting in small groups. Hence, the nestedness of the sexual network in Atlantic salmon may result from the participation of anadromous sneaker males.

Yearly sperm competition variation also indicates variation in the participation of anadromous males exhibiting an alternative reproductive tactic. The sperm competition intensity was higher in average and more variable in 2009 than in 2010, agreeing with a potentially higher participation of anadromous sneaker males in 2009. In a species with alternative reproductive tactics, Muniz *et al.* (2015) found that territorial breeders faced a more variable sperm competition than sneakers. In 2010 individuals exhibiting high sperm competition exhibited low reproductive success, while individuals having high

reproductive success also faced to high sperm competition. The hypothesis of a higher participation of sneaker males in 2009 is also supported by the results of Bacles *et al.* (2018) who found a higher ratio of effective breeders over the number of returning adults ($\frac{N_b}{N_c}$). Indeed, the participation of sneaker males raises the number of effective breeders, the multiple paternity increasing the effective size of salmon populations (Martinez *et al.* 2000). This pattern can also be found by looking at the same ratio with the effective anadromous males and the number of caught individuals: $\frac{10}{17} = 0.59$ and $\frac{22}{46} = 0.48$ in 2009 and 2010, respectively.

Anadromous sneaker males may obscure the global pattern of positive assortment in sexual networks. The negative SCIC — the correlation between males' mating success and the sperm competition that they faced — was similar between the two breeding seasons but was more variable in 2009. McDonald & Pizzari (2017) have shown that a more polyandrous network usually produces a less variable SCIC and a negative SCIC indicates a negative assortment. Thus, the less variable SCIC in 2009 suggested a less polyandrous network compared with 2010. Yet, no difference in pre-copulatory selection (Bateman gradient) on males was found, the two years displaying positive gradient. Yearly variations in the sexual network seem not to affect the pre-copulatory selection but may generate a more variable sperm competition. The more variable SCIC in 2009 can, thus, resulted from the fewer males available in 2009 compared with 2010 leading to more extreme absolute values. Finally, the SCIC values estimated here for Atlantic salmon are similar to other taxa (McDonald & Pizzari 2017), reflecting a global pattern of negative assortment. Hence, the participation of males exhibiting an alternative reproductive tactic diminished the assortativity of the sexual network, which, therefore, increased pre-copulatory selection via the Bateman gradient (McDonald & Pizzari 2015).

Individual body size was found to increase the reproductive success as previously found by Tentelier *et al.* (2016b) but not by Garant *et al.* (2001), Jones & Hutchings (2002). This positive effect paired with our results about selectivity for each female and results of Garant *et al.* (2001), Jones & Hutchings (2002) or Seamons *et al.* (2004) in another salmon species, indicate that some females may mate with small males depending on which males they have encountered. Such effect may dampen the positive effects found in some studies between males' size and their reproductive success. Furthermore, this body size effect was stronger during the first breeding season, supporting the hy-

pothesis of a higher participation of anadromous sneaker males who are smaller, the individual size raising the fertilisation success when simultaneous spawning (Mjølnerød *et al.* 1998). Hence, the global effect of individual phenotype on reproductive success may be dependent on the participation of males exhibiting an alternative mating tactic.

The social environment was found to impact the reproductive success in a contrasting way to the individual phenotype, which may be linked to the mating system varying each year. During the first breeding season, no effect of arrival date of males on their reproductive success was found, whereas the date of arrival diminished the reproductive success in 2010. In comparison, Tentelier *et al.* (2016a) found contrasting results, while Seamons *et al.* (2004) found a weak positive relationship between male reproductive success and their timing of arrival. In addition, a positive social effect on size and a negative one on arrival date during the first season was highlighted. The opposite was found for the second season. These social effects highlight the influence of the competitors' phenotype on the reproductive success of individuals. Our results may be due to the higher aggregation of redds and, therefore, of females in 2009 than in 2010 (Bouchard *et al.* 2018). During the second season, the lowest aggregation enabled first arrived males or bigger ones to access females and to secure them (Seamons *et al.* 2004, Tentelier *et al.* 2016a). In this case, it was best for the focal males to have smaller competitors arriving after it. This generated a negative group phenotype effect on body size but a positive one on arrival date. At the opposite, during the first year, the higher aggregation of females favoured males arriving later to avoid a strong level of competition. In this way, it was better for a male to have large and earlier arriving competitors joining the shuffle. In this case, having larger competitors may increase the number of eggs to fertilise (Makiguchi *et al.* 2016). Hence, the phenotype of competitors may also affect the reproductive success of a focal male. The way of this effect depends on the mating system which clearly appears to be dynamic among years.

Inferring the sexual network of a small population of Atlantic salmon enabled to highlight the existence of a local social structure. The local social structure, even in such a small population, varied between two breeding seasons. Our results highlight the importance of a sexual network approach when investigating sexual selection acting on a phenotypic trait. In addition, the year-to-year variations in social structure seems to be linked to fluctuations of the mating system and, more specifically, in the

frequency of alternative reproductive tactics. Furthermore, we found the mating system of salmon globally exhibited a negative assortment with two different methods. The latter result agrees with previous studies finding that two or three anadromous males may sire juveniles in the same nest (Garant *et al.* 2002, Taggart *et al.* 2001, Weir *et al.* 2010). Finally, investigate such pattern of assortative mating is important, the negative assortment may have several effects at the population level such as an increase in phenotypic diversity (Takahashi & Hori 2008). Finally, a multilevel selection analyses show a strong and variable effect of the local social environment on individual reproductive success. Indeed, the way in which the social environment affects the reproductive success of individuals seems to vary depending on the mating system, also varying among years. The multilevel selection may demonstrate an opposite effect of the social environment to individual effect on individual phenotype, vindicating the necessity to better appreciate the effects of competitors' phenotype.

ACKNOWLEDGEMENTS

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HIGHLIGHTS OF CHAPTER 5

- Spatial distribution of potential breeders affects their encounters which modifies the local Operational Sex Ratio faced by each individual and finally sexual competition that they suffer.
- Using different data type, the sexual network of the salmon population was inferred to assess effects of the spatial structure on the sexual competition and selection.
- A spatial structure varying each year was highlighted in the encounter network and in the mating network.
- Spatial distribution of potential breeders modified the subset of encountered males by each female, accounting for it enabled to advocate that the spatial structure may lead to erroneous conclusions in mate choice and sexual selection.
- Spatial distribution of potential breeders also influenced the social environ-

ment of males as the phenotype of competitors influenced their reproductive success.

SUPPLEMENTARY

PARAMETERS' PRIORS AND POSTERIORS

Table. 5.2: Table of the priors of the different parameters estimated through Bayesian models. Posteriors correspond to the 95% credible interval for the two breeding seasons. † corresponds to the effect of the fork length and ‡ to the effect of the arrival date.

Eq.	Parameter		Prior	Posterior (95%CI)	
	Symbol	Signification		2009	2010
Eq. 5.1	$base$		$\mathcal{C} \sim (0,\ 5)$	$[-10.98;\ 7.99]$	$[-11.77;\ 7.49]$
	α_1	Accounting for encounter probability	$\mathcal{C} \sim (0,\ 5)$	$[1.80;\ 5.34]$	$[1.72;\ 3.95]$
	α_2	Accounting for probability to visit a redd	$\mathcal{C} \sim (0,\ 5)$	$[-0.64;\ 1.73]$	$[-0.39;\ 1.06]$
	α_3	Accounting for female fecundity	$\mathcal{C} \sim (0,\ 5)$	$[-11.30;\ 7.79]$	$[-11.30;\ 8.05]$
Eq. 5.2	β	Accounting for inverted positions	$\mathcal{C} \sim (0,\ 5)$	$[0.04;\ 3.15]$	$[0.01;\ 1.10]$
Eq. 5.11	$\mu_{\text{population}}$	Average phenotype of population	$\mathcal{C} \sim (0,\ 5)$	$[595.59;\ 621.27]$	$[608.79;\ 634.13]$
	$\sigma_{\text{population}}$		$\mathcal{C} \sim (0,\ 5)$	$[21.09;\ 34.77]$	$[38.18;\ 51.67]$
Eq. 5.12	$\mu_{\text{encounter}}$	Average phenotype of encountered	$\mathcal{C} \sim (0,\ 5)$		
	η_f		$\mathcal{C} \sim (1,\ 5)$		
Eq. 5.13	μ_{mated}	Average phenotype of mated	$\mathcal{C} \sim (0,\ 5)$		
	υ_f		$\mathcal{C} \sim (1,\ 5)$		
Eq. 5.9	$intercept$		$\mathcal{C} \sim (0,\ 5)$	$[-0.33;\ 0.34]$	$[-0.19;\ 0.18]$
	$\beta_{M \bullet SCI}$	Bateman gradient for ♂	$\mathcal{C} \sim (0,\ 5)$	$[0.00;\ 2.36]$	$[0.27;\ 2.16]$
	$\beta_{SCI \bullet M}$	Sperm competition effect on reproductive success	$\mathcal{C} \sim (0,\ 5)$	$[-1.86;\ 0.54]$	$[-1.64;\ 0.24]$
	σ_T		$\mathcal{C} \sim (0,\ 5)$	$[0.25;\ 0.95]$	$[0.31;\ 0.61]$
Eq. 5.10	$intercept_{SCIC}$		$\mathcal{C} \sim (0,\ 5)$	$[-0.27;\ 0.27]$	$[-0.09;\ 0.09]$
	$SCIC$	Correlation between M and SCI	$\mathcal{C} \sim (0,\ 5)$	$[0.24;\ 1.28]$	$[0.73;\ 1.11]$
Eq. 5.15	$intercept_{social}$		$\mathcal{C} \sim (0,\ 5)$	$[-24.7285;\ -17.5406]^{\dagger}$ $[20.9474;\ 28.0285]^{\ddagger}$	$[2.4351;\ 6.04.06]^{\dagger}$ $[-7.0274;\ -0.5501]^{\ddagger}$
	α	Effect of focal	$\mathcal{C} \sim (0,\ 5)$	$[0.0161;\ 0.0214]^{\dagger}$ $[0.0200;\ 0.03605]^{\ddagger}$	$[0.0045;\ 0.0066]^{\dagger}$ $[-0.0273;\ 0.0171]^{\ddagger}$
	β_{group}	Effect of group	$\mathcal{C} \sim (0,\ 5)$	$[0.0093;\ 0.0219]^{\dagger}$ $[-0.1275;\ 0. - 0.0963]^{\ddagger}$	$[-0.0098;\ -0.0027]^{\dagger}$ $[0.0333;\ 0.0613]^{\ddagger}$

INFERRING THE SEXUAL NETWORK & ENCOUNTER PROBABILITY

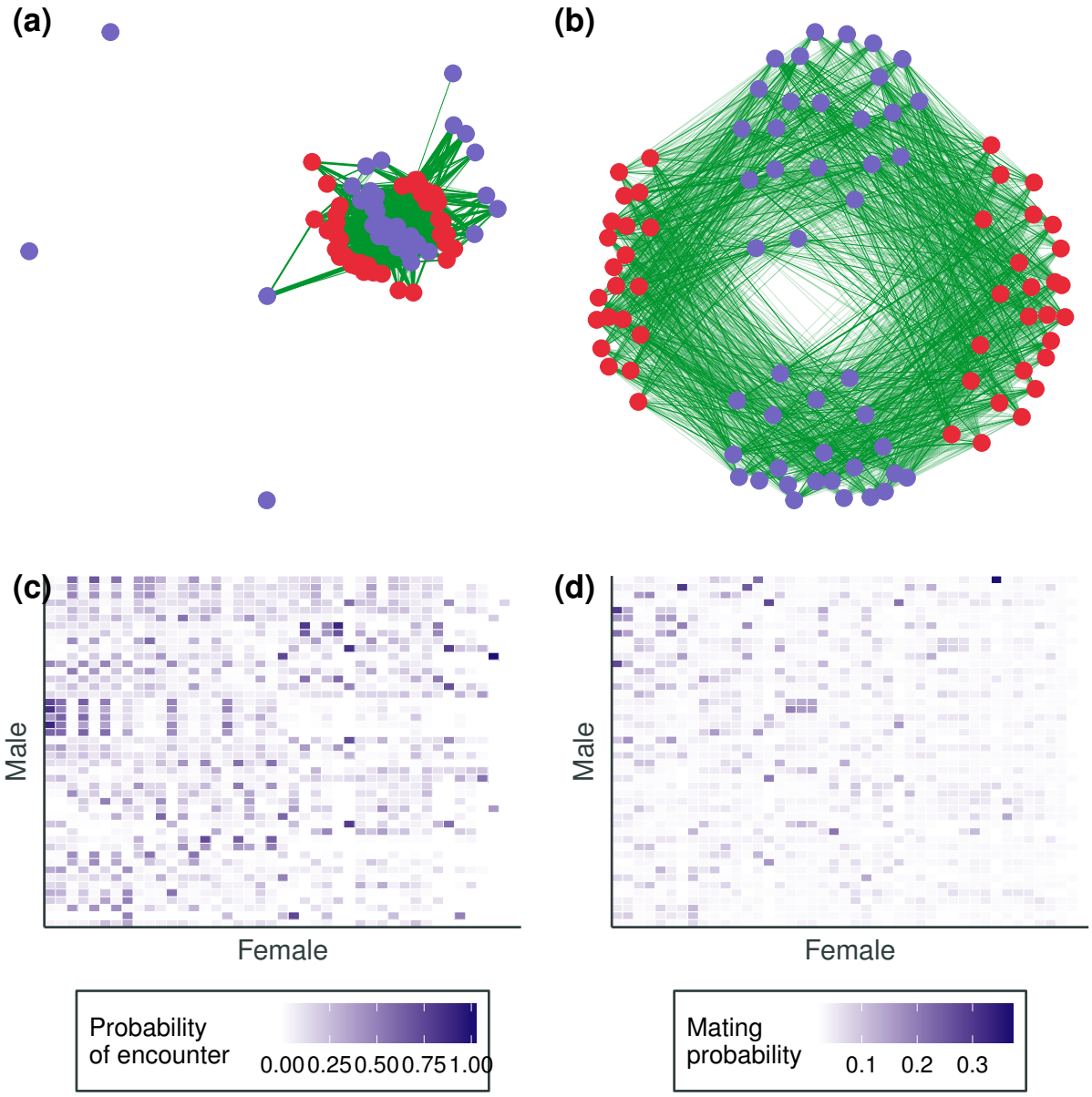


Figure. 5.10: Bi-partite networks of males (red) and females (blue) based on their encounter probability (a-c) and their mating probability (b-d) in 2010. Width of nondirectional edges increases with the corresponding probability. Relationships between individuals are also displayed in matrices. 45 anadromous salmon males and 46 females were tracked during a breeding season enabling with parentage analysis and redd mapping to rebuild these sexual network.

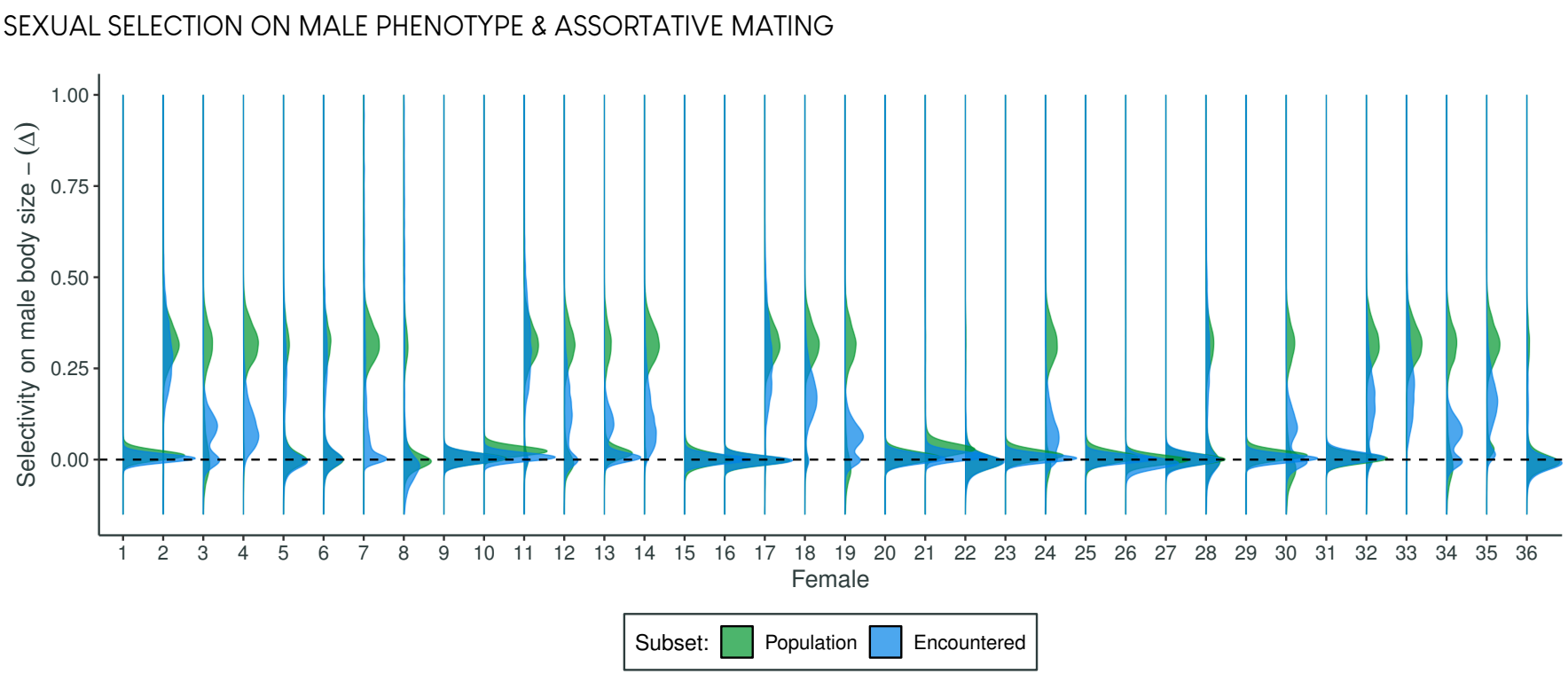


Figure. 5.11: Plot of the salmon female selectivity in male body size during the second breeding season. The average body size of males with whom a female mated has been compared to the average body size of males in the population (subset "Population") or to encountered males (subset "Encountered") for two breeding seasons: $\Delta = \frac{\mu_{\text{subset}} - \mu_{\text{mated}}}{\sigma_{\text{subset}}}$. Only these 36 females, among the 46 tracked females, exhibited encounter probability and mating probability higher than 0.05 with at least one male.

CHAPTER 6

Spatial isolation of females to other females diminishes their number of mates

Contents

6.1 INTRODUCTION

The number of mates of females matters. The number of mates of females has been neglected mainly due to the work of Bateman (1948). Bateman advocated that females had a low Bateman gradient, namely that their reproductive success is weakly related to their number of mates compared to males. However, females reproductive success may be enhanced through an increasing genetic diversity of juveniles (Bernasconi & Keller 2001, Martinez *et al.* 2000, Moran & Garcia-Vazquez 1998) or through an increasing sperm competition of cryptic choice (McDonald & Pizzari 2016; 2017). Number of mates of females may also exacerbate sexual selection faced by males (McDonald *et al.* 2013, McDonald & Pizzari 2017). Hence, Bateman gradient in females may vary between individuals and population because the mating system may affect it. For example, promiscuous species should have a strong and similar gradient between sex (Bergeron *et al.* 2012).

Space use may affect the number of mates of females through the distribution of females. Females usually compete to access breeding sites driving spatial distribution of females between breeding sites (Falcy 2015, Kokko *et al.* 2004, López-Sepulcre *et al.* 2010). In some cases, early arriving females or dominant ones may secure best-breeding sites and exclude subordinate or late arriving females (Falcy 2015). For example, Andren (1990) found that despotic Jays, *Garrulus glandarius*, enhanced their breeding success by occupying the best breeding sites characterised by older trees. Females should, thus, exhibit various spatial isolation to other females. Spatial isolation may diminish the

probability to find a sexual partner like it occurs when females are temporally isolated (Calabrese & Fagan 2004, Calabrese *et al.* 2008). Weak isolation may also allow sneaker males to participate in reproduction due to the increasing size of harems of dominant males. For example, Pérez-González & Carranza (2011) found that Red deer males, *Cervus elaphus*, raised their harem size as the spatial aggregation of females increased. Participation of sneaker males enhances genetic diversity of juveniles (Garant *et al.* 2005, Martinez *et al.* 2000). The effects of female space use on their number of mates and the subsequent effects on their reproductive success were rarely investigated. The consequences of female space use on their reproductive success have mainly been analysed in terms of offspring survival linked to the breeding habitat chose by females.

Atlantic salmon, *S. salar*, is a relevant species to assess the effects of females' spatial isolation on their number of mates and their reproductive success. The typical story is that females choose breeding sites according to physical characteristics to maximise offspring survival, early arriving individuals having access to better habitats (Falcy 2015). Males move from female to female, courting and fighting (intrasexual competition is considered to override female mate preference). In this context, the classical female distribution/EPP point of view has already been analysed (Tentelier *et al.* 2016a). However, the number of mates matters in salmon females because it affects their reproductive success (Garant *et al.* (2005), and also sexual selection in males — chapter 5). The current chapter aims to test whether the space use of females and particularly their spatial isolation affect their number of anadromous mates and their reproductive success originating from anadromous males. I hypothesised that spatial isolation 1) may vary between individuals due to their phenotype or space use behaviour, 2) negatively affects the number of mates; and 3) modifies the reproductive success of females. However, I did not hypothesise the direction of the last effect because of previous findings on habitat quality in females' home range and the density-dependent mortality acting on salmon juveniles.

6.2 METHODS

Like for the previous chapter (chapter 5, page 161), I used the data of Tentelier *et al.* (2016a) and Tentelier *et al.* (2016b). Data corresponded to the radio tracking of anadromous males and females during two breeding seasons (2009 and 2010). Parentage analysis of juveniles caught after these two breeding seasons were available, as well as redd mapping. In this chapter, I used the data from the radio tracking of anadromous, the

parentage analysis and the mating probabilities.

6.2.1 SPATIAL ISOLATION OF FEMALES

Spatial isolation of females from other females was assessed from the radio tracking data of anadromous (Tentelier *et al.* 2016a). The daily distance between each pair of females was stored in a female × female × day array. This array was then reduced to female × female matrices containing respectively the average and the minimum distances between each pair of females over the whole breeding season. Therefore, one average value and one minimum value characterised each pair of females. Each female had one vector of average distances to other females and one vector of minimal distances to other females. For each female the average value of its two vectors was computed leading to characterise each female by two values: its average isolation and its minimal isolation. For example, let one female for which the daily distance to two other females is available during three days. The Figure. 6.1 details the method to compute the average and the minimal spatial isolation of this female.

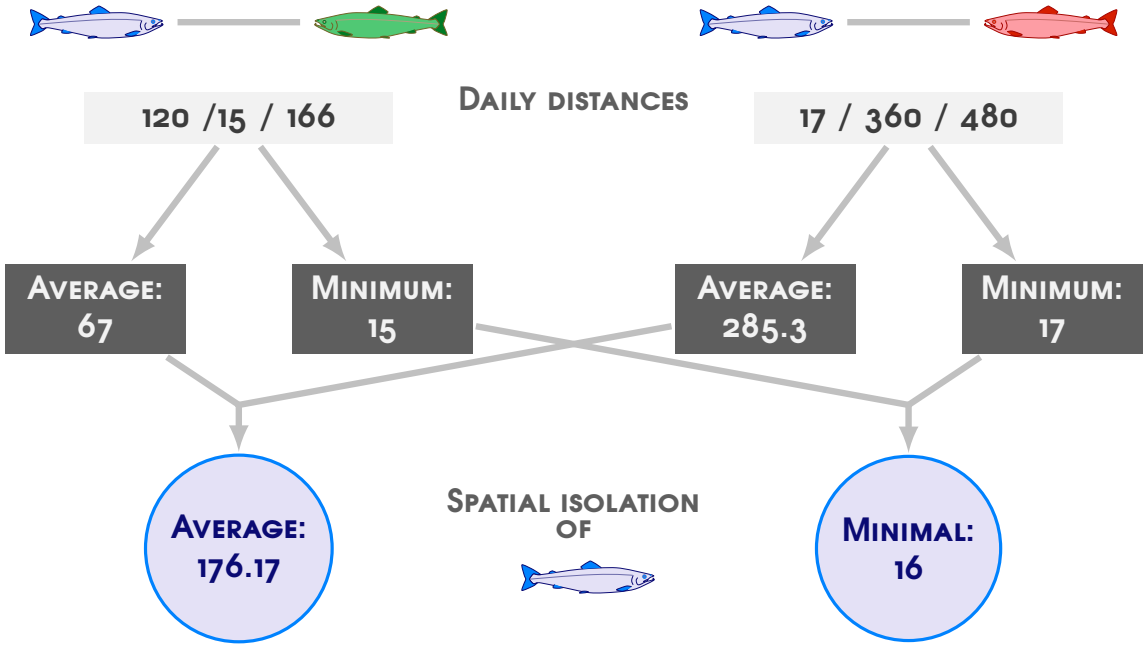


Figure. 6.1: Scheme of the computation of the spatial isolation of one female from two other females (,). The spatial isolation was defined by the "average isolation" and the "minimal isolation" and computed from the daily distances between three days.

The spatial isolation of each female was defined by the average value of 1) the

average distance to each other females (i.e. the "average isolation") and 2) the minimal distance to each other females (i.e. the "minimal isolation"). These two values were then available for 15 females in 2009 and 42 females in 2010. The correlation between these two variables was tested through a Spearman's correlation test. This test was applied on each year separately, as well as by merging the data of the two years.

The effects of four individual variables on the spatial isolation were tested to identify the determinant(s) of the spatial isolation of females. The effects of body length ($FL_{f,j}$), arrival date ($Arrival_{f,j}$), as well as covered distance ($Distance_{f,j}$) and home range ($HR_{f,j}$) were assessed. Body length and arrival date define the phenotype of each female, whereas covered distance and home range define their space use behaviour. The arrival date corresponds to the Julian day on which the female f was tagged when arriving in the study area (Tentelier *et al.* 2016a). The covered distance corresponded to the sum of the absolute daily distance covered by each female throughout the breeding season j. The four effects were tested through a unique model (Eq. 6.2), therefore, variables were standardised. A Student distribution modelled the spatial isolation of the female f which was the "average isolation" or the "minimal isolation".

$$Isolation_{f,j} = \mathcal{S}\left(\nu, \mu_{f,j}, \sigma\right)$$

$$\mu_{f,j} = intercept + \alpha_1 \times FL_{f,j} + \alpha_2 \times Arrival_{f,j} \quad \text{(Eq. 6.1)}$$

$$+\alpha_3 \times Distance_{f,j} + \alpha_4 \times HR_{f,j} \quad \text{(Eq. 6.2)}$$

This model was fitted under a Bayesian framework by calling `Stan` in `R` (Stan Development Team 2018). A Cauchy distribution centred on 0 and with a standard deviation equalled to 5 was used as prior for the five parameters. A total of 30, 000 iterations were saved from three chains with a thinning interval of 5 iterations and a warm-up of 2, 000 iterations. Chains convergence was assessed through graphical examinations, as well as with the scale reduction factor: $\hat{r}$. The effective sample size and the auto-correlation were also checked for each estimated parameter. The following models of this chapter were fitted with similar MCMC settings and the model convergence was assessed in a similar way.

6.2.2 INFLUENCE OF SPATIAL ISOLATION OF FEMALES ON THEIR NUMBER OF MATES

The number of males with whom a female f mated was extracted from data of the previous chapter (chapter 5, see page 169 for methods) and noted M_f. The number of mates used in the current chapter corresponds only to anadromous males. The number of males with whom a female mated was modelled through a Binomial distribution:

$$M_f = \mathcal{B}\left(N_{male,j}, \theta f, j\right)$$
$$\theta_{f,j} = \frac{1}{1 + \exp\left(intercept + \delta \times Isolation_{f,j}\right)} \qquad \text{(Eq. 6.3)}$$

$N_{male,j}$ is the number of effective anadromous male breeders, i.e. the males for whom at least one juvenile was found.

The parentage analysis also permitted to extract the reproductive success of each female — $T_{f,j}$ — originating from anadromous males. The reproductive success was modelled as the same model than the previous one: Eq. 6.3, but with the total number of juveniles ($N_{juv,j}$) replacing the number of effective male breeders ($N_{male,j}$). The yearly effective sizes were similar to those for polyandry with 15 females in 2009 and 42 in 2010.

6.3 RESULTS

6.3.1 SPATIAL ISOLATION OF FEMALES

In 2009, the minimal isolation ranged from 17.81 m to 176.77 m, while the average isolation varied between 82.39 and 361.06 m. During the second season, the minimal isolation ranged from 31.94 m to 871.40 m and the average isolation from 105.4 m to 958.9 m. The two variables displayed highly significant correlation when accounting years separately (Spearman for 2009 and 2010 respectively: $S_{2009} = 100$ and $S_{2010} = 0.940$, $\rho_{2009} = 8214$ and $\rho_{2010} = 0.924$, $p_{\text{value}-2009} < 0.001$ and $p_{\text{value}-2010} < 0.001$) or when merging the two years (Spearman: $S = 1600$, $\rho = 0.949$ and $p_{\text{value}} < 0.001$ — Figure. 6.2).

Because of the correlation between the average and the minimal isolation, only the results focused on the second one are displayed. Then, none of the parameters testing the different effects were significant (Table. 6.1). However, some general trends arose, in particular, the negative effects of the body length, the covered distance and the home

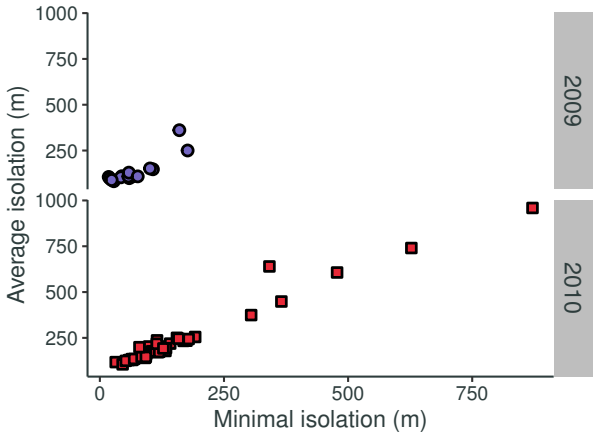


Figure. 6.2: Plot of the average spatial isolation of salmon females to the other females as a function of their minimal spatial isolation during two breeding seasons. Data concerned 15 females in 2009 (blue points) and 42 in 2010 (red points). The spatial isolation was assessed by computing the average daily distance for each pair of females and the minimal daily distance. The mean of each of these values was extracted for each female.

range. The date of arrival displayed the only one positive trend in 2009 but not in 2010. These trends are clearly visible when plotting the observed values of the minimal isolation as a function of the four variables (Figure. 6.3). The positive effect of the arrival date is also clearly visible, and the patterns in 2009 were more pronounced than in 2010 (Figure. 6.3).

6.3.2 SPATIAL ISOLATION DIMINISHED NUMBER OF MATES IN FEMALES

Number of mates ranged from zero to five during the first season and from zero to seven during the second breeding season. In 2009, only a negative trend was found between the spatial isolation of females and their number of mates (effect: -0.0035, CI95 %=[-0.0129;0.0050], 22 % of estimates upper than 0 over the 30,000 values saved). In 2010 a negative significant effect was found (effect: -0.0017, CI95%=[-0.0039;0.0001], 3 % of estimates upper than 0 over the 30,000 values saved). The significant negative effect was notably due to the fact that no females exhibiting high isolation had high number of mates (Figure. 6.4).

6.3.3 REPRODUCTIVE SUCCESS

Concerning the reproductive success, it varied from zero to 143 juveniles in 2009 and from zero to 272 juveniles in 2010 (Figure. 6.5). In 2010, one female displayed a 2.5 times higher reproductive success compared to those of other females (272 against 102), something which was not found in 2009. In 2010, a negative effect of spatial isolation

Table. 6.1: Table of the parameter estimates for the model testing the effect of the females body length, date of arrival, covered distance and home range on their minimal spatial isolation (Eq. 6.2). This model was fitted with data of 15 females in 2009 and 42 in 2010. The Bayesian P_{value} is the percentage of positive values over the 30, 000 estimated for each parameter.

Parameter	Year	Bayesian P_{value}
intercept	2009	0.45
	2010	0.00
α_1 — body length	2009	0.12
	2010	0.06
α_2 — date of arrival	2009	0.63
	2010	0.25
α_3 — covered distance	2009	0.25
	2010	0.14
α_4 — home range	2009	0.17
	2010	0.16

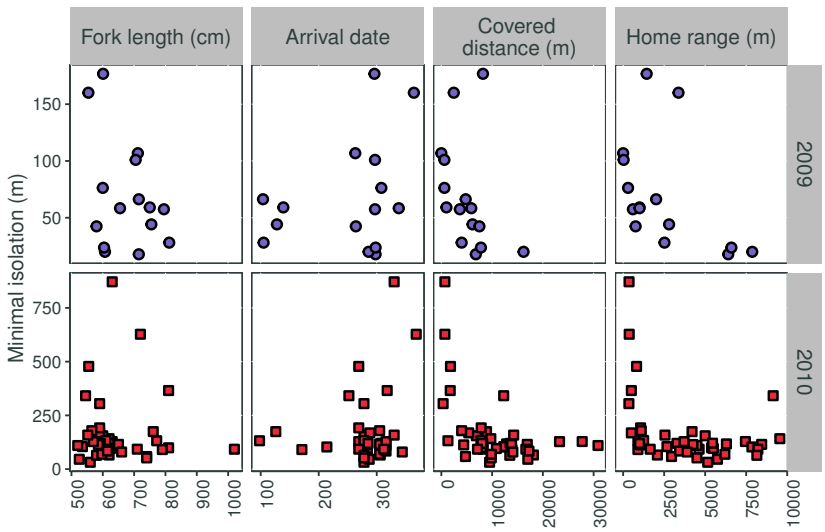


Figure. 6.3: Plot of the minimal spatial isolation of salmon females from other females as a function of their body length (cm), date of arrival (Julian day), covered distance (m), and home range (m) during two breeding seasons. Data concerned 15 females in 2009 (blue points) and 42 in 2010 (red points). The minimal spatial isolation of each female was assessed by computing the mean of the minimum daily distance between this female and the other females.

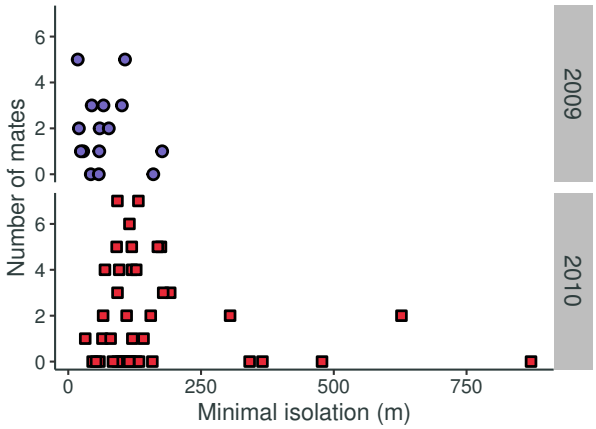


Figure. 6.4: Plot of the number of males with whom females mated as a function of their spatial isolation from the other females in the Nivelle population of Atlantic salmon. Data concerned 15 females in 2009 (blue points) and 42 in 2010 (red points). The spatial isolation of each female was assessed by computing the mean of the minimum daily distance between this female and the other females.

on reproductive success was found (0% of parameter iterations being positive — Figure. 6.6). Yet, in 2009, a positive trend was found (91.45% of parameter iterations being positive).

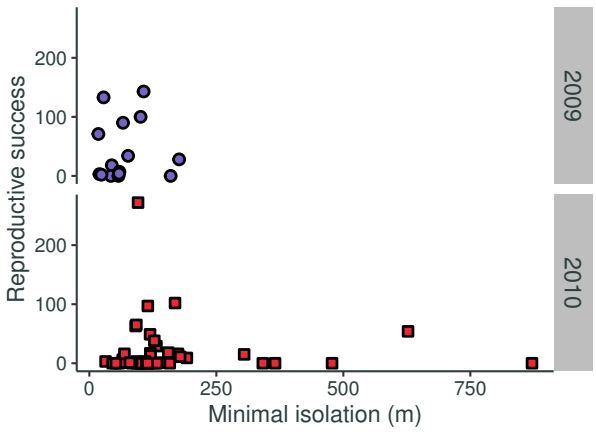


Figure. 6.5: Plot of the reproductive success of anadromous salmon females as a function of their spatial isolation from the other females. Data concerned 15 females in 2009 (blue points) and 42 in 2010 (red points). The spatial isolation of each female was assessed by computing the mean of the minimum daily distance between this female and the other females.

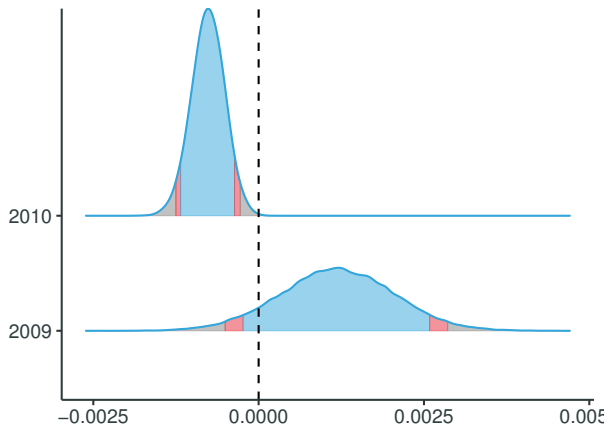


Figure. 6.6: Plot of the spatial isolation effect on the female reproductive success estimated through the model Eq. 6.3. This model describes the reproductive success of anadromous females from a Binomial distribution with the number of effective anadromous male breeders and a probability of success depending of the spatial isolation of females. Data concerned 15 females in 2009 and 42 in 2010 and 30, 000 iterations of the parameter are displayed. Gray areas denote the quantiles 2.5% and 97.5%, while the red areas correspond to the 5% and 95% quantiles.

6.4 DISCUSSION

The current chapter aimed to quantify the spatial isolation of salmon females and to identify its impact in terms of breeding. I found that the spatial isolation varied between individuals and among years. The arrival date of females tended to increase the spatial isolation of females, while their home range did not seem to affect their spatial isolation. I found a negative effect of the spatial isolation of females on their number of mates validating my hypothesis. The spatial isolation of females tended to increase the reproductive success in 2009, whereas the spatial isolation diminished the reproductive success in 2010.

Spatial isolation of females during the breeding season varied between individuals. During the first breeding season, a positive trend was found between the arrival date and the spatial isolation. When the number of individuals increases (e.g. during the second season), the trend disappears. However, only late arrival individuals displayed high values of spatial isolation during the two years. Such findings can be explained by the fact that early arriving individuals aggregate in the best spawning sites. Consequently, some individuals aggregate in lower quality sites while the other individuals disperse to other quality sites where density is low. This explanation agrees with Falcy (2015) who found that early arriving females secure the best-spawning sites. Tentelier *et al.*

(2016a) found similar results in Atlantic salmon. In the Nivelle, the best breeding sites correspond to river part of more than several tens of metres which could explain why females in best-spawning sites are aggregated and not isolated.

The spatial isolation of females diminished their number of mates. Females aggregated with others exhibit weak values of spatial isolation. Monopolisation of females by dominant salmon males can be favoured when females are aggregated generating monogamy in females. However, a strong aggregation of females may favour sneaky males and also make the direct competition between males for females too costly (Weir *et al.* 2011). When females are also too scarcely distributed and isolated, it becomes too difficult for a male to secure females generating polygamy (Debuse *et al.* 2003). Hence, spatial isolation of females may diminish their Environmental Potential for Polygamy (Emlen & Oring 1977).

Despite the observed variations, spatial isolation of females remained weak over these two years. Indeed, apart for two females in 2010, the minimal isolation was lower than 200 m which is two times lower than 500 m, the distance at which a male may stay before to participate in reproduction at a redd as noted by Tentelier *et al.* (2016a). The weak spatial isolation of salmon females potentially originates from their choice to breed at the same location either in relation to the habitat quality or also due to social facilitation and copying (Broly *et al.* 2012, Wagner & Danchin 2003). In all cases, the weak isolation makes the females easily detectable by males which can be another explanation of the absence of effects on their number of mates.

The date of arrival interacts with the breeding site quality and the spatial isolation. A significant negative effect of the spatial isolation of females on their reproductive success was found in 2010, while a positive trend was found in 2009. In 2010, Tentelier *et al.* (2016a) found that early arriving females exhibited best habitat quality in their home range and that habitat quality enhanced their reproductive success. At the opposite, Tentelier *et al.* (2016a) found no effect in 2009. My results, those of Tentelier *et al.* (2016a) and those of Falcy (2015) suggest that when a lot of females are present (in 2010 compared to 2009 here), those arriving early can secure and aggregate in best-breeding sites (i.e. low spatial isolation). The high quality of the secured sites enhanced their reproductive success. Late arriving females are forced to disperse into low-quality

sites (high isolation) diminishing their reproductive success. In 2009, the low number of females allowed early or late arriving females to secure the best sites. Spatial isolation seemed to result from the breeding choices of females which were conditioned by the density of females and their arrival date.

However, the relationship between the spatial isolation and reproductive success remains not strongly pronounced in 2009 and seems to be asymptotic in 2010. The asymptotic pattern could explain why Tentelier *et al.* (2016a) did not find that the habitat quality in the females' home range enhanced their reproductive success in 2010. At the opposite, Tentelier *et al.* (2016a) found that early arriving females displayed a higher habitat quality in their home which improves their reproductive success. Results of Tentelier *et al.* (2016a), those of Falcy (2015) and my results suggest that early arriving females occupy and aggregate (i.e. their spatial isolation decreases) in the best sites. Even if they are in lower quality breeding sites, late arrival females exhibit spatial isolation enabling to dampen the density-dependent mortality which could not be counterbalanced by the habitat quality. The fact that spatial isolation was not higher in 2009 when the number of females was quite lower than in 2010 advocates for aggregation of females in best sites. The positive trend found in 2009 (mean $\pm$ standard deviation: $0.0012 \pm 0.0009 \frac{\text{juvenile}}{m}$) indicates that around 830 m are required to increase the reproductive success of a female by one juvenile. This necessary distance is almost the double of the dispersal distance of salmon juveniles usually found in literature (Beall 1994, Einum & Nislow 2005, Garcia de Leaniz *et al.* 2000). This weak positive effect and the negative effect in 2010 also suggest that carrying capacity or habitat availability (concerning best sites researched by females) could be too low in the Nivelle.

The current chapter demonstrated that spatial isolation of females varies between individuals. The arrival date of females increased their spatial isolation suggesting that early arriving females may secure the best sites. These aggregated females also had a higher number of mates probably because their aggregation favoured sneaky males and polygamy. At the opposite, isolated females seemed to be late arriving individuals choosing habitats of lower quality. Such isolated females demonstrated a lower reproductive success indicating that choosing a lower quality site to diminish density-dependent mortality acting on juveniles (Milner *et al.* 2003, Nislow *et al.* 2004) seemed not to be an adaptive strategy. The spatial distribution of females could, thereby, play a more im-

portant role in larger populations within larger river systems. The approach developed here could be applied and generalised to other salmon populations where the spatial structure could be more pronounced.

HIGHLIGHTS OF CHAPTER 6

- A major part of studies about sexual selection adopts a male's view because in most taxa males have to compete to access females so that sexual selection is mainly acting on them.
- The spatial isolation of females from other females tended to increase with their date of arrival in the river suggesting that early arriving females occupy the best breeding sites and chase other females.
- The spatial isolation of females diminished their number of mates suggesting that aggregation of females favour sneaky males.
- Finally, the weak positive effect of isolation on reproductive success in 2009 and the negative effect in 2010 tend to suggest that availability of good breeding sites are restricting in the Nivelle.

Discussion of Part III

Spatial distribution and local social structure within a population generated yearly variation in mating system and in sexual selection. The spatial aggregation of nests, informing on female aggregation, influenced the effective size of the population (chapter 4, page 153), potentially through the Environmental Potential for Polygamy of males (EPP). The generated local social structure suggests that the mating system of anadromous Atlantic salmon is highly plastic (chapter 5, page 161) especially from the males' view. At the opposite, females exhibited number of anadromous mates which did not vary with their spatial isolation (chapter 6, page 199). The local structure skews encounters between individuals and informs that the subset of encountered individuals modifies the mating system, as well as the social competitive environment (chapter 5, page 161). Finally, my results of the three chapters indicate the local social structure affects the participation of anadromous sneaker males in reproduction.

A LOCAL SOCIAL STRUCTURE WITHIN A SMALL POPULATION

A plastic and local structure within the Nivelle population. Chapter 6 highlights that early arriving females exhibited lowest spatial isolation from other females; the spatial isolation varied between females indicating a local social structure. Chapter 5 strengthens the idea of a local social structure by accounting encounters for matings and between opposite-sex individuals. The structure seemed more pronounced in 2009 agreeing with the smaller home ranges exhibited in 2009 (Tentelier *et al.* 2016a). Spatial isolation was higher on average in 2010 than in 2009 whereas the number of individuals was twice as high in 2010 as in 2009. However, the higher spatial isolation in 2010 was only due to some individuals, the isolation pattern of other individuals was similar to the isolation pattern found in 2009 (Figure. 6.2, page 205). The effect of yearly spatial aggregation of nests on the number of effective breeders in the population also agrees with the idea

of a local social structure (chapter 4).

A stronger structure could be hypothesised in larger and more complex systems. The Nivelle River remains a small river system compared to many systems hosting Atlantic salmon populations. In the Nivelle, only 25 km are available for salmon. The small size of the Nivelle River system could explain why the encounter network between individuals was not strongly nested (chapter 5), as well as the spatial isolation of females from other females which remained weak (chapter 6). In more complex river systems with a higher suitable area for Atlantic salmon (Prevost 2003), the spatial distribution of anadromous individuals could lead to more spatially structured social interactions illustrated by nested networks. For example, in the Sainte-Marguerite River (Canada) exhibiting a "principal branch" of 101.4 km long and a "Northeast branch" of 85 km long, a sub-population structure was already found through a genetic analysis (Garant *et al.* 2000). Some evidence for a genetic substructure within a population was also found in the River Tamar (UK) where multiple tributaries are used by salmon (Ellis *et al.* 2011). Applying a similar approach in such river system should highlight a spatially structured social network around several cores as a determinant of the observed genetic structure.

The spatial distribution of potential breeders generates this structure. The three chapters took three different approaches, either focused at the population level (chapter 4), or at the individual level clustering both sex (chapter 5) or focusing on only one sex (chapter 6). These approaches were all based on the spatial distribution of potential breeders: either on their resultant spatial aggregation (chapter 4) or spatial isolation (chapter 6), or their daily positions (chapter 5). In these chapters, all approaches permitted to suggest that the spatial distribution of potential breeders generated the local structure. Such findings agree with studies focusing on different taxa where authors linked spatial distribution or space use to social interactions (Fisher & Lara 1999, Formica *et al.* 2010, Muniz *et al.* 2015, Robert *et al.* 2012). In addition, isolated females seem to encounter fewer males, which supports that the spatial distribution of potential breeders generates local social structure (box Deeper III.i).

DEEPER III.i: Spatial isolation of females & encountered males

The influence of the spatial distribution of potential breeders on encounters is the main idea of this part. The spatial isolation of females from other females computed in the chapter 6 was, therefore, linked to the number of encountered males. This number was determined from the encounter probability between each female and each male computed in chapter 5. A male was considered as encountered by a female when the probability was upper than 0.05. A Poisson regression was used to test the effect of the minimal isolation of the female f on the number of encountered males N: $N_{f,j} \sim \mathcal{P}\left(\exp\left(\text{intercept} + \alpha \times \text{Isolation}_{f,j}\right)\right)$. This model was separately fitted on each breeding season j.

A similar negative effect was found for the both year (mean and confidence interval at 95%): α_{2009}=-0.42 $[-0.93; 0.03]$ and α_{2010}=-0.70 $[-0.94; -0.47]$ (Figure below).

This relationship clearly supports that the spatial distribution of potential breeders affects their encounters. Interestingly, it seems that a threshold around 250 m was present.

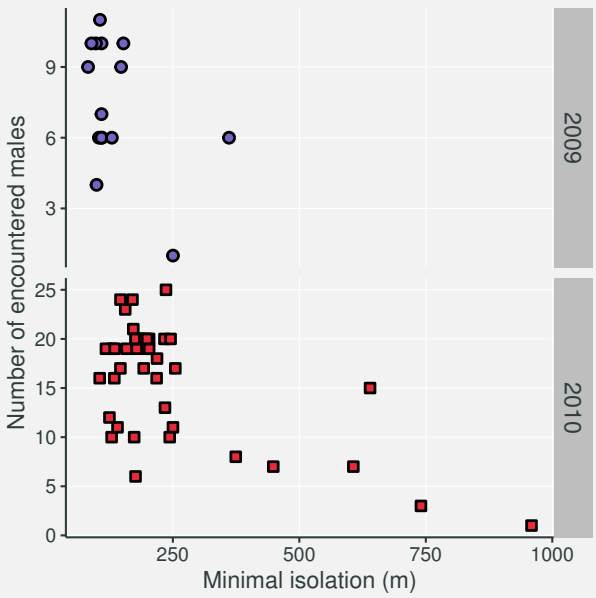


Figure. III.iii: Plot of the number of encountered males estimated from chapter 5 as a function of the minimal isolation of females to other females. Data corresponded to 15 females / 17 males in 2009 and 42 females / 46 males in 2010.

success corresponded to the number of partners with which at least one juvenile was sired. Spatial isolation of females diminished their number of mates and generated variability in the number of mates (chapter 6). Variability in the number of mates found for males (chapter 5) and females (chapter 6) suggest that true mating success (i.e. the number of matings producing juveniles) varies among individuals in both sex as advocated by Garant *et al.* (2001). Thereby, although assessment of the true mating success of males and females remains difficult, obtaining it could be a valuable information source to identify causes of variations in polygamy.

The participation of sneaker males also varies with the spatial distribution of potential breeders. Another complexity of the mating success of Atlantic salmon arises from the participation of sneaker anadromous males. Results of the chapters 4 and 5 suggest that the spatial aggregation of females seems to allow anadromous satellite males to access to eggs by adopting a sneaky behaviour (Figure. III.iv). Indeed, antagonistic interactions diminish when aggregation of females become too high with a strongly skewed OSR(Weir *et al.* 2011). Such findings suggest that some satellite anadromous males may have access to females by adopting a sneaky behaviour as hypothesised by Weir *et al.* (2011) and illustrated by the Figure. III.iv. Such findings were also found in other fishes such as guppies when the OSR becomes skewed (Chuard *et al.* 2016).

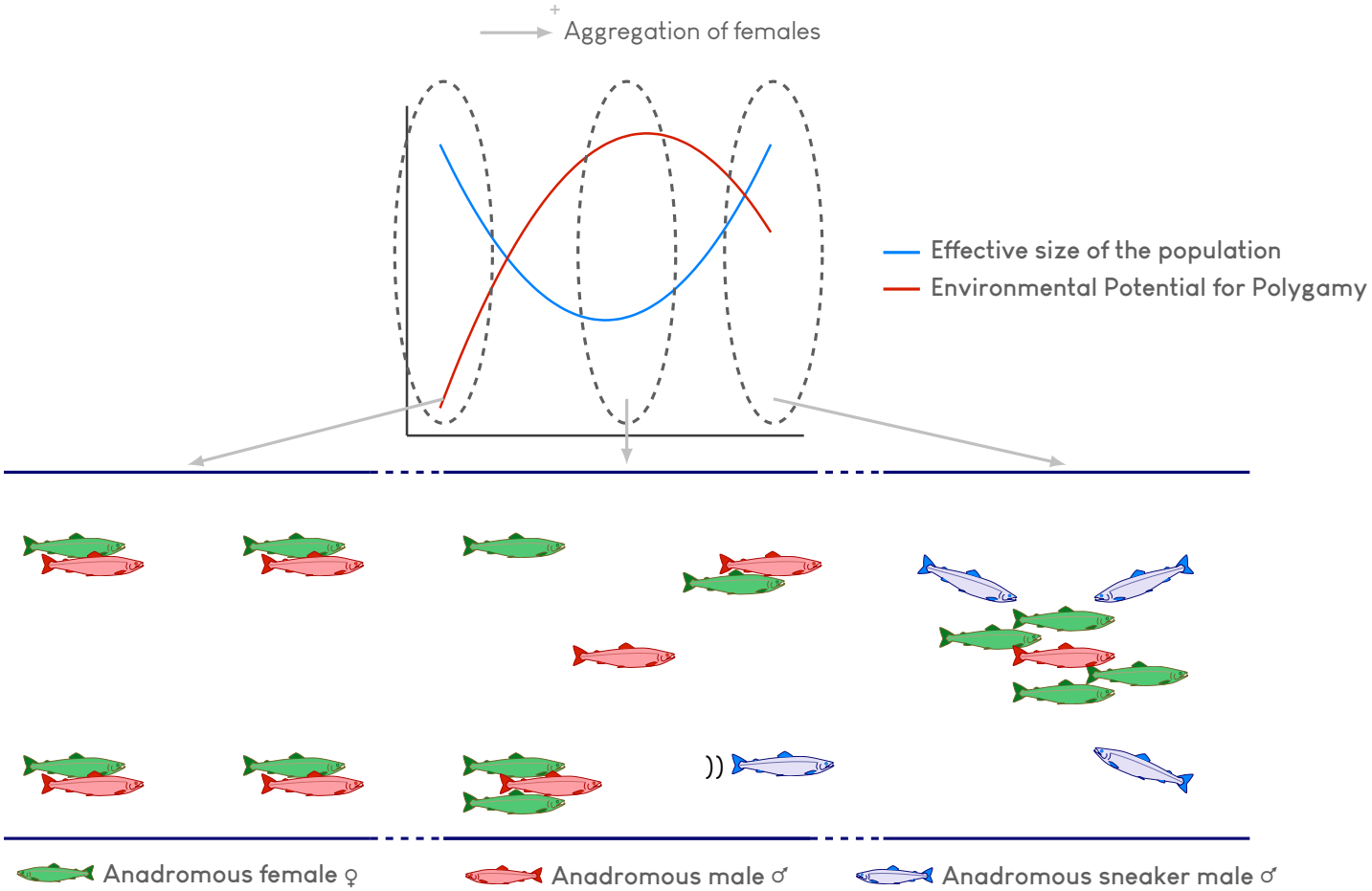


Figure. III.iv: Scheme of three scenarii of spatial aggregation of females — . At weak aggregation (left), males cannot monopolise females, hence numerous males — — have access to females. When aggregation increases (middle), a male may monopolise and secure several females. However a strong aggregation (right) enables several sneaker males — — to participate in reproduction. This scheme illustrates the relation between the spatial aggregation and females and the resultant Environmental Potential for Polygamy of anadromous males, as well as with the effective size of the population.

CONCLUSION

The main approach of the current part was to combine analyses at the population level but also at the individual level to investigate interactions between individuals during the breeding season. In this way, the current part highlighted that the mating system of the Atlantic salmon is highly dynamic and plastic due to the spatial distribution of potential breeders. In addition, I advocate for better accounting for the local structure in encounters between individuals during the reproduction, something which can be especially true in more complex river systems.

However, as exposed previously, the mating success was either estimated or approximated with the number of sexual partners. Succeeding in the assessment of the true mating success (i.e. the number of matings producing juveniles) could be useful to improve the description of the mating system and to determine factors affecting this mating success. A promising approach to investigate these questions could also be to obtain the spawning activity, as well as the parentage analyses at the redd level in the Nivelle and to combine them to the spatial displacements of individuals. However, one remaining factor to really describe mating and sexual competition is the temporal dimension even if a temporal dimension was accounted in the chapter 5. Indeed, like the spatial dimension, the temporal one may generate aggregation and skewed OSR (Calabrese & Fagan 2004). Finally, I have discussed the participation of the anadromous sneakers but salmon exhibit another Alternative Reproductive Tactic siring up to 65% of juveniles within a redd (Martinez *et al.* 2000): mature parr.

Next part: ⇒ page 233

Bibliography

Almeida-Neto, M., Guimarães, P., Guimarães, P.R., Loyola, R.D. & Ulrich, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* **117**, 1227–1239.

Andersson, M. & Simmons, L.W. (2006) Sexual selection and mate choice. *Trends in Ecology & Evolution* **21**, 296–302.

Andren, H. (1990) Despotic distribution, unequal reproductive success, and population regulation in the jay *Garrulus Glandarius* L. *Ecology* **71**, 1796–1803.

Bacles, C.F.E., Bouchard, C., Lange, F., Manicki, A., Tentelier, C. & Lepais, O. (2018) Estimating the effective number of breeders from single parr samples for conservation monitoring of wild populations of Atlantic salmon *Salmo salar*. *Journal of Fish Biology* **92**, 699–726.

Bateman, A.J. (1948) Intra-sexual selection in Drosophila. *Heredity* **2**, 349–368.

Beall, E. (1994) Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. *ICES Journal of Marine Science* **51**, 1–9.

Beauchamp, M.A. (1965) An improved index of centrality. *Behavioral Science* **10**, 161–163.

Bergeron, P., Montiglio, P.O., Réale, D., Humphries, M.M. & Garant, D. (2012) Bateman gradients in a promiscuous mating system. *Behavioral Ecology and Sociobiology* **66**, 1125–1130.

Berghe, E.P.v.d. & Gross, M.R. (1984) Female Size and Nest Depth in Coho Salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 204–206.

Bernasconi, G. & Keller, L. (2001) Female polyandry affects their sons' reproductive success in the red flour beetle *Tribolium castaneum*: Female polyandry and sons' reproductive success. *Journal of Evolutionary Biology* **14**, 186–193.

Blüthgen, N. (2010) Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. *Basic and Applied Ecology* **11**, 185–195.

Bouchard, C., Bardonnet, A., Buoro, M. & Tentelier, C. (2018) Effects of spatial aggregation of nests on population recruitment: the case of a small population of Atlantic salmon. *Ecosphere* **9**.

Broly, P., Mullier, R., Deneubourg, J.L. & Devigne, C. (2012) Aggregation in woodlice: social interaction and density effects. *ZooKeys* **176**, 133–144.

Brun, M., Abraham, C., Jarry, M., Dumas, J., Lange, F. & Prévost, E. (2011) Estimating an homogeneous series of a population abundance indicator despite changes in data collection procedure: A hierarchical Bayesian modelling approach. *Ecological Modelling* **222**, 1069–1079.

Butts, C.T. (2009) Revisiting the foundations of network analysis. *science* **325**, 414–416.

Calabrese, J.M. & Fagan, W.F. (2004) Lost in time, lonely, and single: reproductive asynchrony and the Allee effect. *The American Naturalist* **164**, 25–37.

Calabrese, J.M., Ries, L., Matter, S.F., Debinski, D.M., Auckland, J.N., Roland, J. & Fagan, W.F. (2008) Reproductive asynchrony in natural butterfly populations and its consequences for female matelessness. *Journal of Animal Ecology* **77**, 746–756.

Calsbeek, R. & Sinervo, B. (2002) An experimental test of the ideal despotic distribution. *Journal of Animal Ecology* **71**, 513–523.

Cam, E., Monnat, J.Y. & Hines, J.E. (2003) Long-term fitness consequences of early conditions in the kittiwake. *Journal of Animal Ecology* **72**, 411–424.

Cassini, M.H. (2000) A model on female breeding dispersion and the reproductive systems of pinnipeds. *Behavioural Processes* **51**, 93–99.

Chuard, P.J.C., Brown, G.E. & Grant, J.W.A. (2016) The effects of adult sex ratio on mating competition in male and female guppies (*Poecilia reticulata*) in two wild populations. *Behavioural Processes* **129**, 1–10.

Croft, D.P., Madden, J.R., Franks, D.W. & James, R. (2011) Hypothesis testing in animal social networks. *Trends in Ecology & Evolution* **26**, 502–507.

Cunningham, C., Parra, J.E., Coals, L., Beltrán, M., Zefania, S. & Székely, T. (2018) Social interactions predict genetic diversification: an experimental manipulation in shorebirds. *Behavioral Ecology* **29**, 609–618.

De, P., Singh, A.E., Wong, T., Yacoub, W. & Jolly, A.M. (2004) Sexual network analysis of a gonorrhoea outbreak. *Sexually Transmitted Infections* **80**, 280–285.

de Gaudemar, B., Schroder, S.L. & Beall, E.P. (2000) Nest placement and egg distribution in Atlantic salmon redds. *Environmental Biology of Fishes* **57**, 37–47.

Debuse, V.J., Addison, J.T. & Reynolds, J.D. (2003) Effects of breeding site density on competition and sexual selection in the European lobster. *Behavioral Ecology* **14**, 396–402.

Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* **66**, 973–988.

Dunham, J., Rieman, B. & Davis, K. (2001) Sources and magnitude of sampling error in redd counts for bull trout. *North American Journal of Fisheries Management* **21**, 343–352.

Einum, S. & Nislow, K.H. (2005) Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. *Oecologia* **143**, 203–210.

Einum, S., Nislow, K.H., Mckelvey, S. & Armstrong, J.D. (2008) Nest distribution shaping within-stream variation in Atlantic salmon juvenile abundance and competition over small spatial scales. *Journal of Animal Ecology* **77**, 167–172.

Ellis, J.S., Sumner, K.J., Griffiths, A.M., Bright, D.I. & Stevens, J.R. (2011) Population genetic structure of Atlantic salmon, *Salmo salar* L., in the River Tamar, southwest England: population genetic structure of Atlantic salmon. *Fisheries Management and Ecology* **18**, 233–245.

Ellis, S., Franks, D.W., Nattrass, S., Cant, M.A., Weiss, M.N., Giles, D., Balcomb, K.C. & Croft, D.P. (2017) Mortality risk and social network position in resident killer whales: sex differences and the importance of resource abundance. *Proc. R. Soc. B* **284**, 20171313.

Emlen, S.T. & Oring, L.W. (1977) Ecology, sexual selection, and evolution of mating systems. *Science* **197**, 215–223.

Falcy, M.R. (2015) Density-dependent habitat selection of spawning Chinook salmon: broad-scale evidence and implications. *Journal of Animal Ecology* **84**, 545–553.

Farine, D. (2017) The dynamics of transmission and the dynamics of networks. *Journal of Animal Ecology* **86**, 415–418.

Farine, D.R. & Whitehead, H. (2015) Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology* **84**, 1144–1163.

Finstad, A.G., Einum, S., Ugedal, O. & Forseth, T. (2009) Spatial distribution of limited resources and local density regulation in juvenile Atlantic salmon. *Journal of Animal Ecology* **78**, 226–235.

Finstad, A.G., Okland, F., Thorstad, E.B. & Heggberget, T.G. (2005) Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology* **67**, 919–930.

Fisher, D.O. & Lara, M.C. (1999) Effects of body size and home range on access to mates and paternity in male bridled nailtail wallabies. *Animal Behaviour* **58**, 121–130.

Foldvik, A., Finstad, A.G. & Einum, S. (2010) Relating juvenile spatial distribution to breeding patterns in anadromous salmonid populations. *Journal of Animal Ecology* **79**, 501–509.

Formica, V.A., Augat, M.E., Barnard, M.E., Butterfield, R.E., Wood, C.W. & Brodie, E.D. (2010) Using home range estimates to construct social networks for species with indirect behavioral interactions. *Behavioral Ecology and Sociobiology* **64**, 1199–1208.

Formica, V.A., McGlothlin, J.W., Wood, C.W., Augat, M.E., Butterfield, R.E., Barnard, M.E. & Brodie III, E.D. (2011) Phenotypic assortment mediates the effect of social selection in a wild beetle population. *Evolution* **65**, 2771–2781.

Fretwell, S.D. & Lucas, H.L.J. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16–36.

Garant, D., Dodson, J.J. & Bernatchez, L. (2000) Ecological determinants and temporal stability of the within-river population structure in Atlantic salmon (*Salmo salar* L.)*. *Molecular Ecology* **9**, 615–628.

Garant, D., Dodson, J.J. & Bernatchez, L. (2001) A genetic evaluation of mating system and determinants of individual reproductive success in Atlantic salmon (*Salmo salar* L.). *Journal of Heredity* **92**, 137–145.

Garant, D., Dodson, J.J. & Bernatchez, L. (2005) Offspring genetic diversity increases fitness of female Atlantic salmon (*Salmo salar*). *Behavioral Ecology and Sociobiology* **57**, 240–244.

Garant, D., Fontaine, P.M., Good, S.P., Dodson, J.J. & Bernatchez, L. (2002) The influence of male parental identity on growth and survival of offspring in Atlantic salmon (*Salmo salar*). *Evolutionary Ecology Research* **4**, 537–549.

Garcia de Leaniz, C., Fraser, N. & Huntingford, F.A. (2000) Variability in performance in wild Atlantic salmon, *Salmo salar* L., fry from a single redd. *Fisheries Management and Ecology* **7**, 489–502.

Gasparini, C., Serena, G. & Pilastro, A. (2013) Do unattractive friends make you look better? Context-dependent male mating preferences in the guppy. *Proceedings of the Royal Society of London B: Biological Sciences* **280**, 20123072.

Gelman, A., Jakulin, A., Pittau, M.G. & Su, Y.S. (2008) A weakly informative default prior distribution for logistic and other regression models. *The Annals of Applied Statistics* **2**, 1360–1383.

Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science* **7**, 457–472.

Grimardias, D., Merchermek, N., Manicki, A., Garnier, J., Gaudin, P., Jarry, M. & Beall, E. (2010) Reproductive success of Atlantic salmon (*Salmo salar*) mature male parr in a small river, the Nivelle: influence of shelters: Mature male parr success and shelters. *Ecology of Freshwater Fish* **19**, 510–519.

Hendry, A.P., Berg, O.K. & Quinn, T.P. (2001) Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores). *Oikos* **93**, 407–418.

Holtby, L.B. & Healey, M.C. (1986) Selection for Adult Size in Female Coho Salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 1946–1959.

Hunt, J., Breuker, C.J., Sadowski, J.A. & Moore, A.J. (2009) Male–male competition, female mate choice and their interaction: determining total sexual selection. *Journal of Evolutionary Biology* **22**, 13–26.

James, R., Croft, D.P. & Krause, J. (2009) Potential banana skins in animal social network analysis. *Behavioral Ecology and Sociobiology* **63**, 989–997.

Janicke, T. & Morrow, E.H. (2018) Operational sex ratio predicts the opportunity and direction of sexual selection across animals. *Ecology Letters* .

Järvi, T. (1990) The effects of male dominance, secondary sexual characteristics and female mate choice on the mating success of male Atlantic salmon *Salmo salar*. *Ethology* **84**, 123–132.

Jones, A.G. (2009) On the opportunity for sexual selection, the bateman gradient and the maximum intensity of sexual selection. *Evolution* **63**, 1673–1684.

Jones, M.W. & Hutchings, J.A. (2002) Individual variation in Atlantic salmon fertilization success: implications for effective population size. *Ecological Applications* **12**, 184–193.

Kamath, A. & Losos, J.B. (2018) Estimating encounter rates as the first step of sexual selection in the lizard *Anolis sagrei*. *Proc. R. Soc. B* **285**, 20172244.

Kazakov, R.V. (1981) The effect of the size of Atlantic salmon, *Salmo salar* L., eggs on embryos and alevins. *Journal of Fish Biology* **19**, 353–360.

Kirkpatrick, M. & Ryan, J.R. (1991) The evolution of mating preferences and the paradox of lek. *Nature* **350**, 33–38.

Kokko, H., Harris, M.P. & Wanless, S. (2004) Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. *Journal of Animal Ecology* **73**, 367–376.

Kokko, H. & Rankin, D.J. (2006) Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 319–334.

Kossinets, G. (2003) Effects of missing data in social networks. *arXiv:cond-mat/0306335* ArXiv: cond-mat/0306335.

Krause, J., Croft, D.P. & James, R. (2007) Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology* **62**, 15–27.

Kuijper, B., Pen, I. & Weissing, F.J. (2012) A Guide to sexual selection theory. *Annual Review of Ecology, Evolution, and Systematics* **43**, 287–311.

Lloyd, M. (1967) Mean crowding. *Journal of Animal Ecology* **36**, 1–30.

López-Sepulcre, A., Kokko, H. & Norris, K. (2010) Evolutionary conservation advice for despotic populations: habitat heterogeneity favours conflict and reduces productivity in Seychelles magpie robins. *Proceedings of the Royal Society of London B: Biological Sciences* **277**, 3477–3482.

Louhi, P., Mäki-Petäys, A. & Erkinaro, J. (2008) Spawning habitat of Atlantic salmon and brown trout: general criteria and intragravel factors. *River Res. Applic.* **24**, 330–339.

Makiguchi, Y., Ichimura, M., Kitayama, T., Kawabata, Y., Kitagawa, T., Kojima, T. & Pitcher, T.E. (2016) Sperm allocation in relation to female size in a semelparous salmonid. *Royal Society Open Science* **3**, 160497.

Martinez, J.L., Moran, P., Perez, J., De Gaudemar, B., Beall, E. & Garcia-Vazquez, E. (2000) Multiple paternity increases effective size of southern Atlantic salmon populations. *Molecular Ecology* **9**, 293–298.

McDonald, G.C., James, R., Krause, J. & Pizzari, T. (2013) Sexual networks: measuring sexual selection in structured, polyandrous populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20120356–20120356.

McDonald, G.C. & Pizzari, T. (2015) Mating behaviour: Sexual networks and sexual selection. *Animal social networks*, Oxford University Press, krause edn.

McDonald, G.C. & Pizzari, T. (2016) Why patterns of assortative mating are key to study sexual selection and how to measure them. *Behavioral Ecology and Sociobiology* **70**, 209–220.

McDonald, G.C. & Pizzari, T. (2017) Structure of sexual networks determines the operation of sexual selection. *Proceedings of the National Academy of Sciences* p. 9.

Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S. & Ladle, M. (2003) The natural control of salmon and trout populations in streams. *Fisheries Research* **62**, 111–125.

Mjølnerød, I.B., Fleming, I.A., Refseth, U.H. & Hindar, K. (1998) Mate and sperm competition during multiple-male spawnings of Atlantic salmon. *Canadian Journal of Zoology* **76**, 70–75.

Montiglio, P.O., McGlothlin, J.W. & Farine, D.R. (2018) Social structure modulates the evolutionary consequences of social plasticity: A social network perspective on interacting phenotypes. *Ecology and Evolution* **8**, 1451–1464.

Moran, P. & Garcia-Vazquez, E. (1998) Brief communication. Multiple paternity in Atlantic salmon: a way to maintain genetic variability in relicted populations. *Journal of Heredity* **89**, 551–553.

Muniz, D.G., Guimarães, P.R., Buzatto, B.A. & Machado, G. (2015) A sexual network approach to sperm competition in a species with alternative mating tactics. *Behavioral Ecology* **26**, 121–129.

Myers, R.A. & Hutchings, J.A. (1987) Mating of anadromous Atlantic salmon, *Salmo salar* L., with mature male parr. *Journal of Fish Biology* **31**, 143–146.

Nislow, K.H., Einum, S. & Folt, C.L. (2004) Testing predictions of the critical period for survival concept using experiments with stocked Atlantic salmon. *Journal of Fish Biology* **65**, 188–200.

Oh, K.P. & Badyaev, A.V. (2010) Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *The American Naturalist* **176**, E80–E89.

Okasha, S. (2004) Multilevel Selection and the Partitioning of Covariance: A Comparison of Three Approaches. *Evolution* **58**, 486–494.

Økland, F., Erkinaro, J., Moen, K., Niemelä, E., Fiske, P., McKinley, R.S. & Thorstab, E.B. (2001) Return migration of Atlantic salmon in the River Tana: phases of migratory behaviour. *Journal of Fish Biology* **59**, 862–874.

Opsahl, T. & Panzarasa, P. (2009) Clustering in weighted networks. *Social Networks* **31**, 155–163.

Parker, G.A. (1970) The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scatophagidae): II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. *The Journal of Animal Ecology* **39**, 205.

Parker, G.A. (1974) The reproductive behaviour and the nature of sexual selection *Scatophaga stercoraria* L. (Diptera: Scatophagidae). IX. Spatial distribution of fertilization rates and evolution of male search strategy within the reproductive area. *Evolution* **28**, 93–108.

Pérez-González, J. & Carranza, J. (2011) Female aggregation interacts with population structure to influence the degree of polygyny in red deer. *Animal Behaviour* **82**, 957–970.

Perkins, S.E., Cagnacci, F., Stradiotto, A., Arnoldi, D. & Hudson, P.J. (2009) Comparison of social networks derived from ecological data: implications for inferring infectious disease dynamics: Social networks for inferring disease dynamics. *Journal of Animal Ecology* **78**, 1015–1022.

Pinter-Wollman, N., Hobson, E.A., Smith, J.E., Edelman, A.J., Shizuka, D., de Silva, S., Waters, J.S., Prager, S.D., Sasaki, T., Wittemyer, G., Fewell, J. & McDonald, D.B. (2014) The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behavioral Ecology* **25**, 242–255.

Prevost, E. (2003) Setting biological reference points for Atlantic salmon stocks: transfer of information from data-rich to sparse-data situations by Bayesian hierarchical modelling. *ICES Journal of Marine Science* **60**, 1177–1193.

Procter, D.S., Moore, A.J. & Miller, C.W. (2012) The form of sexual selection arising from male-male competition depends on the presence of females in the social environment: Social influences on sexual selection. *Journal of Evolutionary Biology* **25**, 803–812.

Quevillon, L.E., Hanks, E.M., Bansal, S. & Hughes, D.P. (2015) Social, spatial, and temporal organization in a complex insect society. *Scientific Reports* **5**, 13393.

Robert, K., Garant, D. & Pelletier, F. (2012) Keep in touch: Does spatial overlap correlate with contact rate frequency? *The Journal of Wildlife Management* **76**, 1670–1675.

Schlicht, L., Valcu, M. & Kempenaers, B. (2015) Spatial patterns of extra-pair paternity: beyond paternity gains and losses. *Journal of Animal Ecology* **84**, 518–531.

Seamons, T.R., Bentzen, P. & Quinn, T.P. (2004) The effects of adult length and arrival date on individual reproductive success in wild steelhead trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 193–204.

Shuster, S.M. & Wade, M.J. (2003) *Mating systems and strategies*. Monographs in behavior and ecology, Princeton University Press, Princeton.

Sih, A., Hanser, S.F. & McHugh, K.A. (2009) Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology* **63**, 975–988.

Silk, M.J., Finn, K.R., Porter, M.A. & Pinter-Wollman, N. (2018) Can multilayer networks advance animal behavior research? *Trends in Ecology & Evolution* **33**, 376–378.

Stan Development Team (2016) Rstan: the r interface to stan .

Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.17.3.

Steen, R.P. & Quinn, T.P. (1999) Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. *Canadian Journal of Zoology* **77**, 836–841.

Taggart, J.B., McLaren, I.S., Hay, D.W., Webb, J.H. & Youngson, A.F. (2001) Spawning success in Atlantic salmon (*Salmo salar* L.): a long-term DNA profiling-based study conducted in a natural stream. *Molecular Ecology* **10**, 1047–1060.

Takahashi, T. & Hori, M. (2008) Evidence of disassortative mating in a Tanganyikan cichlid fish and its role in the maintenance of intrapopulation dimorphism. *Biology Letters* **4**, 497–499.

Tentelier, C., Larranaga, N., Lepais, O., Manicki, A., Rives, J. & Lange, F. (2016a) Space use and its effects on reproductive success of anadromous Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 1461–1471.

Tentelier, C., Lepais, O., Larranaga, N., Manicki, A., Lange, F. & Rives, J. (2016b) Sexual selection leads to a tenfold difference in reproductive success of alternative reproductive tactics in male Atlantic salmon. *The Science of Nature* **103**.

Teplitsky, C., Mills, J.A., Yarrall, J.W. & Merilä, J. (2010) Indirect genetic effects in a sex-limited trait: the case of breeding time in red-billed gulls. *Journal of Evolutionary Biology* **23**, 935–944.

Thorpe, J.E., Miles, M.S. & Keay, D.S. (1984) Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. *Aquaculture* **43**, 289–305.

Tinghitella, R.M., Weigel, E.G., Head, M. & Boughman, J.W. (2013) Flexible mate choice when mates are rare and time is short. *Ecology and Evolution* **3**, 2820–2831.

Trillmich, F. & Trillmich, K.G.K. (1984) The mating systems of pinnipeds and marine iguanas: convergent evolution of polygyny. *Biological Journal of the Linnean Society* **21**, 209–216.

Wacker, S., Mobley, K., Forsgren, E., Myhre, L.C., de Jong, K. & Amundsen, T. (2013) Operational sex ratio but not density affects sexual selection in a fish: effects of OSR and density on sexual selection. *Evolution* **67**, 1937–1949.

Wagner, R.H. & Danchin, E. (2003) Conspecific copying: a general mechanism of social aggregation. *Animal Behaviour* **65**, 405–408.

Wei, D., Deng, X., Zhang, X., Deng, Y. & Mahadevan, S. (2013) Identifying influential nodes in weighted networks based on evidence theory. *Physica A: Statistical Mechanics and its Applications* **392**, 2564–2575.

Weir, L.K., Breau, C., Hutchings, J.A. & Cunjak, R.A. (2010) Multiple paternity and variance in male fertilization success within Atlantic salmon *Salmo salar* redds in a naturally spawning population. *Journal of Fish Biology* **77**, 479–493.

Weir, L.K., Grant, J.W.A. & Hutchings, J.A. (2011) The influence of operational sex ratio on the intensity of competition for mates. *The American Naturalist* **177**, 167–176.

West-Eberhard, M.J. (1983) Sexual selection, social competition, and speciation. *The Quarterly Review of Biology* **58**, 155–183.

Wey, T., Blumstein, D.T., Shen, W. & Jordán, F. (2008) Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour* **75**, 333–344.

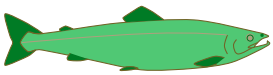
Wolf, J.B., Brodie III, E.D., Cheverud, J.M., Moore, A.J. & Wade, M.J. (1998) Evolutionary consequences of indirect genetic effects. *Trends in Ecology & Evolution* **13**, 64–69.

Wolf, J.B.W., Mawdsley, D., Trillmich, F. & James, R. (2007) Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Animal Behaviour* **74**, 1293–1302.

Zahavi, A. (1975) Mate selection—A selection for a handicap. *Journal of Theoretical Biology* **53**, 205–214.

PART IV

When salmon take another pathway; implication and space use of parr exhibiting an alternative reproductive tactic.



Introduction to Part IV

The previous part highlighted that the space use of anadromous breeders influences the sexual selection and their reproductive success. More precisely at the individual level, spatial isolation of females diminished the number of their sexual partners (chapter 4). The spatial aggregation of females also influences the effective number of breeders in the population through a U-shaped relationship (chapter 6). The two chapters suggested that mate monopolisation by dominant males and the participation of satellite males are dependent on the spatial distribution of females. Individuals explore and move within their environment to find potential mates during reproduction. Then, space use of salmon should be determined by the spatial distribution of females to maximise encounters. At least partly, because some individual traits such as body length may influence space use tactics in salmon Baglinière *et al.* (1991), Finstad *et al.* (2005). Space use of individuals also influenced their social environment that affects the reproductive success of individuals (chapter 5). Nevertheless, chapters 5 and 6 focused on anadromous salmon and did not account for individuals exhibiting an alternative reproductive tactic.

AN ALTERNATIVE REPRODUCTIVE TACTIC

Salmon exhibit complex life histories. Besides anadromous individuals, some Atlantic salmon deploy an alternative reproductive tactic by maturing at the parr stage before their seaward migration (Bagliniere & Maisse 1985, Kazakov 1981, Myers 1984). Early maturation involves a threshold size, mature parr inheriting this life history trait through inheritance of the juvenile growth (Garant *et al.* 2003a, Lepais *et al.* 2017). Then, early maturation usually concerns individuals belonging in the upper size mode (Simpson 1992). Early maturing individuals therefore display usually the highest growth rate (Berglund 1995), as well as the highest Mesenteric Fat Index (Simpson 1992), but these factors are not inescapable (Berglund 1995) and vary between studies (Kristinsson *et al.*

1985, Myers *et al.* 1986). Since the gonadal maturation requires high levels of energy (Brokordt & Guderley 2004), female maturation usually involves a higher expenditure than male maturation (Fleming 1996). For that reason, only a few early maturing females have been found in the southern part of the Atlantic salmon distribution including some in France (Bagliniere & Maisse 1985). In addition, environmental factors may also affect early maturation. For example, Letcher & Terrick (1998) found that flood may increase the proportion of early maturing males by raising food availability. Early maturation causes a drop-off in survival probability until the smoltification (Buoro *et al.* 2010, Myers 1984), the stage before seaward migration. Early maturation in salmon does not exclude anadromy, anadromous males may have previously been a mature parr.

Mature parr as sneaker. Alternative reproductive tactics usually involve different phenotypes and behaviours (Taborsky *et al.* 2008). Such differences are exacerbated in Atlantic salmon between anadromous males and mature parr [1]. Emlen (1997) linked the size differences between males in dung beetles (*Onthophagus acuminatus*) to alternative reproductive tactics and different behaviours. Smaller males developed rudimentary horns and adopted a sneaky behaviour, whereas larger males developed longer horns and guarded tunnels containing females. The dichotomy of breeding behaviours — guarding versus sneaking — is typically the dichotomy of behaviours observed between anadromous salmon males and mature parr (Fleming 1996). The extremely lower body size of mature parr compared to anadromous — Figure. IV.i — favours such sneaky behaviour (Fleming 1996).

PARTICIPATION IN REPRODUCTION FOR MATURE PARR: FROM TACTIC LEVEL TO AN INDIVIDUAL LEVEL

Mature parr may have strong genetic effects within populations. In their recent study, Tentelier *et al.* (2016b) found that mature parr fathered at least 14% of juveniles caught in a river, while Martinez *et al.* (2000) found that mature parr viewed as a group sired 65.1% of eggs in several redds. The last study demonstrated the strong effect of mature parr on genetic variability in small populations of Atlantic salmon. Indeed, the participation in reproduction of mature parr raises the effective population size N_e (Ardren & Kapuscinski 2003, Saura *et al.* 2008) amplifying the genetic variability between juveniles and ultimately the fitness of females (Garant *et al.* 2005). In addition, Garant

[1] here and thereafter I refer to male mature parr

et al. (2002) found juveniles fathered by mature parr demonstrated higher growth rates than juveniles sired by anadromous. At the opposite, mature parr diminish gene flows between populations by the absence of migration and may also decrease the number of returning anadromous. Moreover, reproduction of mature parr favours introgression of hatchery fish in wild populations (Garant *et al.* 2003b), something which can be in concern with recent aquaculture escapements. Finally, mature parr may break fecundity selection on arrival date because increasing variance on arrival date (Arnaud *et al.* 2013) and may also mitigate natural selection operating at sea.

Success is more complicated at an individual level. The individual reproductive success of mature parr is weaker than the one of anadromous. Until the 2000s, a majority of studies focused on mature parr as a group. For example, Hutchings & Myers (1988) found that mature parr fertilised less than 25% (5% - 23%) of eggs in a redd. Recent studies have used polymorphic genetic markers to isolate individual participation in reproduction. In this way, Martinez *et al.* (2000) found an individual fertilised 46.7% of eggs in a redd [2]. However, individual reproductive success of mature parr varies a lot between individuals. Tentelier *et al.* (2016b) found a variance of individual reproductive success at 67.62 (number of offspring[2]) within a river, while Thomaz *et al.* (1997) found an average reproductive success varying from 5% to 25% of eggs fertilised in egg pocket. The variations between studies relate to the level of analysis: redds, egg pockets, rivers, experiments. (for more examples see Jordan *et al.* 2007).

A LACK OF KNOWLEDGE ABOUT SEXUAL SELECTION AND SPACE USE

The sexual competition faced by mature parr remains an opened question. Mature parr are seldom considered in studies about salmon sexual selection despite their influence within small populations and the variability in their reproductive success. Some studies focused on differences in individual reproductive success between the two alternative reproductive tactics (Garcia-Vazquez *et al.* 2001, Tentelier *et al.* 2016b). In their study, Tentelier *et al.* (2016b) found a stronger opportunity for selection in mature parr compared to anadromous but without accounting for variations in sperm competition between reproductive tactics. Anadromous males compete with each other to access females, causing sexual selection (Fleming 1996, Järvi 1990). In comparison, mature parr compete with anadromous by sneaking. Mature parr also struggle with other ma-

[2]This percentage is for one mature parr, while the percentage of 65.1% in the previous paragraph is the overall parr reproductive success.

ture parr because dominance hierarchy influences distance to nest (Myers & Hutchings 1987). Salmon females are polyandrous what exacerbates sperm competition. Indeed, males have to compete to access females but also to fertilise the most of eggs at each laying event. Therefore, males are concerned by i) the sexual competition impacting their mating success and ii) the sperm competition impacting the number of fertilised eggs, both affecting their reproductive success. Hence, sexual selection may differ between reproductive tactics and selection operating on mature parr might be linked to competition among anadromous.

Early maturation may lead to a specific space use. Like sexual selection, space use of mature parr related to breeding activity is under-investigated. The differences in their body size and in their breeding behaviour compared to anadromous might lead them to opt for a specific space use tactic. Since mature parr are smaller than anadromous, they have a lower search efficiency raising the question about how they move to maximise their probability to encounter females. Mature parr might opt for a staying behaviour rather than a cruising one because of their smaller body size and their limited resources. Nevertheless, they should also leave their natal habitats (i.e. foraging habitats of salmon parr) to go to breeding ones to maximise their encounter probability with females, whereas immature should stay in their natal habitats to feed. Such habitat shifts should spatially segregate immature parr and mature parr in terms of habitat use.

Three different chapters constitute the current part (Figure. IV.ii). Chapter 7 (page 241) aimed to compare sexual selection between reproductive tactics by using data of Tentelier *et al.* (2016b). Chapter 8 (page 257) intended to assess the space use of mature parr caused by breeding activity and their maturity level. To do this, I compared their space use to those of immature parr in order to detect a potential modification of their space by their maturity level. Finally, chapter 9 (page 283) aimed to test whether maturity involves a shift of habitats for Atlantic salmon parr.

Figure. IV.i: Photograph of a male anadromous Atlantic salmon and a mature male parr in the Nivelle River — ©INRA—O. Lepais

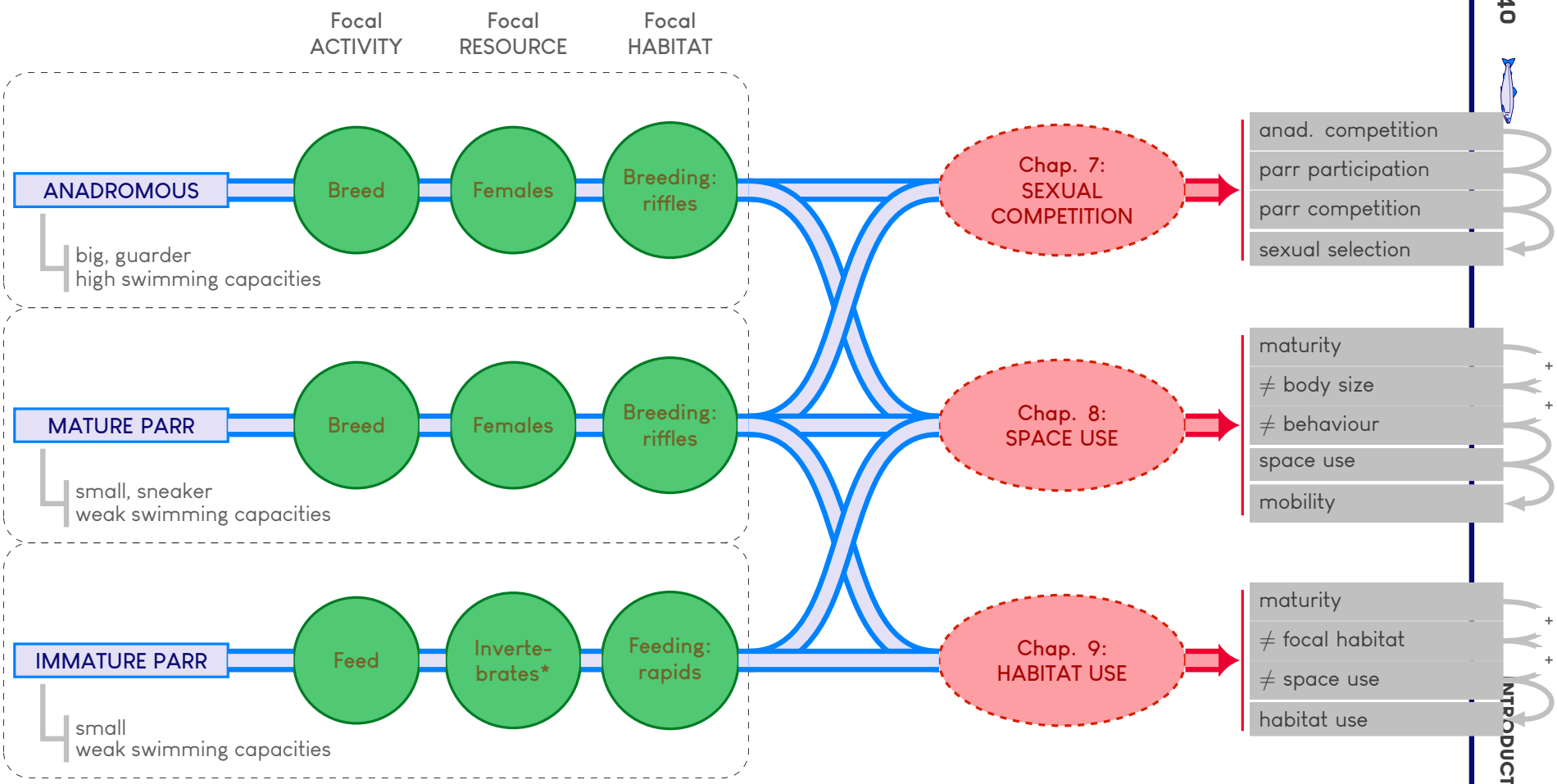


Figure. IV.ii: Scheme to explain conceptual ideas of the Part IV and the different chapters. The chapter 7 aimed to compare the sexual selection operating on the two different reproductive tactic (anadromous male vs mature parr). The chapter 8 assessed the space use of salmon parr related to breeding activity by comparing mature parr and immature ones. The chapter 9 assessed the effect of maturity on the habitat use of salmon parr. *: drifting invertebrates.

CHAPTER 7

Salmon parr as hackers of sexual networks

Contents

7.1 CONTEXT

The Nivelle River remains a small river network and its salmon population as a small salmon population in comparison to populations in North America or in Norway. Several authors have emphasised the potential importance of mature parr in participation in reproduction in such small populations (Bagliniere & Maisse 1985, Garcia-Vazquez *et al.* 2001, Jones & Hutchings 2001; 2002, Juanes *et al.* 2007). Moreover, most of the studies working on salmon reproduction focused on mature parr as a group without accounting for individual variability (Jordan *et al.* 2007).

A recent study by Tentelier *et al.* (2016b) emphasised individual variability in participation in reproduction by mature parr within the Nivelle population. Authors showed that the reproductive success of mature parr was weak and variable (2.24 offspring $\pm$ 67.62) depending on their mating success (83% having no mate) but not on their body size. Other studies found the individual reproductive success of parr varying with their body size (Myers & Hutchings 1987, Thomaz *et al.* 1997). But participation in reproduction by mature parr usually varies between 25% to 87% (Grimardias *et al.* 2010b).

Although such a level of contributions is hard to put aside, studies rarely discuss effects on the resulting competition experienced by anadromous.

Anadromous salmon males compete between each other to access to multiple females (up to 16: Garant *et al.* 2001). The dominant male which can be the larger one (Järvi 1990), the one with the larger "kype" — elongation of the jaws in males — (Fleming 1996), or the more aggressive one (Hendry & Beall 2004), usually chase other males (Fleming 1996). Mature parr also compete between each other to access redds, a hierarchical dominance existing between them (Myers & Hutchings 1987). Sexual competition between males related to a skewed operational sex-ratio modulates the relation between the mating success and the reproductive success of individuals (Bateman gradient).

Aggregation of females (Bacles *et al.* 2018), as well as heterogeneity in male size, may favour sneaking behaviour by other anadromous males. Additionally to competition between anadromous, mature parr may actively participate in reproduction (Hutchings & Myers 1988), their size giving them an advantage of exhibiting a sneaky behaviour. Thus, male reproductive success strongly depends on sperm competition. Indeed, the number of sneaker males may impact the number of eggs fertilised by a focal male during a laying event. In this way, the sperm competition intensity (SCI) corresponds to the harmonic mean of a males partners mating success which may impact the reproductive success of an individual (McDonald & Pizzari 2016). The sperm competition and the resultant effect on reproductive success may, therefore, vary between reproductive tactics and fertilisation of eggs by mature may significantly increase the SCI suffered by anadromous males.

How the SCI is linked to the mating success of individuals is critical for individuals. The "sperm competition intensity correlation" (SCIC) is the measure of the correlation between the SCI and the mating success of individuals (McDonald & Pizzari 2016). The SCIC can be view as a measure of the trade-off between mate-searching and mate-guarding. Comparing the SCIC between individuals or tactics is equivalent to comparing the ability of individuals or tactics in guarding mates. Mature parr exhibit a sneaky behaviour, therefore, they may have a SCI increasing as their mating success increases. If numerous sneakers are present, the cost of having multiple females for an anadromous male is to have also a lot of sneakers which increases its SCIC.

The current chapter aimed to compare the sexual competition between two reproductive tactics and to evaluate how mature parr influence the competition faced by anadromous. First, I tested the importance of accounting for mature parr or not when calculating the sperm competition through the SCI and the SCIC that anadromous faced by using the data of Tentelier *et al.* (2016b). Second, I compared the sexual competition experienced by each reproductive tactic (i.e. mature parr vs anadromous males). I hypothesised differences in sexual selection between the two reproductive tactics because mature parr exclusively exhibit sneaky behaviour which necessarily involves sperm competition at each mating event.

7.2 METHODS

7.2.1 VARIATIONS IN THE SCI WHEN ACCOUNTING OR NOT INDIVIDUALS EXHIBITING THE OTHER REPRODUCTIVE TACTIC

Data of Tentelier *et al.* (2016b) allowed me to compute the reproductive success and the mating success of anadromous females, anadromous males, and mature parr during the two breeding seasons: 2009 and 2010 — for details see Part III, page 145. The current section describes analyses to test if accounting for the other reproductive tactic significantly modify the values of sperm competition faced by anadromous males and mature parr.

The sperm competition intensity — SCI (McDonald & Pizzari 2016) — was computed for each anadromous male — m — for the two breeding seasons — j:

$$\text{SCI}_{m,j} = \frac{1}{\frac{1}{M_{m,j}} \times \sum_{f=1}^{M_{m,j}} \frac{1}{k_{f,j}}} \qquad \text{(Eq. 7.1)}$$

with $M_{m,j}$ the mating success of the focal male m during the breeding season j, and $k_{f,j}$ the mating success of the female f during the same season j. The model only included individuals with no-null mating success ($M_{m,j} > 0$). I computed the SCI for each reproductive tactic: 9 anadromous individuals in 2009, 22 anadromous individuals in 2010, 18 mature parr in 2009, and 21 mature parr in 2010. Two values of SCI characterised each focal male: one value by accounting only individuals exhibiting the same reproductive tactic in the mating success of females ($k_{f,j}$ in Eq. 7.1) and one value by accounting all individuals in the mating success of females. For instance, one value of SCI accounted for all individuals and one value of SCI accounted for only mature parr if the focal male is

a mature parr. In the latter case, the focal mature parr could have only mature parr as competitors. In this way, I was able to test whether accounting for individuals belonging in the other reproductive tactic significantly alter the values of the sperm competition, but also to compare the SCI between reproductive tactics. Then, four different levels denoted the context of the SCI computation as shown in the Table. 7.1:

Table. 7.1: Table of the different levels characterising the context when computing the Sperm Competition Intensity as defined by McDonald & Pizzari (2016).

Level	Reproductive tactic	
	Focal Male	Competitors
`Ana-Ana`	Anadromous	Anadromous
`Ana-All`		All
`Parr-Parr`	Mature parr	Mature parr
`Parr-All`		All

A normal distribution modelled the distribution of the $log(\text{SCI}_{m,j})$:

$$log\left(\text{SCI}_{m,j}\right) \sim \mathcal{N}\left(\mu[Level[m]]_j,\ \sigma[Level[m]]\right) \qquad \text{(Eq. 7.2)}$$

Then, $\mu[Level[m]]_j$ denoted the average value of SCI for the breeding season j, the "Level" characterising the focal male m, and the context of the SCI computation (see Table. 7.1). The model was fitted two times: once for anadromous individuals for the levels `Ana-Ana` and `Ana-All`, and once for mature parr for the levels `Parr-Parr` and `Parr-All`.

Weak informative priors (Cauchy distribution) were used for μ and σ. A total of 12,000 iterations were saved from three chains. An overlap (noted Bayesian P_{value}) lower than 0.05 representing 5% of overlapping between the distributions of estimated values for different levels indicated a significant difference.

7.2.2 DIFFERENCES IN SEXUAL SELECTION BETWEEN REPRODUCTIVE TACTICS

The current part describes analyses comparing the effects of sexual competition on reproductive success of anadromous males and mature parr. Another model linked the reproductive success of individuals ($T_{m,j}$) to their mating success ($M_{m,j}$) and the SCI

that they faced ($SCI_{m,j}$):

$$T_{m,j} = \mathcal{N}\left(intercept + \beta_{M\bullet SCI} \times M_{m,j} + \beta_{SCI\bullet M} \times SCI_{m,j},\ \sigma\right) \qquad \text{(Eq. 7.3)}$$

$\beta_{M\bullet SCI}$ in Eq. 7.3 represents the usual male Bateman gradient controlling for variations in SCI (McDonald & Pizzari 2016), while the parameter $\beta_{SCI\bullet M}$ assessing the effect of $SCI_{m,j}$. The model Eq. 7.3, like the others models, included only individuals with no-null mating success and was fitted for anadromous and for mature parr separately. Values of SCI ($SCI_{m,j}$) corresponded to those computed in the previous paragraph for the different levels. Within each level context, the reproductive success ($T_{m,j}$), the mating success ($M_{m,j}$), and the SCI ($SCI_{m,j}$) were standardised by dividing each individual value by the population mean (either anadromous males or mature parr McDonald & Pizzari 2016). Such standardisation enabled me to compare parameters estimated between each level context. Data on 9 anadromous and 18 mature parr were used in 2009, while 22 anadromous and 21 mature parr were incorporated in analyses in 2010.

The sperm competition intensity ($SCI_{m,j}$) may increase as the mating success of individuals ($M_{m,j}$) raised. A last model tested the effect of $M_{m,j}$ on $SCI_{m,j}$.

$$SCI_{m,j} = \mathcal{N}\left(intercept_{SCIC} + SCIC[RT_{m,j}] \times M_{m,j},\ \sigma_{SCIC}\right) \qquad \text{(Eq. 7.4)}$$

SCIC in Eq. 7.4 assesses the relationship between a male mating success ($M_{m,j}$) and the sperm competition he faced which represents the partners' polyandry (SCI, Eq. 7.1, McDonald & Pizzari 2017). A Cauchy distribution ($\mathcal{C}(0,2)$) was used as prior for parameters of both models Eq. 7.4 and Eq. 7.3. The three parameters: $\beta_{M\bullet SCI}$, $\beta_{SCI\bullet M}$, and $SCIC$ had specific prior distributions $\mathcal{C}\left(0, \sigma_{\text{parameter}}\right)$, "parameter" being one of the three. As the model Eq. 7.2, 6,000 iterations were saved and the test of significance was also the same. $T_{m,j}$, $SCI_{m,j}$, and $M_{m,j}$ were standardized by then population mean within each level context (McDonald & Pizzari 2017). Data on 9 anadromous and 18 mature parr were used in 2009, while 22 anadromous and 21 mature parr were incorporated in analyses in 2010.

7.3 RESULTS

7.3.1 VARIATIONS IN THE SPERM COMPETITION INTENSITY

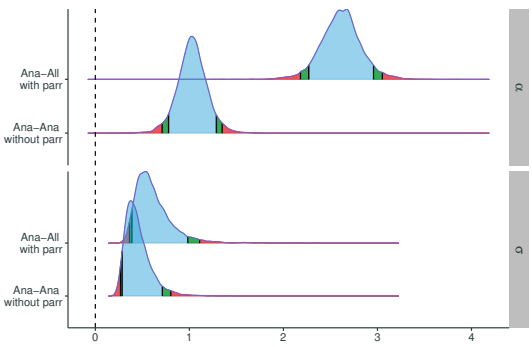
7.3.1.1 Effects of accounting for the competitors exhibiting the other reproductive tactic

In 2009, the log(SCI) of anadromous (N=9) ranged from 1.64 to 05.00 when not accounting for mature parr in sexual competitors (level: `Ana-Ana`), whereas the values varies between 5.40 to 30.00 when accounting for them (`Ana-All`). The log(SCI) estimated by the model (Eq. 7.2) were significantly lower (Bayesian $P_{value} < 0.001$) but not less variable (Bayesian $P_{value} = 0.6$) when not accounting for mature parr than when accounting for them ((a) in Figure. 7.1). During the same season, mature parr (N=16) exhibited values of log(SCI) ranging from 1.97 to 10.00 when not accounting for anadromous competitors (level: `Parr-Parr`) and from 4.55 to 30.00 when accounting for them (level: `Parr-All`). The difference was significant (Bayesian $P_{value} < 0.001$) and the log(SCI) varied similarly between the both cases (Bayesian $P_{value} = 0.7$ for σ, (c) in Figure. 7.1).

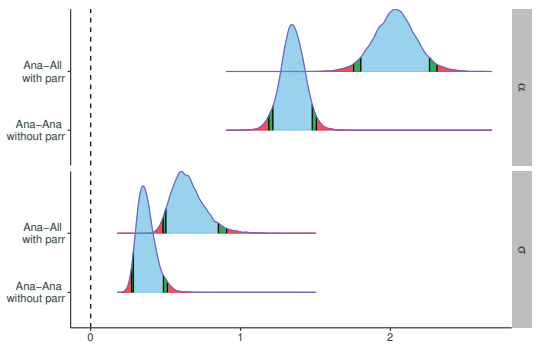
In 2010, anadromous (N=22) exhibited a log(SCI) varying between 1.67 and 07.00 when not accounting for mature parr (level: `Ana-Ana`), whereas the values varies between 3.11 to 26.00 when accounting for them (`Ana-All`). The difference was significant (Bayesian $P_{value} = 0.004$) and the log(SCI) tended to vary more when accounting for mature parr (Bayesian $P_{value} = 0.09$ for σ, (b) in Figure. 7.1). Mature parr (N=21) displayed values of log(SCI) ranging from 1.50 to 07.00 when not accounting for anadromous competitors (level: `Parr-Parr`) and from 2.86 to 26.00 when accounting for them (level: `Parr-All`). The log(SCI) was significantly lower when not accounting for anadromous (Bayesian $P_{value} < 0.001$ but not less variable (Bayesian $P_{value} = 0.2$ for σ, (d) in Figure. 7.1).

7.3.1.2 Differences between reproductive tactics when accounting all sperm competitors

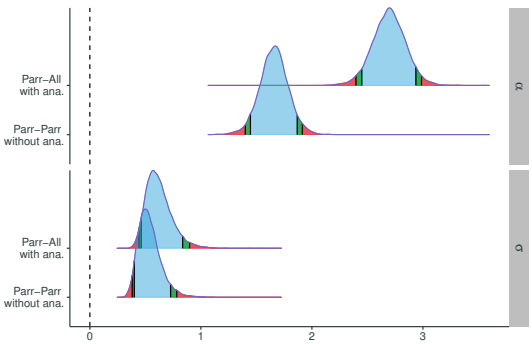
During the two seasons, the variability of the log(SCI) was similar between reproductive tactics when accounting all sperm competitors (levels `Ana-All` and `Parr-All`, Bayesian $P_{value} = 0.8$ in 2009 and 0.9 in 2010). Anadromous and mature parr exhibited similar values of log(SCI) in 2009, whereas anadromous tended to display lower values of log(SCI) than mature parr in 2010 (Bayesian $P_{value} = 0.1$, Figure. 7.1).



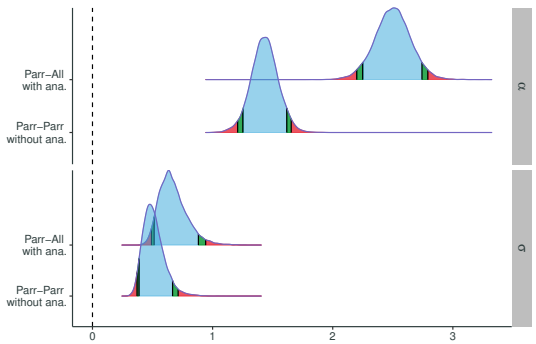
(a) Anadromous in 2009 (levels "Ana-Ana" and "Ana-All")



(b) Anadromous in 2010 (levels "Ana-Ana" and "Ana-All")



(c) Mature parr in 2009 (levels "Parr-Parr" and "Parr-All")



(d) Mature parr in 2010 (levels "Parr-Parr" and "Parr-All")

Figure. 7.1: Density plots of the mean (parameter α) and deviation (parameter σ) of the normal distribution estimated for the Sperm Competition Intensity computed like in McDonald & Pizzari (2016) (Eq. 7.1). The SCI was separately computed for anadromous salmon (N=9 in 2009 and N=22 in 2010) and mature parr (N=16 in 2009 and N=21 in 2010) while accounting for only individuals exhibiting the same reproductive tactic ("Ana-Ana" and "Parr-Parr") or all individuals ("Ana-All" and "Ana-All", see Table. 7.1). Blue areas represent the values between the quantiles 5% and 95%. Red areas represent the values between the quantiles 0 and 2.5% and the values between the quantiles 97.5% and 1. Green areas represent the values between the quantiles 2.5% and 5% and the values between the quantiles 95% and 97.5%.

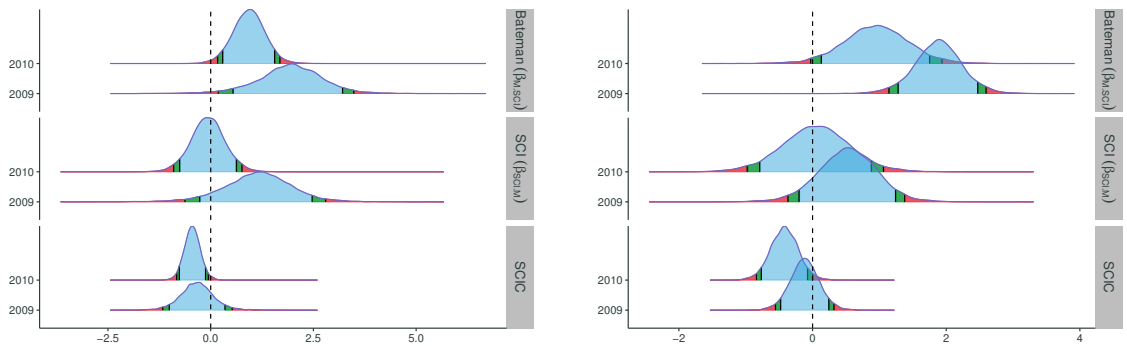
7.3.2 DIFFERENCES IN SEXUAL SELECTION BETWEEN REPRODUCTIVE TACTICS

In 2009, mature parr tended to exhibit lower and less variable values of $\beta_{SCI \bullet M}$ (Eq. 7.3) than anadromous (Bayesian $P_{value} = 0.5$ when considering all individuals as sperm competitors, Table. 7.2). The values estimated for the two reproductive tactics were not significantly different to zero (Table. 7.2). Mature parr exhibited positive Bateman gradient that was similar to the one displayed by anadromous individuals (Bayesian $P_{value} = 0.6$). Finally, the correlation between the mating success of individuals and

the sperm competition suffered by them — SCIC (Eq. 7.3), was not significantly different between reproductive tactics but anadromous tended to have lower values (SCIC: -0.33 for anadromous against -0.12 for mature parr, Bayesian $P_{value} = 0.6$).

For the second breeding season, mature parr exhibited similar values of $\beta_{SCI \bullet M}$ but more variable than anadromous (Bayesian $P_{value} = 0.8$ when considering all individuals as sperm competitors, Table. 7.2). The values estimated for the two reproductive tactics were not significantly different to zero (Table. 7.2). Both reproductive tactics exhibited positive Bateman gradient at strongly similar values (Bayesian $P_{value} = 0.9$). Finally, the correlation between the mating success of individuals and the sperm competition suffered by them — SCIC (Eq. 7.3), was not significantly different between reproductive tactics (SCIC: -0.45 for anadromous against -0.42 for mature parr, Bayesian $P_{value} = 0.96$).

The two previous paragraphs compared the values when accounting all individuals as sperm competitors. Accounting for only individuals exhibiting a similar reproductive tactic did not significantly modify the parameter estimates. Concerning yearly differences, the values of $\beta_{SCI \bullet M}$ for anadromous tended to be lower in 2009 than in 2010 (Bayesian $P_{value} = 0.2$, Figure. 7.2), whereas mature parr exhibited similar values between years (Bayesian $P_{value} = 0.6$). The Bateman gradient tended to diminish between 2009 and 2010 for the two reproductive tactics (Bayesian $P_{value} = 0.34$ for mature parr and 0.27 for anadromous). Finally, the SCIC tended to decrease between 2009 and 2010 for the two reproductive tactics (Bayesian $P_{value} = 0.58$ for mature parr and 0.65 for anadromous).



(a) Anadromous males (b) Mature parr

Figure. 7.2: Density plots of Bateman gradient ($\beta_{M \bullet SCI}$) and the effects of the Sperm Competition Intensity (SCI — parameter $\beta_{SCI \bullet M}$) on the reproductive success either of anadromous males (a, N=9 in 2009 and N=22 in 2010) or mature parr (b, N=16 in 2009 and N=21 in 2010). The SCI was computed like in McDonald & Pizzari(2016, Eq. 7.1) and separately for anadromous salmon (N=9 in 2009 and N=22 in 2010) and mature parr (N=16 in 2009 and N=21 in 2010). The SCIC corresponds to the correlation between the mating success of individuals and the SCI they face. Blue areas represent the values between the quantiles 5% and 95%. Red areas represent the values between the quantiles 0 and 2.5% and the values between the quantiles 97.5% and 1. Green areas represent the values between the quantiles 2.5% and 5% and the values between the quantiles 95% and 97.5%.

Table. 7.2: Table of the parameters estimated in the models Eq. 7.4 and Eq. 7.3 enabling to characterised pre-copulatory competition between salmon males. The mean and the 95% Highest Posterior Density interval were displayed for each parameter. Symbol "*" indicates that a parameter was significantly different than zero. Data on 9 anadromous and 18 mature parr were used in 2009, while 22 anadromous and 21 mature parr were incorporated in analyses in 2010. Either all individuals or only individuals exhibiting the same reproductive tactic was accounted in the computation of the sperm competition intensity of focal males. The level indicates the reproductive tactic of the focal male ("Ana" for anadromous individuals and "Parr" for mature parr) and the reproductive tactic of sperm competitors ("All" or the same reproductive tactic than the focal male).

Year	Parameter	Level	Mean 95%HPD
2009	SCIC — Eq. 7.4	Ana-Ana	$-0.45^*[-1.01; -0.28]$
		Ana-All	$-0.33[-1.17; 0.52]$
		Parr-Parr	$-0.22[-0.61; 0.18]$
		Parr-All	$-0.12[-0.56; 0.32]$
	$\beta_{M\bullet SCI}$ — Eq. 7.3	Ana-Ana	$1.95^*[-0.11; 3.88]$
		Ana-All	$1.93^*[0.18; 3.48]$
		Parr-Parr	$1.91^*[1.16; 2.66]$
		Parr-All	$1.88^*[1.14; 2.60]$
	$\beta_{SCI\bullet M}$ — Eq. 7.3	Ana-Ana	$0.93[-1.75; 3.45]$
		Ana-All	$1.14[-0.63; 2.80]$
		Parr-Parr	$0.47[-0.50; 1.46]$
		Parr-All	$-0.12[-0.56; 0.32]$
2010	SCIC — Eq. 7.4	Ana-Ana	$-0.21^*[-0.40; -0.03]$
		Ana-All	$-0.45^*[-0.83; -0.06]$
		Parr-Parr	$-0.34^*[-0.67; -0.01]$
		Parr-All	$-0.42^*[-0.84; 0.00]$
	$\beta_{M\bullet SCI}$ — Eq. 7.3	Ana-Ana	$1.01^*[0.25; 1.76]$
		Ana-All	$0.93^*[0.17; 1.68]$
		Parr-Parr	$1.02^*[0.06; 1.99]$
		Parr-All	$0.95^*[-0.03; 1.94]$
	$\beta_{SCI\bullet M}$ — Eq. 7.3	Ana-Ana	$0.22[-1.44; 1.89]$
		Ana-All	$-0.07[-0.90; 0.76]$
		Parr-Parr	$0.26[-1.04; 1.55]$
		Parr-All	$0.05[-0.98; 1.06]$

7.4 DISCUSSION

The current chapter aimed to compare the sexual competition between anadromous males and mature parr but also to test the importance of accounting for individuals exhibiting the other reproductive tactic when assessing sperm competition. Accounting for mature parr may strongly increase the computed values of SCI than when not considering them, especially during years where their participation is high. Sperm competition suffered by males diverged between reproductive tactics and can be linked to their spawning behaviour. Nevertheless, the way that the pre- and post-copulatory competition affect the reproductive success was similar between reproductive tactics. Nonetheless, some trends could be identified.

The average value of the sperm competition intensity (SCI) that anadromous males faced differ when accounting or not for mature parr. The SCI when considering mature parr was more than twice as high than when not accounting for mature parr. The difference was less pronounced in 2010 which can be due to the lower proportion of juveniles fathered by a mature parr compared to 2009. Indeed, Tentelier *et al.* (2016b) found that $\frac{123}{733+123} = 14\%$ of juveniles were sired by a mature parr, while in 2010 the proportion dropped off to $\frac{45}{1006+45} = 4\%$. In addition, the number of juveniles whose father was not known was higher in 2009 (821 offsprings in 2009 against 299 in 2010). A high proportion of this number is likely to be mature parr (anadromous being caught at two fish passes). The difference in SCI is, thus, probably under-estimated in two years and especially in 2009.

Anadromous salmon and mature parr exhibited similar values of SCIC. The Sperm Competition Intensity Correlation measures how the number of sperm competitors increases with the mating success of individuals. Negative SCIC indicates disassortative mating on mating success (McDonald & Pizzari 2017). Although the SCIC was not significantly different between reproductive tactics, anadromous tended to exhibit lower values of SCIC than mature parr in 2009. The number of sperm competitors tended to increase less as mating success raised for anadromous than for mature parr. A higher value for mature parr can be explained by their sneaky behaviour implying sperm competitors (the sneaked males), whereas anadromous males can mate without having sperm competitors if they secure females.

Ignoring individuals exhibiting the other reproductive tactic may blur the measures of sexual competition. The SCIC was not significantly different when accounting or not for individuals expressing the other reproductive tactic. Nevertheless, anadromous males exhibited significant negative values of SCIC in 2009 when not accounting for mature parr as sperm competitors. The SCIC was not different to zero when accounting for mature in 2009. Which individuals accounted as sperm competitors greatly impacted the Sperm Competition Intensity. Accounting for all individuals in the population significantly increased the SCI for both tactics. Not considering mature parr in computations of post-copulatory competition faced by anadromous, may, therefore, lead to erroneous conclusions.

The effect of the number of sperm competitors on their reproductive success was not different to zero for both reproductive tactics and during the two seasons. Nevertheless, the values of $\beta_{SCI \bullet M}$ tended to be higher in 2009 indicating a "benefit" to have sperm competitors on the reproductive success. One explanation could be that most of the sperm competitors in 2009 could be mature parr because mature parr sired a low number of juveniles (Tentelier *et al.* 2016b). The non-negative values of $\beta_{SCI \bullet M}$ for mature parr were surprising. Indeed, Garant *et al.* (2003b), Hutchings & Myers (1988), Thomaz *et al.* (1997) found negative effect of the number of implicated mature parr on their individual reproductive success. Some authors found the opposite and have suggested that a high number of mature parr favours their participation in reproduction (Hutchings & Myers 1988, Weir *et al.* 2005). An explanation of differences could be the level of the studies, especially because the current chapter was at the river scale while others were at egg nest, egg pocket or an experimental treatment.

Mature parr exhibited a negative SCIC in 2010 but a SCIC not different to zero in 2009 suggesting a more positive assortment in 2009 than in 2010. Then, mature parr mated with less polyandrous females in 2010 than in 2009. The participation of mature parr in 2009 was higher than in 2010 (Tentelier *et al.* 2016b). A low number of competitors may increase the dominance hierarchy between individuals and therefore the competition. Myers & Hutchings (1987) found that mature parr size influenced their position in dominance hierarchy as well as proximity to the nest. Their participation is also favoured by the high number of anadromous competitors weakening aggression by guarding males due to costs of competition which increase as the number of competitors

increased (Weir *et al.* 2011). The number of competitors was higher because of the high number of other mature parr competitors to access females in 2009. Yearly variations of SCIC for mature parr could then be linked to their participation in the reproduction. For anadromous, the SCIC in 2009 was not different to zero, while in 2010, it was lower than zero suggesting a negative assortment in 2010 (McDonald & Pizzari 2017). The lower value of SCIC in 2010 indicates that the number of sperm competitors increased less with mating success than in 2009, suggesting that dominant anadromous males were more able to guard and monopolise females in 2010 than in 2009.

For anadromous, SCIC was lower in 2010 than in 2009, while SCI was higher in 2009 than in 2010. Theory predicts that negative values of SCIC accentuate the slope of the male Bateman gradient (Wolf *et al.* 1999), and therefore increase the pre-copulatory competition. Hence, pre-copulatory competition suffered by anadromous was stronger in 2010 than in 2009. One explanation could be the lower number of anadromous competitors in 2009, or the opposite, namely a too high number of anadromous competitors exacerbating costs of competition. Weir *et al.* (2011) suggested that antagonist interactions decrease as the number of competitors increased. The second hypothesis seems right because i) the number of sperm competitors was higher in 2009 (higher SCI), ii) the positive effect of SCI on their reproductive success in 2009 (positive value $\beta_{SCI \bullet M}$, Shuster & Wade 2003), and iii) the higher participation of mature parr in 2009.. Again, results agree with a higher participation of mature parr in 2009.

During the two years, mature parr exhibited values of pre-copulatory competition ($\beta_{M \bullet SCI}$) similar to those of anadromous. The similar effect was quite surprising because mature parr usually fertilised fewer eggs than anadromous males during a laying event. Moreover, some studies have demonstrated the potential existence of sperm depletion during spawning, their reproductive success within a nest decreased as the order of nest construction increased (Hutchings & Myers 1988, Thomaz *et al.* 1997). Both tactics exhibited a lower Bateman gradient in 2010 than in 2009 suggesting a pre-copulatory competition tending to be lower in 2010 than in 2009. For anadromous, a lower pre-copulatory competition indicates a potentially facilitated mate monopolisation in 2010.

The current chapter is the first study comparing measures of sexual competition among reproductive tactics (anadromous against mature parr) *in natura*. Years' effect

and reproductive tactics' one seem to interact depending on the mating system. The two reproductive tactics had similar Bateman gradients ($\beta_{M \bullet SCI}$) indicating that multiplying mating events was also advantageous for mature parr. However, raising the number of mating events increased the number of sperm competitors. Effect of having sperm competitors on reproductive success tend to vary between years and among tactics but seemed not impacting the reproductive success. Nevertheless, the presence of sperm competitors seemed beneficial for individuals in terms of reproductive success suggesting that most of the competitors were mature parr because they usually fertilise fewer eggs than anadromous males. Year variations in this effect for anadromous indicated that anadromous shared mated females with mature parr in 2009 and other anadromous in 2010. The mating system of salmon appeared to tend to vary among years and resulted in variable sexual competition among reproductive tactics. Environmental factors may have strong effects on sexual selection among reproductive tactics because mate guarding for anadromous and sneaking ability for mature parr may depend on environmental factors (Grimardias *et al.* 2010b, Part II).

HIGHLIGHTS OF CHAPTER 7

- Despite their high participation in population reproduction, mature parr are rarely accounted in studies about sexual competition in salmon.
- How operate sexual competition on mature parr is also rarely investigated, although they exhibit sneaky behaviour, and, therefore, compete to access females.
- Accounting for mature parr increased the number of sperm competitors faced by anadromous males. Not accouting for them may lead to erroneous conclusions about sperm competition.
- Number of mature parr competitors and number of anadromous interplay to favour or not the participation of mature parr in reproduction.
- Sexual competition faced by mature parr corresponds to their sneaky behaviour and, therefore, tend to differ to the sexual competition faced by anadromous salmon.

CHAPTER 8

Maturity increases mobility and heterogeneity in individual space use in Atlantic salmon

Contents

Authors: Bouchard, C., F. Guéraud, F. Lange, J. Rives and C. Tentelier

Abstract:

1. The space use of mobile organisms is linked to the spatio-temporal distribution of their focal resources. Focal resources include territories, food and potential mates and may differ between developmental stages. In particular, individuals have to consider the probability of mate encounter which affects their space use and behaviour when becoming mature.

2. Space use of immature and mature animals should be compared between individuals of the same cohort to control for a potential age effect. Atlantic salmon *Salmo salar* are a good model for this study because of the facultative early maturation of male parr. The early maturation in salmon parr permits comparing space use between mature and immature individuals belonging in the same cohort.

3. Space use of 40 one-year old Atlantic salmon parr (immature and mature) was monitored throughout the breeding season. The link between the space use of mature individuals and their probability to encounter redds (female nests) was also tested.

4. Mature individuals were more mobile than immature ones. Overall, they covered greater upstream distances and absolute distances than immature individuals and had wider home ranges. Mature individuals also exhibited more heterogeneity in space use.

5. Space use tactics of mature individuals impacted their probability to participate in reproduction. Among mature parr, those that exploited a wider home range or those favouring to move upstream exhibited a higher probability of encountering redds. Covering greater upstream distances potentially increases the reproductive success of mature individuals but also potentially involves higher energetic costs and a greater risk of predation compared to immature parr.

6. By monitoring space use of salmon parr we identify that dams may constrain displacements of mature individuals like for anadromous individuals. Improving the understanding of distribution of individuals provide valuable information to enhance management of populations, especially when this distribution is modified by a developmental stage (i.e. maturity here).

Keywords: Alternative reproductive tactic, Atlantic salmon, individual heterogeneity, maturity, radio-tagging, spatial movements, spatial distribution, telemetry

8.1 INTRODUCTION

The developmental stage of individuals may plays an important role in the spatio-temporal distributions of individuals within their populations. An organisms developmental status can be characterised at different scales. Life stage or developmental stage refers to the distinct phase in an organisms life cycle, e.g. embryo, young of the year or adult. Mobile organisms select one or more focal resources such as food, territories, shelter, or potential mates; each resource having a specific distribution with both a spatial and a temporal component (Kamath & Losos 2018, Moorcroft & Barnett 2008, Moorcroft *et al.* 2006, Silk *et al.* 2018). As individuals grow and develop, their need for certain focal resources changes and they move around according to their new priorities.

In this way, the spatio-temporal distribution of focal resources drives the spatio-temporal distribution of individuals within populations (Moorcroft & Barnett 2008).

The relationship between individual distribution and their required resources constitutes the central idea of several "optimal theories" such as the *optimal foraging theory* or the *ideal free distribution* (Fretwell & Lucas 1969, MacArthur & Pianka 1966). Numerous studies have used such relationships between animal distribution and the distribution of their resources to extrapolate and better predict the distribution of individuals based on resource distribution (Moorcroft & Barnett 2008, Moorcroft *et al.* 2006, Potts & Lewis 2014). Knowing individual distribution enables improving species management by mitigating the potential specific threats to each environment.

Individual variability within developmental stages exacerbates the diversity of spatial distributions among individuals. Accounting for individual variability both in life histories and in spatial distributions is a growing area of research (Gimenez *et al.* 2018, Hamel *et al.* 2018, Kamath & Losos 2018, Maldonado-Chaparro *et al.* 2018). Reproductive stage contributes greatly to individual variability due to the changes of focal resources related to development (Long *et al.* 2009, Veilleux *et al.* 2004). In Woodland caribou, for example, females have been shown to adapt their habitat selection according to their reproductive stage (Viejou *et al.* 2018). Females with calves selected habitats maximising predator avoidance, while females without calves chose habitats according to food availability. The reproductive stage of females influenced their consideration of predator risk and therefore their focal resource: habitat. While reproductive stage is an indication of availability as a breeder, sexual maturity, however, has only two levels: mature and immature. Whether or not an individual is sexually mature being the only factor considered.

Maturation involves switches of focal resources by adding mates to the set of coveted resources, as does reproductive stage progression (Jonsson & Jonsson 1993, Lucifora *et al.* 2009). In this way, maturation may lead to the divergence of space use as well as an individual variability in space use of mature individuals because mating systems can involve different space use tactics (Forchhammer & Boomsma 1998, Sandell & Liberg 1992). For instance, Hoyos-Padilla *et al.* (2016) found that adult white sharks *Carcharodon carcharias* presented larger home ranges than juveniles in Guadalupe Island.

Comparing the effect of maturity levels on spatial distribution and space use across species with variable life histories enables the isolation of maturity effects from mere age effects. Reproductive stages usually follow each other in time. This temporal succession of stages may confound the pure effects of maturity with season or age effects (Péron & Grémillet 2013). A similar issue arises when all individuals of the same cohort mature at once, age effects consequently mixing with maturity effects (Lucifora *et al.* 2009). Testing the effects of sexual maturity on space use usually consists of comparing the space use of juveniles to that of adults, which therefore implies that age possibly masks maturity effects (Hoyos-Padilla *et al.* 2016, Péron & Grémillet 2013). Disentangling maturity effects from these co-effects requires studying a species with a life history varying among individuals, so that both mature and immature individuals belong within the same cohort.

Atlantic salmon *Salmo salar* parr are relevant biological models for the investigation of the effects of maturity on distribution and space use. In salmonids, some individuals mature at the parr stage in rivers, while the major part of individuals mature at sea (Myers *et al.* 1986). The early maturation in river which is an alternative reproductive tactic allows us to test the effects of sexual maturity on space use within the same cohort, avoiding a potential bias. Salmon parr, as multiple central-place foragers, occupy and defend small feeding territories in which they move and stay at feeding stations (Steingrímsson & Grant 2003; 2008). Numerous studies have also explored how they move within small scales (Roy *et al.* 2013a;b), which territories they choose (Dolinsek *et al.* 2007, Kim *et al.* 2011), as well as their circadian and seasonal activity patterns (Fraser & Metcalfe 1997, Hiscock *et al.* 2002, Metcalfe *et al.* 1999, Robertson *et al.* 2003). In an experimental elliptic flume, Thorpe *et al.* (1988) detected that mature individuals moved more than immature ones in November, just before the breeding season. In a comparable setting, Armstrong *et al.* (2001) highlighted differences of detectability between mature and immature individuals around one nest. However, to our knowledge, no study has investigated how maturity affects individual space use *in natura* and during the breeding season in salmon.

The main purpose of this study was to test whether sexual maturity impacts the space use of Atlantic salmon parr at an individual level. To do this, the space use of radio tagged mature and immature individuals belonging in the same cohort (one-year

old individuals) was monitored in a river throughout the breeding season. Firstly, we hypothesised that the space use of mature individuals would be significantly different to that of immature individuals due to switching to, or at least coveting a new focal resource: anadromous females. Secondly, we hypothesised that this new focal resource would increase the heterogeneity of space use among mature individuals compared to the heterogeneity among immature individuals. Several studies highlight variable behaviours among mature parr trying to gain access to nests as well as high variations in individual reproductive success (Garant *et al.* 2002, Grimardias *et al.* 2010b, Jones & Hutchings 2002, Myers & Hutchings 1987, Tentelier *et al.* 2016b). All of these studies highlight a more heterogeneous space use in mature individuals. Finally, we linked individual space use of mature parr was linked to their probability to participate in reproduction. A good understanding of the distribution of mature parr may improve salmon population management by identifying human-induced constraints in their displacements, as well as how their displacements influence their participation in population reproduction.

8.2 METHODS

8.2.1 STUDY AREA, CATCHING AND TAGGING

This study was conducted in a 2.4 km section in the 39 km long Nivelle River situated in the south west of France (Figure. 8.1). An impassable dam defined the upstream limit of the study area. This dam formed the upper limit of the available area for the population of Atlantic salmon in the river. A flood control dam, defined the downstream limit of our study area. Although the flood control dam can be crossed by the salmon, the riverbed along the 500 m downstream of it does not constitute a suitable breeding area. The study area has supported a significant yearly number of redds (salmon spawning nests) over recent years: 19 nests (representing 23 % of the nests found in the whole river), 34 nests (52 %), 51 nests (46 %), 21 nests (27 %), and 34 nests (41 %) respectively from 2011 to 2015 (Bouchard *et al.* 2018, Tentelier *et al.* 2016a). The study area was chosen because of the abundance of breeding activity, the ability to monitor the river section by walking along it and the presence of an impassable upstream limit. The section of river studied has an average width of 10 m $\pm$ 2 m, an average depth of 41 cm $\pm$ 26 cm and an average velocity of 37 cm.s^{-1} $\pm$ 20 cm.s^{-1}, and contains a succession of riffles, pools and runs.

One-year-old salmon parr (N=72) were caught by electro-fishing along the study

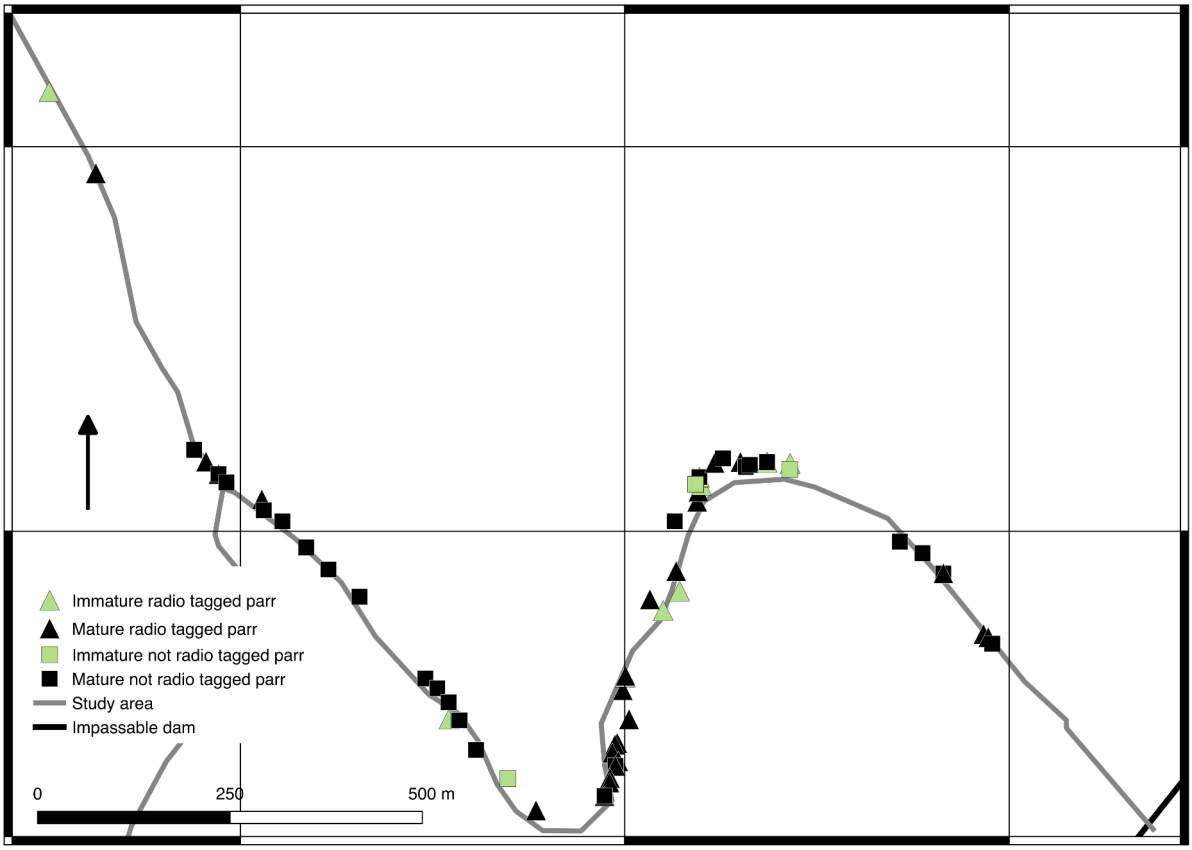


Figure. 8.1: Map of the study area in grey where space use by one-year old Atlantic salmon parr was monitored in the Nivelle River (France). Triangles indicate the location of each radio-tagged individual: black triangles for mature individuals and green triangles for immature individuals (n = 40). Squares indicate the location of caught but not radio-tagged individuals (n = 32). Of the 72 individuals caught, 40 were tagged with radio transmitters.

Figure. 8.2: One-year-old Atlantic salmon parr (measuring 134 mm and 26.30 g) tagged with an external radio transmitter in sub-dorsal position (ref: F1945 by ATS ™, ©INRA/S. Glise).

area over three days in November 2017 (20th, 21st and 22nd). The fishing period was just before the breeding season (in December with an activity peak around the 15th), allowing us to discriminate between mature and immature individuals by the presence or absence of milt when gently stripped (Lepais *et al.* 2017). The caught individuals were anaesthetised with benzocaine at 20 mg.L^{-1} before we weighted them, measured their fork length, took a fin clip sample, and checked their maturity state. Of the 72 individuals, 40 one-year old individuals belonging in the same cohort (30 mature and 10 immature) were tagged with external radio transmitters (ref: F1945 ATS^{TM}, 1.1 g, 40 ppm) in a sub-dorsal position (Figure. 8.2). The 40 that were tagged were selected to depict a representative sample of the distributions of weight and of body size in the population. These distributions were assessed by sampling 77 individuals in the study area one month earlier. The catching point of each parr during the electro-fishing was marked and each individual was released at its catching point after handling. This precaution was taken in order to limit the disturbance of capture on subsequent territorial and space use behaviour. To prevent a sex effect when comparing mature and immature parr, the genetic sex of the radio-tagged immature individuals was determined by genotyping at one sex-specific locus — `sd-Y` (Yano *et al.* 2013) — following the methods used by Lepais *et al.* (2017). The 10 tagged immatures were all genetic males.

The location of each individual was recorded daily from the 24th of November 2017 to the 9th of January 2018. Locations accurate to 5 m were determined by manual radio-tracking using a mobile receiver (R2100 ATS^{TM}) and a loop antenna while walking along the river (there were two days without data). Each GPS position was recorded using a mobile GPS tablet (Trimble®Yuma^{TM}). An accurate redd survey was not possible for this year due to unfavourable weather conditions and resultant poor water visibility.

8.2.2 THE EFFECT OF MATURITY ON SPACE USE

Space use can be defined by two determinants: the distances covered and the resulting area used. We represented the covered distances from individual positions by computing the sum of the upstream distances covered by each individual throughout the breeding season, as well as the sum of the absolute distances (Figure. 8.3). The vital area of an individual was defined by their individual home range (shortest distance containing 95% of their positions), centroid position (average position), and relocation distance (absolute distance between the catching point and the centroid position). The model described in Eq. 8.1 was fitted to the data under a Bayesian framework to explain these five variables (noted Y) according to the maturity level of each individual i. This model allowed us to test whether the distribution of Y was similar between the two groups both in terms of location parameter (μ) and in terms of variability (σ).

$$\begin{aligned} \mu_i &= \alpha\,[\text{Maturity}_i]\,, \\ \sigma_i &= \beta\,[\text{Maturity}_i]\,, \\ Y_i &\sim \mathcal{S}\,(\nu, \mu_i, \sigma_i)\,. \end{aligned} \qquad \text{(Eq. 8.1)}$$

The fork length and weight of individuals were also compared between maturity levels with a similar model. A generalised Student distribution was chosen to deal with potential outliers, while a Cauchy distribution ($\mathcal{C}(0, 1000)$) — a weakly informative distribution — was used as prior of the μ parameter as recommended by Gelman *et al.* (2008). A more informative gamma distribution ($\Gamma(0.01, 100)$) was used as prior of the σ parameter (Gelman *et al.* 2014). After a burn-in of 1,000 iterations, a total of 6,000 iterations were saved from three chains by calling `MC Stan` with the `R` package `RStan` (Stan Development Team 2018). Chain convergence was assessed by graphical examinations and the scale reduction factor, $\hat{\mathrm{r}}$, as well as the effective sample size and the autocorrelation of parameter estimates. The overlap percentages between the posterior distributions of α or β for the two maturity levels were computed with the `R` package `overlapping` (Pastore 2017) and defined our Bayesian P_{value} to test the maturity effect. An overlap percentage lower than 5% indicated a significant effect. The Bayesian models that followed were analysed similarly. The number of days during which locations of individuals were recorded in the study area did not differ between maturity levels (Wilcoxon: W=85, $p_{value} = 0.07$, N=30 and 9 mature and immature individuals, respectively), thus this variable was not included in models comparing maturity levels (Eq.

8.1).

The effect of fork length on the upstream distance (Y_i) covered by each mature individual i, was tested with the following model:

$$\begin{aligned} \mu_i &= \alpha_0 + \beta \times \text{distance start}_i + \delta \times \text{body size}_i + \gamma \times \text{NDay}_i, \\ Y_i &\sim \mathcal{S}\left(\nu, \mu_i, \sigma\right), \end{aligned} \qquad \text{(Eq. 8.2)}$$

Here `distance start`$_i$ represents the distance at catching of individual i, therefore individuals caught higher upstream had a lower distance to cover to reach the upstream dam. The variable `NDay`$_i$ corresponds to the number of days during which the individual i was located in the study area. Indeed, individuals could exit through the downstream limit and potentially re-enter in the study area. Yet, all individuals that exited the study area did not re-enter in. For this model, the thinning interval was increased to 10 to prevent autocorrelation in parameter estimates. The percentage of parameter estimates lower than 0 for a negative parameter and greater than 0 for a positive parameter defined the Bayesian P_{value}.

8.2.3 SPACE USE TACTICS IN MATURE INDIVIDUALS AND PROBABILITY OF REDD ENCOUNTERS

The 30 mature individuals were separated in three categories based on their space use tactics. The three groups allowing us to discriminate individuals in two dimensions and ensuring an adequate number of individuals per group. After scaling and centring variables, we used the function `discrimin` from the `R` package `ade4` for discrimination. The five variables used in the previous steps (upstream and absolute distances, home range, centroid position, relocation distance) were combined with the number of direction switches and the sum of covered distances. The latter two variables were not compared between maturity levels to avoid having too many tested variables but were included in this discrimination analysis. In the computation of the sum of the covered distances, upstream distances were assigned to be positive and downstream distances negative (Figure. 8.3). A one direction switch occurred when an individual went upstream one day and downstream the following day or *vice versa* (for example between position 2 and 3 or 3 and 4 in Figure. 8.3). In this analysis, the individual number of direction switches made per individual was normalised by the number of days during which the individual was found in the study area to prevent a potential bias, since these two variables were

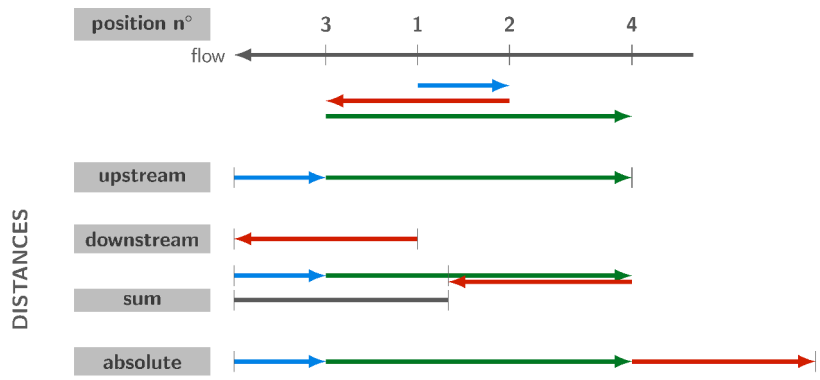


Figure. 8.3: Scheme of the different distances computed in the study to define space use of one-year old Atlantic salmon parr. Numbers indicate temporal positions along the river from position 1 to position 4. The river flows from right to left. Three movements are displayed, arrow direction corresponds to the movement direction. The blue and green movements correspond to a fish moving upstream.

correlated (Spearman: S = 722.8, $\rho = 0.84$, $p_{value} < 0.001$). The same normalisation was done for the upstream distance, since the correlation was also significant (Spearman: S = 2781.8, $\rho = 0.38$, $p_{value} = 0.04$). The other variables did not correlate to the number of days that individuals were present in the river. Immature individuals were included in this analysis as a control group. We applied a Monte-Carlo test with 1000 permutations allowed us to test the significance of the discrimination between the four groups.

The positions of redds recorded between 2011 and 2015 along the study area allowed us to predict locations of breeding activity during the 2017 breeding season. Habitat quality of breeding sites were assumed to have remained constant between 2011-2015 and our study period. The density of redds was then computed along the study area as well as the density of each parr from their daily positions. From these densities, it was possible to plot the density curves of each of the parr's positions and redd positions along the study area (Figure. 8.4). The individual cumulative probability to encounter redds, Pr [Encounter redd] was defined by the area under the intersecting curve between the redd density curve and the parr density curve. These probabilities provided a proxy of an individual's participation in reproduction (Figure. 8.4).

The individuals probabilities of encountering redds were compared between the three space use groups of matures. Immature individuals were included in this analysis again as a control group. The overlap percentage between the estimated average value of this probability in each group defined the Bayesian P_{value} of the comparison:

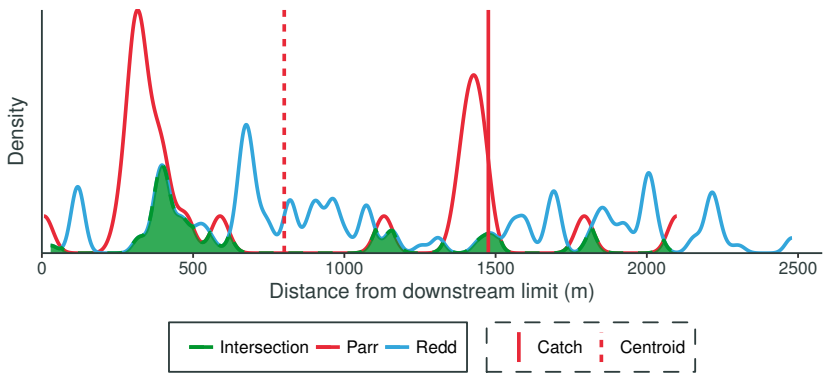


Figure. 8.4: Density curves of one Atlantic salmon parr's positions (red line) and redd positions (blue line) monitored in the study area. An external radio transmitter enabled the daily recording of the parr's positions throughout the breeding season in the Nivelle population. Redd positions were based on data from 2011 and 2015. The area of intersection below both density curves, indicated in green, defines the individual's probability to encounter redds.

$\Pr\left[\text{Encounter redd}\right]_i \sim \mathcal{S}\left(\nu, \alpha\left[\text{Group}_i\right], \sigma\right)$. The $\Pr\left[\text{Encounter redd}\right]$ was standardised in this model to enable a better model fit. This comparison allowed us to test the link between the space use tactics and the probability to encounter redds of each individual i. This method was used in order to test variables direct effect on the probability and in order to prevent multiple comparisons. This analysis also allowed us to account for possible paired effects of variables and provided a comprehensive understanding of the effect of space use on the probability of encountering redds.

8.3 RESULTS

No spatial segregation or specific pattern was found between maturity levels at catching in November (Figure. 8.1). Weight and fork length did not significantly differ between mature (mean $\pm$ standard deviation: 39.42 g $\pm$ 7.5 g and 149.9 mm $\pm$ 9.1 mm) and immature parr (38.6 g $\pm$ 8.3 g and 152.3 mm $\pm$ 12.8 mm) — Bayesian $P_{value} = 0.81$ and 0.34. Tags weighed between 1.86 % and 4.36 % of the total fish mass.

During radio-tracking, eight different individuals reached the impassable dam at the upstream limit of the study zone. On the last day, the 47th day after tagging, 22 individuals (eight immature) among the 40 tagged individuals were still in the study area. The other individuals had either moved out of the study area or became untraceable (a battery life of 27 days is guaranteed for the tags). One immature individual, the smallest of the parr caught (129 mm) and the one caught furthest downstream (20 m

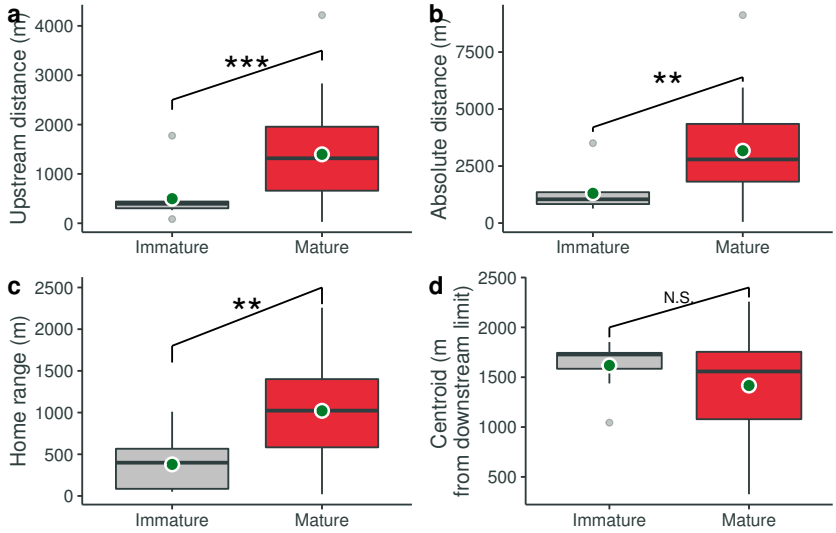


Figure. 8.5: Boxplots of (a) upstream covered distance, (b) absolute covered distance, (c) home range, (d) centroid position , and (e) relocation distance — distance between catch sites and centroid — of Atlantic salmon parr. Parr from the population in the Nivelle River were tagged with radio transmitters and their positions were monitored daily throughout breeding season. Thirty mature individuals (red) and nine immature individuals (grey) were tagged. The mean value of each variable for each maturity state is displayed in green.

upstream the downstream limit of the study area), moved out the study area on the first day of tracking. Only nine immature individuals were therefore included in subsequent analysis.

8.3.1 THE EFFECT OF MATURITY ON SPACE USE

Mature individuals covered longer upstream distances than immature individuals (mean of parameter estimates and 95% credible interval: $\mu = 1285.25$ m $[968.44; 1596.78]$ against 363.78 m $[260.71; 460.65]$, Bayesian $P_{value} < 0.001$ — Figure. 8.5), and travelled longer absolute distances (2831.09 m $[2188.42; 3508.04]$ against 998.13 m $[739.02; 1301.00]$, Bayesian $P_{value} = 0.002$). Mature individuals also had wider home ranges (1008.38 m $[801.51; 1212.11]$ against 363.36 m $[154.83; 569.12]$, Bayesian $P_{value} = 0.005$) compared to immature ones. No significant differences were found for the centroid positions (1441.90 m $[1259.84; 1617.20]$ against 1646.19 m $[1480.34; 1788.63]$, Bayesian $P_{value} = 0.24$) and relocation distances (2.48 m $[0, 90.06]$ against 29.54 m $[12.63; 45.12]$, Bayesian $P_{value} = 0.17$).

Upstream and absolute distances were significantly more variable for mature individuals than immature ones ($\sigma = 584.53$ m $[390.39; 825.66]$ against 115.87 m $[43.14; 255.23]$,

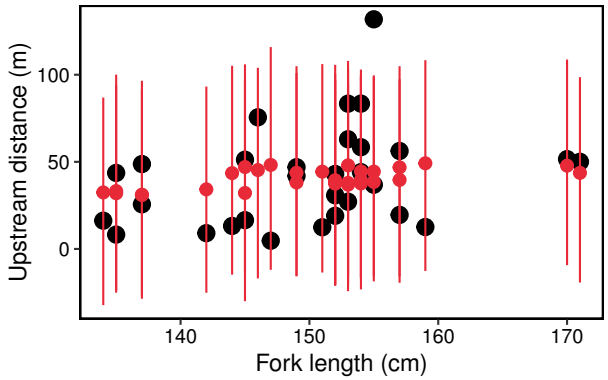


Figure. 8.6: Plot of the upstream distance covered by radio-tagged salmon parr in the Nivelle population as a function of their fork length. Thirty mature individuals were tagged. Black dots represent observed values and red symbols indicate estimates of the model with the credible interval at 95%.

Bayesian $P_{value} = 0.03$ for upstream distance; 1028.52 m $[656.95; 1454.09]$ against 268.27 m $[118.00; 489.51]$, Bayesian $P_{value} = 0.02$ for absolute distance — Figure. 8.5). The variance of the normal distributions (absolute and upstream distances) was three times greater in mature individuals than immature individuals, while three times as many mature individuals were tagged. Home ranges and centroid positions were not more variable in mature parr than immature ones. Relocation distances were ten times more variable among mature individuals than among immature ones (285.38 m $[177.71; 393.14]$ against 21.66 m $[10.25; 39.14]$, Bayesian $P_{value} < 0.001$). We tested whether the upstream distances covered by mature individuals were dependent on their fork length in order to explain this higher variability. The upstream distance was normalised by the number of days during which individuals were detected. Individual fork length had a significant but weak positive effect ($\delta = 0.24\ \frac{\text{m}}{\text{day}}.\text{mm}^{-1} \pm 0.00\ \frac{\text{m}}{\text{day}}.\text{mm}^{-1}$, Bayesian $P_{value} = 0.03$, Eq. 8.2).

8.3.2 SPACE USE TACTICS IN MATURE INDIVIDUALS AND PROBABILITY OF REDD ENCOUNTERS

The discrimination of the 30 mature individuals into different groups on the basis of their space use was significant ($\text{p}_{\text{value}} < 0.001$ — Figure. 8.7 c). In Figure. 8.7 a, axis 1 carries information about home range while axis 2 represents other variables. Centroid position, number of position switches, and sum of covered distances had little influence on the discrimination (Figure. 8.7 a). The first group of parr had higher values of covered distances (individuals favouring upstream movement) and absolute distances covered (Figure. 8.7 a and b). The second group had lower home range values and

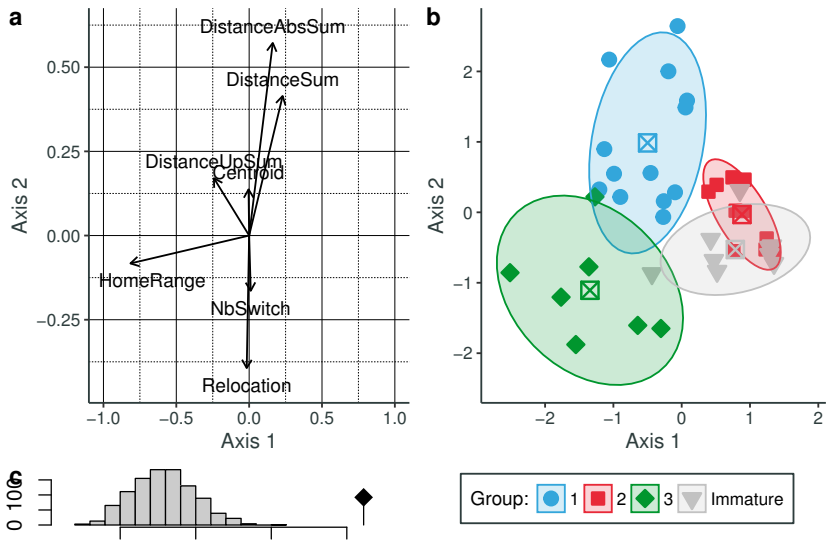


Figure. 8.7: Plots of the discriminant analysis according to the space use of mature and immature salmon parr throughout the breeding season (N_{group}= 15, 9, 6, and 9 respectively for groups 1, 2, 3, and immature parr). Immature parr are included as a control group. (a) The relative importance of each variable on the two selected axes. (b) The groups resulting from the discrimination of the 30 mature individuals and 9 immature ones. (c) The Monte-Carlo test output of the discriminant analysis testing if the groups were similar or not (significant test) to random groups.

lower average values of covered distances. The third group had broader home ranges and longer relocation distances. The control group, immature parr, held a "central" position with the three groups of mature around (Figure. 8.7 b). There was a notable overlap between group 2 and the immature group.

The probabilities of encountering redds were similar for groups 1 and 3 (Bayesian $P_{value\ 1-3} = 0.12$, Figure. 8.8), both of which were significantly higher than group 2 (Bayesian $P_{value\ 1-2} = 0.045$ and Bayesian $P_{value\ 2-3} < 0.01$, Figure. 8.8). Immature individuals, representing "control" probabilities, displayed significantly lower probabilities of encountering redds than groups 1 and 3 (Bayesian $P_{\text{value immature}-1} < 0.01$ and $P_{\text{value immature}-3} < 0.001$), but there was no significant difference between the control and group 2 (Bayesian $P_{\text{value immature}-2} = 0.35$).

8.4 DISCUSSION

The monitoring of individual displacements of Atlantic salmon parr throughout the breeding season enabled us test the effect of maturity on space use. As hypothesised, maturity affected the displacements of individuals throughout the breeding season. Ma-

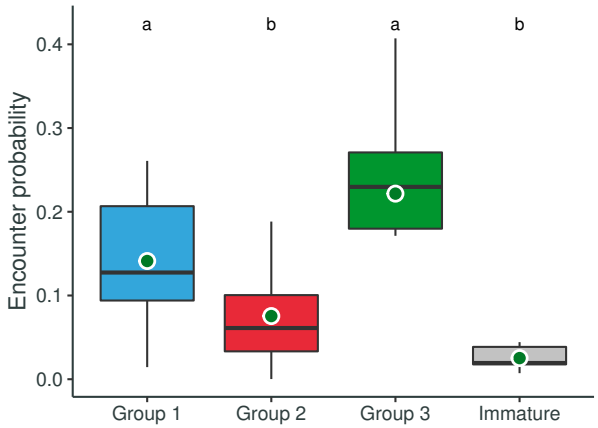


Figure. 8.8: Plots of the probability of redd encounter for mature salmon parr (groups 1 to 3) and for the immature salmon parr during the breeding season. The 30 individuals were discriminated on the basis of their space use (N_{group}= 15, 9, 6 and 9 respectively for groups 1, 2, 3, and immature parr). Groups with different letters are significantly different.

ture individuals displayed both a higher average mobility and a larger inter-individual variability in space use tactics. Between mature individuals, those which had broader home ranges or those which favoured travelling upstream to moving downstream (positive sum of the covered distances) exhibited higher probabilities of encountering redds.

Obtaining similar distributions of age, size (fork length) and weight between maturity levels was a challenging methodological issue. The length and weight was homogeneous between maturity levels, which ensured that differences in space use between mature and immature individuals were not related to difference in size. In addition, tag mass was below 5% of body weight in all cases, much lower than the 8% limit recommended by Lacroix *et al.* (2004). Despite the relatively low tag mass, we recognise that external tagging could still have had a negative impact on the movement and hydrodynamics of individuals. If the tags affected the movement and behaviour of individuals, the observed differences in space use between maturity levels would have then been underestimated and not overestimated. This tag effect may have encouraged downstream movements rather than upstream ones (constraints against flow are higher) and may have negatively impacted the length of covered distances.

8.4.1 THE EFFECT OF MATURITY ON SPACE USE IN RELATION TO DIFFERENT FOCAL RESOURCES

Maturity involves a switch to broader home ranges as well as an exacerbated mobility in relation to different focal resources. In this study, mature individuals exhibited broader home ranges and covered longer upstream distances than immature individuals, which was linked to a higher probability of encountering redds. The difference in probability of encountering redds between maturity levels is consistent with the expectation that immature individuals focus predominantly on food while for mature individuals, females and breeding activity are greater priorities. The smaller home ranges and the smaller covered distances of immature parr are consistent with the fact that salmon parr are territorial feeders (Steingrímsson & Grant 2003). Mature individuals, however, move in search of anadromous females, a sparsely distributed and mobile resource (Tentelier *et al.* 2016a). Greater mobility and a higher probability to encounter redds in mature individuals, associated with redd searching agrees with some previous results obtained in experimental elliptical flumes. Thorpe *et al.* (1988) found that mature parr moved more than immature ones in November, and Armstrong *et al.* (2001) found that mature individuals stayed near a redd for longer than immature ones. The extreme variability in relocation distances of mature individuals that we found supports these findings. Some individuals dispersed from their feeding territories (assumed from their location at catching) to another river zone to search for a new resource: females. Hence, these results indicate that individuals with different maturity states adopt different space use tactics due to focusing on different resources.

Multiple central-place foragers may move within wider home ranges than expected. Immature salmon parr like other multiple central-place foragers defend feeding territories, moving and staying at feeding stations within these territories (Steingrímsson & Grant 2008). Steingrímsson & Grant (2003; 2008) found an average territory size of around 1 m^2 for young of the year salmon. Roy *et al.* (2013a) found an average of 28.2 m (maximum at 43 m) for one-year-old parr monitored from 24 July to 30 October. In our study, immature individuals had home ranges varying from 50 m to 1 km, much larger territory sizes than previously reported for immature Atlantic salmon. Differences with Steingrímsson & Grant (2003; 2008) may be due to the different ages — young of the year in their studies and parr in ours —, while differences with Roy *et al.* (2013a) may be due to the season of the study — summer against autumn. These findings suggest

that the feeding territory size of salmon parr may be strongly dependent on season and age.

8.4.2 SPACE USE AS A BEHAVIOURAL TRAIT

The higher variability in distances covered by mature individuals compared to distances covered by immature ones suggests that a diversity of behavioural traits exists in mature individuals. The lower variability in distances covered by immature individuals was despite the fact that they experienced the same environmental conditions as the mature ones. This suggests that maturity level is responsible for the heterogeneity, probably reflecting a diversity of behavioural traits in mature parr as is the case for anadromous males (Tentelier *et al.* 2016a). Some individuals may have stayed near one female or a group of females at one site, adopting a staying behaviour; others may have moved a lot to find several females or groups favouring a roaming behaviour (Forchhammer & Boomsma 1998, Sandell & Liberg 1992). An intermediate tactic may also be to use a few nearby breeding sites, like multiple central-place foragers.

The discrimination of mature individuals into three groups based on their space use revealed a similar variability. It is also interesting to note that the group of immatures occupied a central place with the three groups of matures dispatched around. Space use tactics of mature individuals could radiate from a "basic" space use displayed by immatures. Some individuals may favour a similar tactic to multiple central-place foragers (group 2 — Figure. 8.8), others a broader home range (group 3), and others could favour upstream displacements over downstream displacements (group 1).

8.4.3 LINKS BETWEEN SPACE USE AND PARTICIPATION IN REPRODUCTION

Heterogeneity in individual space use arising from maturity could also be linked to heterogeneity in participation in reproduction. The three space use groups displayed significant differences in probabilities of encountering redds. Wider home ranges and the favouring of upstream movements seem to be reproductively beneficial for mature individuals. Despite the lack of temporal dimension, and despite inferring redd positions from recent years, these results are in accordance with previous studies. This type of relationship between space use and participation in reproduction, or at least the probability of encountering a mate, is known to exist in anadromous Atlantic salmon (Tentelier *et al.* 2016a) and in other species (Fisher & Lara 1999, Formica *et al.* 2010, Kamath & Losos 2018). Recent studies have focused on the links between space use and

social or sexual networks (Cunningham *et al.* 2018, McDonald *et al.* 2013, Silk *et al.* 2018). New studies are needed to monitor successful encounters of redds by mature parr and their actual participation in reproduction. Such monitoring was planned to do in this study but could not be due to the unusually high flow conditions preventing us from accurately mapping redds.

The decision to participate in reproduction or adopting a particular space use tactic relative to the participation in reproduction may depend of individual body size. Fork length was positively correlated to upstream distances covered: the larger the mature parr, the longer the covered upstream distance. A potential explanation for this is that larger parr have better swimming abilities, one probable mechanistic cause of space use diversity (Webb *et al.* 1973, Weihs 1973). In addition, some individuals increased their probability to encounter redds by favouring to upstream displacements rather than downstream ones (positive sum of covered distance). The effect of size on mobility lines up with size effects already reported in mature parr. Myers & Hutchings (1987) previously described the effect of mature parr size on their dominance in gaining access to redds, while Garant *et al.* (2002), Grimardias *et al.* (2010a), Jones & Hutchings (2002) have reported that size has an affect on the reproductive success of mature parr.

8.4.4 POTENTIAL IMPLICATIONS FOR SURVIVAL AND BEHAVIOURAL DIVERSITY

Individual heterogeneity in space use brought on by maturity may lead to differences in survival rates. Individuals adopt tactics and movement behaviours which require varying amounts of energetic resources. Displacement heterogeneity, for instance, should cause heterogeneity in energetic costs. Under the principle of energy allocation (Cody 1966), any energetic costs related to the various behaviour and space use tactics would be additional to the existing energetic demands associated with gonadal maturation (Brokordt & Guderley 2004). Heterogeneity in space use potentially further drive heterogeneity in survival probabilities for mature individuals (Buoro *et al.* 2010, Myers 1984). Moreover, longer displacements and potential changes of habitats induced by maturity may lead to potential higher predation risks but something which was impossible to assess with the tags employed in this study.

The different space use groups indicated that the space use of mature parr can be considered as an expression of behavioural traits (Dingemanse *et al.* 2003). The space

use of may be directly influenced by parental behaviour (although this is probable for salmon) or by a modification of their phenotype (e.g. via genes, Dingemanse *et al.* 2003). Further studies are needed to test whether the variability of behaviours and resulting reproductive success within early maturing individuals may impact the evolution of behaviours under a game-theoretic approach as suggested by Smith & Blumstein (2008).

Understanding how maturity shapes spatial distribution, either in usual maturation or in early maturation, provides useful information to improve species management. Identifying potential threats due to space use or factors reducing survival among developmental stages enables establishments of new management directives. In their study, Starking-Szymanski *et al.* (2018) provided valuable information about a management program by monitoring displacements and habitat use of Blandings turtle *Emydoidea blandingii*. Additionally, identifying whether and how individuals move in habitats threatens by human-induced disturbances also enables to improve management directives. For instance, Rio-Maior *et al.* (2018) found that breeders in Iberian wolves *Canis lupus* may be affected by human activities during breeding seasons.

8.5 CONCLUSION

Maturity has an important effect on space use and displacements of Atlantic salmon parr. Mature individuals covered longer distances than immature individuals implying potential costs for their survival. Maturity may, therefore, affect individual survival also by modifying their spatial distribution. Space use of mature individuals was linked to their probability to participate in reproduction suggesting also an effect of space use on their fitness. Further studies in salmon may investigate the true link between space use reproductive success of early maturing salmon which may impact genetic diversity and the effective population size of a population (N_e, Jones & Hutchings 2001; 2002, Juanes *et al.* 2007, Saura *et al.* 2008). Impacts of displacements and space use tactics in terms of energetic costs and survival probability also remain to be studied. Finally, a possible extrapolation of our results to other taxa might be useful to identify proximal and ultimate causes of space use tactics in relation to age at first reproduction.

DEEPER IV.i: First elements of the space use of mature parr during the breeding season

Alternative reproductive tactics should also cause a divergent dispersal of juveniles. A strong size difference exists between the two alternative reproductive tactics (Bagliniere & Maisse 1985, Kazakov 1981). The strong size difference generates weaker swimming abilities (Webb *et al.* 1973, Weihs 1973), as well as lower energetic reserves for mature parr compared to anadromous males. According to the principle of allocation, mature parr should have a spatially constrained participation in reproduction. The spatial distribution of juveniles fathered by each individual should, thereby, be reduced for mature parr in comparison to anadromous.

Parentage data and capture location of juveniles of Tentelier *et al.* (2016b) — for details see Part III, page 145 — permitted computing the distance between the two furthest juveniles fathered by each male. A value of the distance range characterised each anadromous male and each mature parr which sired at least two juveniles. The capture location of each juvenile, as well as of each mature parr, allowed us to know if juveniles were upstream or downstream their father mature parr. In 2009, 18 mature parr fathered 475 juveniles, while in 2010, 21 mature parr sired 148 juveniles. 11 anadromous males produced 735 juveniles in 2009, while 24 anadromous males fathered 1015 juveniles in 2010 (Tentelier *et al.* 2016b).

To better understand how varied the distance between the two furthest juveniles of the same father, we modelled it by the number of mated females (mating success) and the number of produced juveniles (reproductive success). A simple generalised linear model was fitted for each year (j) with the reproductive tactic ($RT_{m,j}$) of the male j as a fixed effect and with the mating success ($M_{m,j}$) or the reproductive success ($T_{m,j}$) as an explanatory variable:

$$Distance_{m,j} \sim \mathcal{S}(\nu, RT + M_{m,j} + RT \times M_{m,j}, \sigma) \quad \text{(Eq. 8.3)}$$

$$Distance_{m,j} \sim \mathcal{S}(\nu, RT + T_{m,j} + RT \times T_{m,j}, \sigma) \quad \text{(Eq. 8.4)}$$

The variable $Distance_j$ was standardised (each year separately) to increase the efficiency of these models.

The range between the two furthest juveniles fathered by the same father displayed a similar pattern between the two reproductive tactics (Figure. 8.9). Over the two years, four mature parr displayed a range longer than seven kilometres.

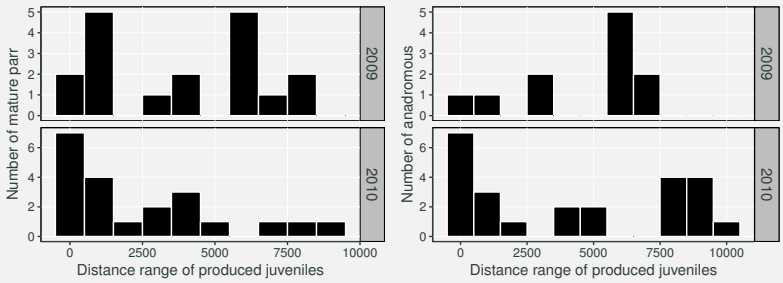


Figure. 8.9: Plot of the distance between the two furthest juveniles fathered by a male mature parr (left) or an anadromous male (right) during two breeding seasons in the Nivelle River. Data concerned 18 and 21 mature parr in 2009 and 2010, respectively, while data on 11 and 24 anadromous were used in 2010.

When looking at the position of the juveniles fathered by a mature parr, most of the juveniles were found upstream from the position of their father (Figure. 8.10 a). It was especially true when the distance between a mature parr and its juveniles increased. At the individual level, the proportion of juveniles at an upstream position from their father was extremely variable between each mature parr. Indeed, some individuals displayed a high proportion of juveniles either upstream or downstream, whereas some individuals displayed similar proportions of juveniles upstream and downstream (Figure. 8.10 b).

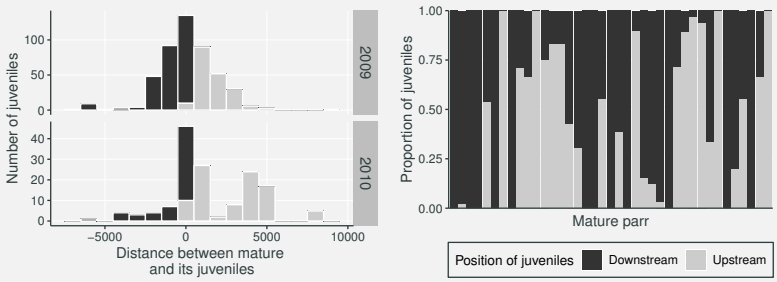


Figure. 8.10: Histogram of the distance between each mature parr and its juveniles (left) and proportion of juveniles found upstream or downstream to each parr father (right) during two breeding seasons in the Nivelle River (2009 and 2010). Data concerned 18 and 21 mature parr in 2009 and 2010, respectively, while data on 11 and 24 anadromous were used in 2010.

Over both breeding seasons, the distance between the two furthest juveniles increased as the mating success raised (Table. 8.1). Reproductive tactics had no effect on this relationship through the fixed effect or the interaction (Table. 8.1), reproductive tactics clearly exhibiting the same pattern (Figure. 8.11). The reproductive success did not affect the distance in 2009 but a positive trend appeared in 2010. Interaction effect with reproductive tactics appeared significant for the second year (Table. 8.1).

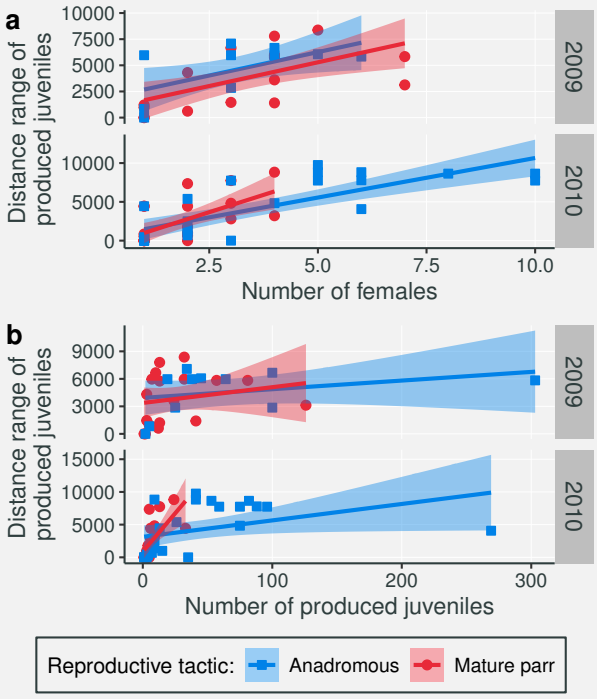


Figure. 8.11: Plot of the distance between the two furthest juveniles fathered by a mature parr (in red) or an anadromous male (in blue) as a function of the number of mated females (a) or the number of produced juveniles (b). A simple linear model was fitted for each couple of variables with a fixed effect of the reproductive tactic, lines correspond to estimated median with the confidence interval at 95%.

Table. 8.1: Results of the generalised models Eq. 8.3 and Eq. 8.4 to test the effects of the mating success ($M_{m,j}$), the reproductive success ($T_{m,j}$) and reproductive tactic (RT_m) on the distance between the two furthest juveniles fathered by a same anadromous males or mature parr.

Model	Year	Variable	p_{value}
$Distance_{m,j} \sim RT_{m,j} + M_{m,j} + RT \times M_{m,j}$	2009	RT	0.24
		$M_{m,j}$	< 0.001
		$RT \times M_{m,j}$	0.98
	2010	RT	0.68
		$M_{m,j}$	< 0.001
		$RT \times M_{m,j}$	0.16
$Distance \sim RT + T_{m,j} + RT \times T_{m,j}$	2009	RT	0.80
		$T_{m,j}$	0.22
		$RT \times T_{m,j}$	0.73
	2010	RT	0.49
		$T_{m,j}$	< 0.001
		$RT \times T_{m,j}$	0.01

Mature parr and anadromous exhibited similar dispersal patterns of their juveniles. Both tactics displayed range between the two furthest juveniles of the same male which may exceed 7 km. In addition, both tactics exhibited high variability between father individuals. Even if juveniles have been caught after potentially small dispersal, this distance reflects the space use of the father. Indeed, a lot of studies have worked on the juvenile dispersal in Atlantic salmon. Usually, salmon fry stay near the redd from which they emerged for one week or two (Garcia de Leaniz *et al.* 2000, Gustafson-Greenwood & Moring 1990). Even if some authors found various dispersal

distances and a dispersal speed estimated at around five m.day^{-1} (Garcia de Leaniz *et al.* 2000), dispersal distances remain in a similar range of variability from 20 m downstream to less than 100 m downstream (Beall 1994, Crisp 1995, Einum & Nislow 2005, Gustafson-Greenwood & Moring 1990). However, salmon fry may disperse to 400 m downstream (Beall 1994, Webb *et al.* 2001) and 50 m upstream the redd (Einum *et al.* 2006) at late emergence season because of competition to settle in feeding territories. These scales of variations remaining small in comparison to dispersal ranges found here, and especially when father was found downstream than its juveniles (for mature parr). Hence, ranges found here suggest that mature parr exhibited a diversity in space use during the breeding season like anadromous males.

ACKNOWLEDGEMENTS

This research followed both national and European regulations. Fish capture and field work were conducted with ethical approval from the legal representative (prefectural decree n°64-2017-05-22-001) and the ethical committee for birds and fishes in the French region Nouvelle Aquitaine (n°10126-2017071013218091).

HIGHLIGHTS OF CHAPTER 8

- Maturity involves a switch of focal resources or at least may involve new focal resources.
- Maturity may therefore affects the space use of individuals.
- Indeed, mature individuals covered longer distances which can increase the predation risk.
- Maturity also increased diversity of space use between individuals which can favour appearance in a diversity of energetic costs.
- Space use tactic of mature individuals was linked to their probability to participate in reproduction.

Maturity may, therefore, affect survival and fitness of individuals through space use of individuals.

CHAPTER 9

Accounting for maturity level when investigating habitat use of individuals

Contents

9.1 CONTEXT

The previous chapter discussed the modification of individual space use by maturity. Individual space use may be determined by covered distances, home ranges and centroid positions (Armstrong *et al.* 1999, Moorcroft *et al.* 2006, Tentelier *et al.* 2016a). Nevertheless, individuals may also differentially use space in terms of habitat use (Cameron *et al.* 2018, Dinkins *et al.* 2017, Morris 1987). A habitat corresponds to a portion of a species' ecological niche whose characteristics, biotic and/or abiotic, satisfy needs of individuals accomplishing specific activities such as feeding, breeding, harvesting, ...

In a recent special issue in *Oïkos* (Hamel *et al.* 2018), several authors stressed the necessary inclusion of individual heterogeneity in population modelling and in Capture-Mark-Recapture modelling. Individual heterogeneity may arise from different causes, either measurable traits or states (e.g. individual size, sex, or age) or unobservable sources as discussed by Gimenez *et al.* (2018). Maturity levels (immature vs mature) can generate such heterogeneity in space use as found in the previous chapter (chapter 8, page 257).

Maturity levels (immature vs mature) might also cause such individual heterogeneity in habitat use. Searching for anadromous females, mature individuals should be found near breeding habitats. At the opposite, immature parr, continuing to feed (Fraser & Metcalfe 1997), should be found in foraging habitats. However, breeding habitats and feeding habitats of salmon parr may overlap. Indeed, both habitats are characterised by

close values in terms of velocity ($35-65$ cm.s^{-1} vs $60-75$ cm.s^{-1} for breeding habitat and feeding habitat respectively) and depth ($20-50$ cm vs $60-75$ cm for breeding habitat and feeding habitat respectively, Louhi *et al.* 2008, Nislow *et al.* 1999, Roy *et al.* 2013a).

DEEPER IV.ii: Longitudinal gradient of maturity within a river

One question relating both to space and to Atlantic salmon mature parr is to know if there is a longitudinal gradient of maturation within a population. Indeed, food availability may vary along a river as well as habitat complexity. These two factors affect the growth of individuals, one important determinant of early maturation. However, studies found divergent results. In the Ste. Marguerite River (Québec, Canada), Aubin-Horth *et al.* (2006) found that the frequency of mature individuals increases as the upstream distance. At the opposite, Bagliniere & Maisse (1985) found that the maturation was higher downstream in the Scorff River (France). I then assessed if such longitudinal gradient occurs in the Nivelle River.

We used the population monitoring in the Nivelle River (Chapter 2, page 65) consisting of young of the year caught at 22 sites along the river from 2003 to 2015. The probability that a caught individual (i) was mature at each site (s) in a year (y) was computed under a Bayesian framework as follows:

$$\Pr[\text{Mat.} = 1|\text{i, y, s}] = \frac{1}{1 + exp\left(-\left(\text{intercept} + \alpha_{y,i} + \beta_{s,i} + \delta \times \text{LF}_i\right)\right)} \quad \text{(Eq. 9.1)}$$

with LF_i the fork length of individual i.

Although the more upstream site displayed the higher positive effect on the probability that the individual i was mature (Figure. 9.1), no clear pattern appeared.

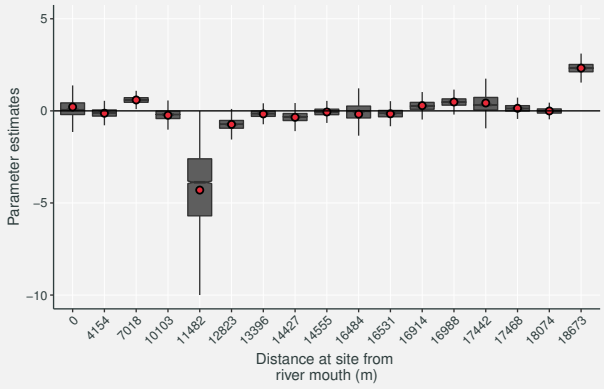


Figure. 9.1: Plot of the probability that a Atlantic salmon parr caught along the Nivelle river was a mature parr.

Maturity might also generate more movements between habitats. Immature individuals still feeding in winter (Fraser *et al.* 1995), while maturation did not affect appetite of mature parr (Simpson *et al.* 1996) suggesting that mature individuals also keep feeding. Maturity may, therefore, increase movements between feeding habitats and breeding ones.

In salmon parr, some studies have worked on activity rhythms (Fraser *et al.* 1995, Hiscock *et al.* 2002, Metcalfe *et al.* 1999, Roy *et al.* 2013a, Simpson *et al.* 1996), as well as on habitat use (Robertson *et al.* 2003, Roy *et al.* 2013a, Steingrímsson & Grant 2008). However, most of studies were focused on immature or did not account for maturity levels (Fraser & Metcalfe 1997, Fraser *et al.* 1995, Hiscock *et al.* 2002, Metcalfe *et al.* 1999, Roy *et al.* 2013a). Most of studies about habitat use were also only to describe the preferred habitat or how individuals move within them. How salmon parr use habitat in a dynamic way, movements among habitats, was never assessed at fine scale (e.g. Robertson *et al.* 2003 compared movements among lacustrine and fluvial habitats), especially when accounting for maturity effect.

Hypothesising a clear different habitat uses between maturity levels of salmon parr would be an assumption too strong. Nevertheless, I can hypothesise that mature and immature individuals display different movement probabilities between habitat types in a river. Similar movement probabilities would be assigned to different habitat types for mature parr due to their shifts in habitats to breed and feed. At the opposite, immature

would exhibit a higher movement probability to go to one habitat type. To test this, a capture-mark-recapture (CMR) approach was used to estimate movement probabilities between habitat types with the data of the previous chapter (chapter 8, page 257).

9.2 METHODS

9.2.1 DATA

During the study of Tentelier *et al.* (2016a), the upper zone of the Nivelle (upstreal Olha dam, Figure. I.viii) was divided in 618 stretches based on morpho dynamic changes of habitat, dams, bridges for instance. Each stretch was characterised according to five different types of morpho dynamic habitats: riffles, rapids, flat-flowing, flats (or runs or glides), pools, with increasing depths and reducing velocities (Prevost & Chaput 2001, page 100). For each stretch, the proportion of area defined by each flow pattern was noted, the higher proportion defining the stretch. A habitat type "mixed" was also considered when two or more proportion were equivalent for the considered stretch. The stretch delimitation was a more precise and more contemporary delimitation than the division by stretches used in the Part II (page 49).

I used the daily positions obtained during the field study described in the previous chapter (chapter 8, page 257). A type of habitat was associated to each individual daily position. Because some individuals left the study area, a seventh type of habitat was also defined to notify a position outside the study area: "out".

9.2.2 ESCAPEMENT AND MOVEMENT PROBABILITY

The escapement probability (leave the study area), as well as the movement probabilities between habitat types, were assessed with a multistate Hidden Markov Model (HMM). Observed states were defined as either one of the habitat types or "not seen". Previous chapter (chapter 8, page 257) shown that maturity levels ("immature" vs "mature") has modified space use of individuals. Therefore, the model developed here assessed the effect of maturity on survival, escapement and movement probability between habitats.

The usual survival probability in such CMR models, ϕ, depicted here the probability to remain detectable, combining tag issue, tag battery life, survival, ... rather than to purely survive (Figure. 9.2). Some models of radio tags change their pulse rate after hours of complete immobility offering possibility to detect dead individuals. Tags used in this study did not have this option so dead individuals could not be discriminated

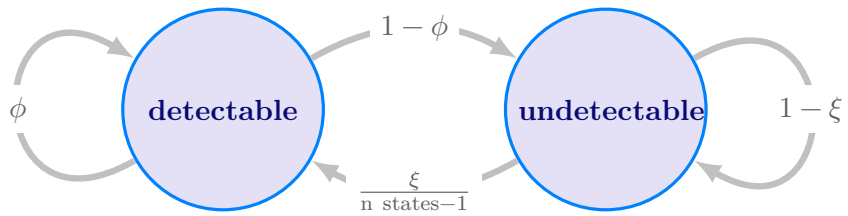


Figure. 9.2: Diagram of the probabilities to be undetectable or not in the multistate Hidden Markov Model written to explain the habitat use of Atlantic salmon parr throughout a breeding season. The undetectable state replaces the usually dead state. The state "alive" displayed here, pools multiple states (Figure. 9.3) but allow to simply represent the probability to remain detectable (ϕ) and the probability to remain undetectable ($1-\xi$).

from living individuals. The probability $1-\xi$ defined the probability to remain undetectable (Figure. 9.2). Indeed, the state "undetectable", replacing the state "dead", pooled individuals not found due to a radio-transmitter error but remaining within the study area and individuals not found and being outside the study area. Therefore, an individual can be detected after not being found; ξ estimating this probability. Recapture probability, p, estimated the probability of observation at day d — $O(d)$ — given the state $S(d)$ (Figure. 9.3). Thus the observation matrix of the model was:

$$\begin{pmatrix} & \text{out} & \text{k} & \text{undetectable} \\ \text{out} & p & 0 & 1-p \\ \text{k} & 0 & p & 1-p \\ \text{undetectable} & 0 & 0 & 1 \end{pmatrix} \qquad \text{(Eq. 9.2)}$$

Here, k indicates any habitat within the study area and *out* a position outside the study area.

One state of the model represented individuals alive outside the study area. This state enabled to estimate the movement probability between habitats in the study area to outside the study area: the escapement probability — $\psi_{\text{k-out}}$, Figure. 9.3. The movement probability also estimated the probability to move between each other habitat types noted k: $\psi_{\text{k-k}}$.

The model accounts for a potential effect of maturity (immature vs mature parr)

on the probability to remain detectable (ϕ^{maturity}), as well as the movement probability ($\psi^{\text{maturity}}_{\text{k-k}}$), and the escapement probability ($\psi^{\text{maturity}}_{\text{k-out}}$ — Figure. 9.3). The differences of mobility observed in chapter 8 (page 257) motivated incorporation of a potential effect of maturity on ϕ. Therefore, the following matrix corresponds to the state-transition matrix of the model:

$$\begin{pmatrix} & \text{out} & \text{k} & \text{undetectable} \\ \text{out} & \phi^{\text{maturity}} \times \psi^{\text{maturity}}_{\text{out-out}} & \phi^{\text{maturity}} \times \psi^{\text{maturity}}_{\text{out-k}} & 1-\phi^{\text{maturity}} \\ \text{k} & \phi^{\text{maturity}} \times \psi^{\text{maturity}}_{\text{k-out}} & \phi^{\text{maturity}} \times \psi^{\text{maturity}}_{\text{k-k}} & 1-\phi^{\text{maturity}} \\ \text{undetectable} & \frac{\xi}{\text{n states}-1} & \frac{\xi}{\text{n states}-1} & 1-\xi \end{pmatrix} \quad \text{(Eq. 9.3)}$$

Weakly informative prior was assigned to ψ: $logit(\psi^{\text{maturity}}) \sim \mathcal{N}(0, sqrt(1000))$. Analyses were performed by calling `MC Stan` with the `R` package `RStan` (Stan Development Team 2018). A total of 4,002 iterations were saved from three chains with a thin of 3, and after a warm-up of 1,000 iterations. Graphical examinations and the scale reduction factor — $\hat{r}$ — allowed us to assess chain convergence. The overlap percentages between the posterior distributions of ϕ^{mature} and ϕ^{immature} or between ψ estimates were computed with the `R` package `overlapping` (Pastore 2017) and defined our Bayesian P_{value}, 5% of overlap defining a significant effect.

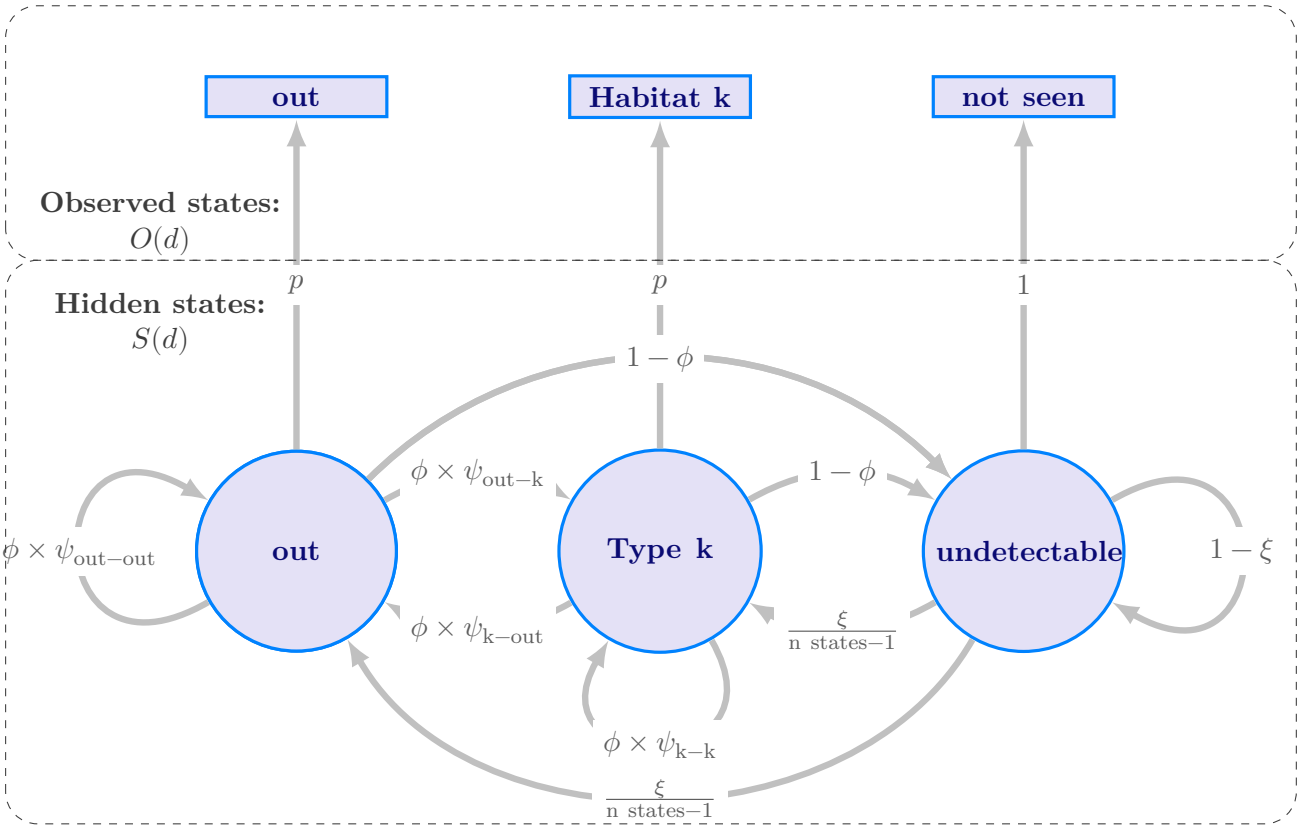


Figure. 9.3: Diagram of the daily observed ($O(d)$) and hidden states ($S(d)$) of our multistate Hidden Markov Model written to explain the habitat use of Atlantic salmon parr throughout a breeding season. The model takes into account a potential effect of the maturity state (immature vs mature) on the probabilities ϕ (remaining detectable probability) and ψ (movement probability). This effect was not display in this diagram to lighten writing. The state "Type k" represents six different types of morpho-dynamic habitat in the river where an individual is located: riffles, rapids, flat-flowing, flat, pool and mixed. The state "out" concerned individuals seen and being outside the study area.

9.3 RESULTS

The model estimated a high value for the recapture probability at $p = 0.9871$ $[0.9798; 0.9933]$ as well as for the probability to remain undetectable at $1 - \xi = 0.9453$ $[0.9081; 0.9717]$ (Table. 9.1). The probability to remain detectable did not differ between mature and immature parr ($\phi^{\text{immature}} = 0.9891$ and $\phi^{\text{mature}} = 0.9813$ —Bayesian $P_{value} = 0.38$ — Table. 9.1).

Table. 9.1: Table of three different probabilities of our multistate Hidden Markov Model written to explain the habitat use of Atlantic salmon parr throughout a breeding season. The model incorporated a potential effect of maturity (immature vs mature) on the probabilities ϕ (remaining detectable probability). For each probability, the Credible Interval at 95% accompanied the estimated average value.

Parameter		Mean [CI 95%]	Bayesian P_{value}
Name	Symbol		
Recapture probability	p	0.9871 $[0.9798; 0.9933]$	/
Probability to remain detectable	ϕ^{immature}	0.9891 $[0.9757; 0.9971]$	0.38
	ϕ^{mature}	0.9813 $[0.9724; 0.9888]$	
Probability to remain undetectable	$1 - \xi$	0.9453 $[0.9081; 0.9717]$	/

The following matrices display the average values of estimated movement probabilities for immature individuals $\psi^{\text{immature}}_{\text{k-k}}$ (Eq. 9.4), and mature individuals $\psi^{\text{mature}}_{\text{k-k}}$ (Eq. 9.5). The symbol "$*$" in both matrices indicates significant differences between immature and mature.

$$\psi^{\text{immature}}_{\text{k-k}} = \begin{pmatrix} & \text{mixed} & \text{riffles} & \text{rapids} & \text{flat} & \text{flowing flat} & \text{pool} & \text{out} \\ \text{mixed} & 0.16* & 0.16 & 0.17* & 0.17* & 0.17 & 0.18 & 0.02 \\ \text{riffles} & 0.00 & 0.81 & 0.00 & 0.06 & 0.12 & 0.00 & 0.00 \\ \text{rapids} & 0.17* & 0.18 & 0.16 & 0.17 & 0.14 & 0.17* & 0.02 \\ \text{flat} & 0.00 & 0.57 & 0.05 & 0.33 & 0.05 & 0.00 & 0.00 \\ \text{flowing flat} & 0.00 & 0.16 & 0.00 & 0.00 & 0.82* & 0.00* & 0.00 \\ \text{pool} & 0.00 & 0.98* & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\ \text{out} & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.98 \end{pmatrix} \quad \text{(Eq. 9.4)}$$

$$\psi^{\text{mature}}_{\text{k-k}} = \begin{pmatrix} & \text{mixed} & \text{riffles} & \text{rapids} & \text{flat} & \text{flowing flat} & \text{pool} & \text{out} \\ \text{mixed} & 0.00* & 0.50 & 0.00* & 0.00* & 0.16 & 0.33 & 0.00 \\ \text{riffles} & 0.00 & 0.74 & 0.00 & 0.11 & 0.11 & 0.03 & 0.00 \\ \text{rapids} & 0.00* & 0.21 & 0.45 & 0.04 & 0.31 & 0.00* & 0.00 \\ \text{flat} & 0.01 & 0.33 & 0.01 & 0.56 & 0.07 & 0.01 & 0.01 \\ \text{flowing flat} & 0.00 & 0.24 & 0.03 & 0.05 & 0.65* & 0.03* & 0.00 \\ \text{pool} & 0.05 & 0.28* & 0.00 & 0.19 & 0.19 & 0.27 & 0.00 \\ \text{out} & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 1 \end{pmatrix} \quad \text{(Eq. 9.5)}$$

Few differences appeared between the two maturity levels. However, the estimated probabilities shown that mature individuals stayed in rapids while immature moved to another habitat defined by a lower flow velocity ($\psi^{\text{immature}}_{\text{rapids-mixed or pool}} > \psi^{\text{mature}}_{\text{rapids-mixed or pool}}$). At the opposite, immature individuals stood in flowing flats while mature went to another habitat, preferentially riffles characterised by a higher flow velocity ($\psi^{\text{immature}}_{\text{flowing flat-flowing flat}} > \psi^{\text{mature}}_{\text{flowing flat-flowing flat}}$). Immature displayed a strong probability to move from pools to riffles, while mature moving from pools went to multiple habitat types. Apart these points, the resulting patterns of movement probabilities did not clearly differ between maturity levels (Eq. 9.4 and Eq. 9.5). The cumulative probabilities to move into each habitat type did not differ between maturity levels and varied in same ways (Figure. 9.4) with the higher value of cumulative probability was to move in riffles. Despite the visual similarity, the movement probabilities seem split into habitats (Figure. 9.4).

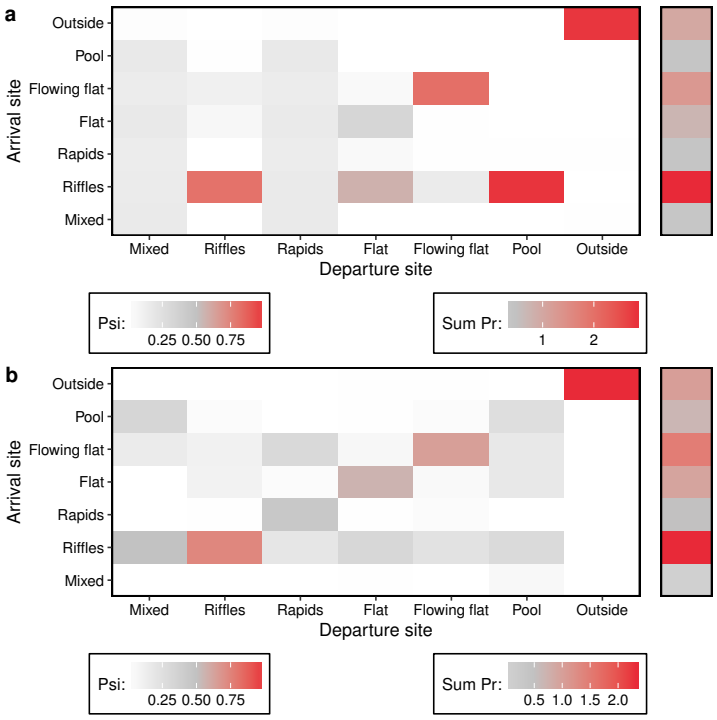


Figure. 9.4: Plot of the movement probability (ψ_{k-k}) of immature (a) and mature (b) Atlantic salmon parr between different types of habitat. Each daily position of each individual throughout the breeding season was translated into an habitat type where the fish was. The type "outside" corresponded to individuals located outside the study area while the type "mixed" denoted habitat with undifferentiated type. The column at the right of the graphical matrix indicated the cumulative probabilities to migrate into each habitat type.

9.4 DISCUSSION

The purpose of this chapter was to test whether maturity implied a different habitat use in salmon parr. In the previous chapter (chapter 8, page 257) an effect of maturity on space use was found, mature parr covering longer distances. Despite this difference in movements, no differences in probability to remain detectable emerged. The multistate HMM's results suggested that both maturity levels displayed broadly similar patterns of movements between habitat types. However, maturity levels exhibited some differences in movements between some habitat types.

The cumulative probability to move into each habitat type did not differ between mature and immature individuals. For both maturity levels, individuals move more to go to riffles characterised by high flow velocity and shallow depth. Breeding activity of Atlantic salmon occurs at riffles (Louhi *et al.* 2008) and mature parr move more

than immature (chapter 8). The research of anadromous females during the breeding season could explain the preference for riffles expressed by mature parr, while riffles also correspond to potentially suitable feeding habitats for immature parr (Boavida *et al.* 2017, Roy *et al.* 2013a). Mature parr seemed to move more among habitats only at the margin, no clear difference with immature parr was found.

Salmon parr exhibited variable habitat uses. In their studies, Boavida *et al.* (2017), Roy *et al.* (2013a) found similar habitat uses in terms of velocity and depth. However, individuals in these studies demonstrated variable habitat uses. For example, in the study of Boavida *et al.* (2017), mean water velocity experienced by individual varied from 0.05 $m.s^{-1}$ to 0.71 $m.s^{-1}$ and mean depth from to 0.30 m to 3.03 m. Then, even if salmon immature parr prefer habitats characterised by a shallow depth and high velocity, some individuals may display more variable habitat uses. The matrix of movement probabilities with no strong patterns and movements between all habitat types agrees with these variable habitat uses found in other systems. In addition, seasons, as well as floods, may involve such variations of habitats chosen by salmon parr (Boavida *et al.* 2017, Nislow *et al.* 1999). At the opposite, mature individuals stayed in habitats when the flow velocity in these habitats was high, while immature sometimes preferred to stay in deeper habitats with slower flow velocity in accordance to their drifting foraging abilities (Nislow *et al.* 1999).

Yet, some limitations should be pointed out. First, the positions of immature parr only originated from 10 immature individuals compared to the 30 mature individuals. The low number of immature individuals could have overestimated some movement probabilities for this maturity level. In addition, the stretch and habitat scale did not match with the radio-tracking precision scale which was more accurate. A study at the micro-habitat scale could be preferential even if this study provides some valuable information as a complement to the previous chapter (chapter 8).

The temporal dimension could also be a lack of this study. Salmon parr exhibit nycthemeral and seasonal rhythms leading to a foraging activity at night in winter (Fraser *et al.* 1995). Monitoring positions at the same hour at day was not a limitation because salmon parr are central place foragers and, therefore, occupy a small feeding territory (Steingrímsson & Grant 2008). The issue can be for mature parr because breeding

activity also occurs at night (Beall & De Gaudemar 1999). Absence of differences in movement probabilities may be due to this lack of temporal dimension. Redoing this study with one point at night may had valuable information concerning this issue. Yet, some fixed station to monitor fish near them were positioned at two locations, and individuals detected at day were also detected at night and *vice versa* (unreported data).

Maturity seems not to imply a strong different habitat use by Atlantic salmon parr. However, some differences caused by maturity have been pointed out such as immature individuals staying in flowing flats while mature preferentially went to riffles characterised by a higher flow velocity. Accounting for individual heterogeneity when investigating habitat use by salmon parr should involve working at the microhabitat scale. In addition, maturity levels materialised individual heterogeneity in this model. However, accounting for individual fork length or swimming abilities could be useful to better characterised individual heterogeneity in habitat uses by salmon parr and identify mechanistic causes of this heterogeneity.

HIGHLIGHTS OF CHAPTER 9

- Although mature and immature parr have different focal resources the feeding habitats and breeding habitats may overlap.
- Movement probabilities between habitat types were compared between maturity levels.
- Similar probabilities of movements between habitat types were found for the two maturity levels.
- Mature parr did not move more among habitat types than immature.
- Yet, mature parr tended to favour habitats with higher flow velocity, while immature tended to stay in flowing flats.

Discussion to Part IV

Sexual selection may differ between reproductive tactic especially through different levels of sperm competition. Mature parr tended to exhibit a higher mating assortment than anadromous which can be linked to their sneaky behaviour (chapter 7, page 241). Mature parr faced, thus, to a higher sperm competition but displayed a similar pre-copulatory competition to that of anadromous. Despite the differences in body length, these alternative reproductive tactics displayed similar ranges of juvenile dispersal (box Deeper IV.i). In salmon parr, maturity involves a modification of space use (chapter 8, page 257). Individual space use affected the probability to encounter redds, individuals having a broader home range increasing their probability. Finally, despite this change in space use, no clear differences emerged in terms of habitat use between maturity levels in salmon parr (chapter 9, page 283).

DENSITY OF ANADROMOUS AFFECTS HOW MATURE PARR MAY HACK MATING SYSTEM

A density-dependent participation of mature parr. Competition between males and mate acquisition trait are frequency dependent (Kokko & Rankin 2006). Here, mature parr participated more in reproduction in 2009 when anadromous-anadromous competition tended to be higher (chapter 7, page 241). Indeed, the Bateman gradient without accounting for parr tended to diminish between 2009 and 2010 ($\beta_{M \bullet SCI}$ level `Ana-Ana` in Table. 7.2, 251). In addition, dispersal distance of their juveniles was longer at low anadromous-anadromous competition (box Deeper IV.i, page 277). The effect of the anadromous density on the parr participation results from high costs of competition associated with a too high number of competitors (Weir *et al.* 2011, chapter 7). Mature parr's participation in reproduction is also density-dependent in regard of their own density (Hutchings & Myers 1988, Weir *et al.* 2005). Nevertheless, some studies

found opposite results Garant *et al.* (2003b), Hutchings & Myers (1988), Thomaz *et al.* (1997). The differences between studies should be the result of an interaction between the density-dependent effect of the parr density with the density-dependent effect of the anadromous salmon density.

Space use of mature parr seemed also dependent of the density of anadromous. Potentially covered distances and home ranges of mature parr seemed dependent of the density of anadromous. The distance range between the two furthest juveniles of a mature parr displayed a bi-modal distribution in 2009 and a unimodal one in 2010 (Figure. 8.9, 278). Some individuals displayed, thus, high mobility during the breeding season with the stronger competition between anadromous which resulted in harder accesses to females for mature parr (Box Deeper IV.i, page 277). Such density-dependent variations of space use are common in predator-prey interactions. For example, predators exhibit long relocation distances and small steps when exploiting sparsely distributed resources (Humphries *et al.* 2010, Sims David W. *et al.* 2011). Such density-dependent variations could be generalised with potential mates as resources.

MATURE PARR EXHIBIT VARIOUS RANGES OF DISPLACEMENTS

Mature parr exhibit wide sexual home ranges. The space use of mature parr suggested by the range between their two furthest juveniles (box Deeper IV.i) supported the results of chapter 8. Nevertheless, I found an average home range at one kilometre long during the field study, whereas the dispersal distance of juveniles was higher than seven kilometres for some individuals in 2009 and 2010. The observed difference could result from the spatial scale of the study, here fieldwork monitored displacements in a small part of the river, whereas the study of Tentelier *et al.* (2016b) was at the river scale. Another explanation could be the upstream dam constraining mature parr's upstream displacements during my field study while Tentelier *et al.* (2016b) also sampled more downstream redds in 2009-2010.

Roaming versus staying. The trade-off on covering long distances or not for mature parr should vary throughout the breeding season and may also depend on whether they have already spawned or not. Mature parr displayed various space use during the fieldwork (chapter 8) but also in 2009 and 2010 (Box Deeper IV.i, page 277). The size of their home range increased their probability to encounter redds (chapter 8) and their reproductive

success was positively linked to the distance between their two furthest juveniles, a proxy of their space use in 2009-2010 (Box Deeper IV.i). Mature parr should, thus, favour a roaming tactic to raise their reproductive success. Nevertheless, several Atlantic salmon females usually spawn at the same breeding site (Hendry *et al.* 2001), and a female may also spawn several times at the same site (de Gaudemar *et al.* 2000) giving numbers possibilities to mature parr to mate without having to move. The latter possibility and the costs associated of covering long distances (e.g. high predation risk, energetic demand) should favour a staying tactic. In the early breeding season, the benefit to move to find females should overpass the costs of moving, whereas stay at breeding sites should be beneficial at the end of the season, especially because sperm depletion occurs in mature parr (Hutchings & Myers 1988, Thomaz *et al.* 1997), staying behaviour of mature parr after their first mates. Such results have been already found concerning the temporal dynamic of the movements by anadromous males. For example, Rich *et al.* (2006) found that movements of anadromous male sockeye salmon (*Oncorhynchus nerka*) decreased as a function of time spent on the breeding grounds.

CONCLUSION

Mature parr may affect genetic structure within the population. The effects of mature parr participation on population genetic received a lot of attention in literature (Ardren & Kapuscinski 2003, Martinez *et al.* 2000, Saura *et al.* 2008). In their study on another salmonid, Rich *et al.* (2006) hypothesised from their results that homing to precise natal locations may generate genetic structures of populations at fine spatial scale. The absence of a distinct pattern in habitat use by mature parr from immature ones was paired with the absence of a gradient of maturation along the river (box Deeper IV.ii). Associated with the high mobility of mature parr throughout the breeding season, these absences suggested potential participation of mature parr in all parts of the Nivelle. The Nivelle River is a small and simple system compared to the one studied by Rich *et al.* (2006) which suggests a low population viscosity in the Nivelle. The pervasive participation of mature parr along the Nivelle may mitigate the gene flows triggered by anadromous coming from other populations. Such effects of mature parr were hypothesised by Jordan & Youngson (1992) and could be exacerbated in small populations like the Nivelle.

Mature parr may have a complex effect on demography. The wide space use of mature parr and their variable participation in reproduction raises the question about the importance of mature parr in kin selection in such small populations. Our findings suggest parr tend to better access females when anadromous males guarding females chase other anadromous males. Then, mature parr may diminish kinship levels within redd. Moreover, Atlantic salmon parr are able to recognise and discriminate kin from non-kin parr (Brown & Brown 1992, Moore *et al.* 1994). However, several studies found a fitness benefit aggregating with kin rather than non-kin for mature parr (Brown & Brown 1996, Ward & Hart 2003). This general effect is modulated by environmental conditions especially in winter (Griffiths *et al.* 2003), avoiding kin-related individuals becoming advantageous (Griffiths & Armstrong 2001). Hence, mature parr may modify kin relations between juveniles which complicates the understanding of their overall effects on demography. Indeed, this effect combines with the negative effects on their own survival (Buoro *et al.* 2010, Myers 1984), on the survival of juveniles (Garant *et al.* 2002), or on the number of returning anadromous for example.

A substantial number of questions remain to investigate. Indeed, the link between individual reproductive success and space use of mature parr could be investigated to highlight the best space use tactic in terms of fitness. However, many factors may be involved in such a question. Environmental conditions and individual states — condition, metabolism, swimming abilities — may influence the costs of different space use tactics. Is it better for an individual to diminish its covered distance and its reproductive success at parr stage in order to increase its probability to survive and to participate in reproduction as an anadromous increasing its lifetime reproductive success? The response of this question is probably frequency-dependent, depending on the density of anadromous, their sex-ratio, and the density of mature parr. A first work by applying a best-of-n-rule within simulations could permit to point out the first response elements.

BESIDE IV.i: Transposition of Lévy flight foraging hypothesis

Effects of maturity on space use, as well as on habitat use, were assessed in this part. However, daily movements between maturity levels were not compared. Immature Atlantic salmon parr still feed drifting invertebrates in the water column in winter (Fraser & Metcalfe 1997, Fraser *et al.* 1995),

a feeding resource which can be considered as a widely distributed. At the opposite, mature parr have to find anadromous females to breed, a mobile and scarcely distributed resource especially in small populations like in the Nivelle River (Bouchard *et al.* 2018, Tentelier *et al.* 2016a).

Some studies have assessed the link between the distribution of foraging resources and individual displacements. Thus, individuals opt for Brownian motions, defined by small and random steps, when feeding on abundant and predictable resources (Humphries *et al.* 2010, Sims David W. *et al.* 2011). At the opposite, Lévy flights characterised by many small steps connected by longer relocation distances, are favoured when resources are sparsely distributed (Humphries *et al.* 2010, Sims David W. *et al.* 2011).

A hypothesis could be that mature parr tend to exhibit such Lévy flights, while immature favour Brownian motions. Mature individuals and immature ones showed clear different patterns of distance from previous observation (figure below). Mature exhibited longer relocation distances which might characterise Lévy flight while immature clearly exhibited small steps in comparison. This analysis could be done in another work to test this hypothesis.

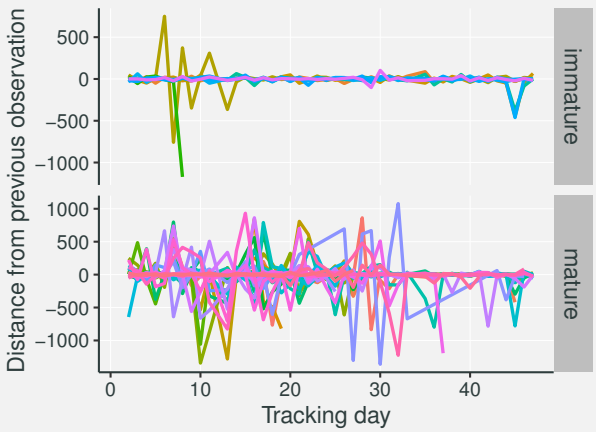


Figure. IV.iii: Plot of the individual distance covered from the last observation throughout the breeding season for immature and mature Atlantic salmon parr.

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Bibliography

Ardren, W.R. & Kapuscinski, A.R. (2003) Demographic and genetic estimates of effective population size (Ne) reveals genetic compensation in steelhead trout. *Molecular Ecology* **12**, 35–49.

Armstrong, J.D., Einum, S., Fleming, I.A. & Rycroft, P. (2001) A method for tracking the behaviour of mature and immature salmon parr around nests during spawning. *Journal of Fish Biology* **59**, 1023–1032.

Armstrong, J.D., Huntingford, F.A. & Herbert, N.A. (1999) Individual space use strategies of wild juvenile Atlantic salmon. *Journal of Fish Biology* **55**, 1201–1212.

Arnaud, C.M., Becker, P.H., Dobson, F.S. & Charmantier, A. (2013) Canalization of phenology in common terns: genetic and phenotypic variations in spring arrival date. *Behavioral Ecology* **24**, 683–690.

Aubin-Horth, N., Bourque, J.F., Daigle, G., Hedger, R. & Dodson, J.J. (2006) Longitudinal gradients in threshold sizes for alternative male life history tactics in a population of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2067–2075.

Bacles, C.F.E., Bouchard, C., Lange, F., Manicki, A., Tentelier, C. & Lepais, O. (2018) Estimating the effective number of breeders from single parr samples for conservation monitoring of wild populations of Atlantic salmon *Salmo salar*. *Journal of Fish Biology* **92**, 699–726.

Bagliniere, J. & Maisse, G. (1985) Precocious maturation and smoltification in wild Atlantic salmon in the Armorican massif, France. *Aquaculture* **45**, 249–263.

Baglinière, J.L., Maisse, G. & Nihouarn, A. (1991) Radio-tracking of male adult Atlantic salmon, *Salmo salar* L., during the last phase of spawning migration in a spawning stream (Brittany, France). *Aquatic Living Resources* **4**, 161–167.

Beall, E. (1994) Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. *ICES Journal of Marine Science* **51**, 1–9.

Beall, E. & De Gaudemar, B. (1999) Plasticité des comportements de reproduction chez le saumon atlantique (*Salmo salar*) en fonction des conditions environnementales. *Cybium* **23**, 9–28.

Berglund, I. (1995) Effects of size and spring growth on sexual maturation in 1+ Atlantic salmon (*Salmo salar*) male parr: interactions with smoltification. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2682–2694.

Boavida, I., Harby, A., Clarke, K.D. & Heggenes, J. (2017) Move or stay: habitat use and movements by Atlantic salmon parr (*Salmo salar*) during induced rapid flow variations. *Hydrobiologia* **785**, 261–275.

Bouchard, C., Bardonnet, A., Buoro, M. & Tentelier, C. (2018) Effects of spatial aggregation of nests on population recruitment: the case of a small population of Atlantic salmon. *Ecosphere* **9**.

Brokordt, K.B. & Guderley, H.E. (2004) Energetic requirements during gonad maturation and spawning in scallops: Sex differences in *Chlamys islandica* (Muller 1776). *Journal of Shellfish Research* **23**, 25–32, wOS:000221403900005.

Brown, G.E. & Brown, J.A. (1992) Do rainbow trout and Atlantic salmon discriminate kin? *Canadian Journal of Zoology* **70**, 1636–1640.

Brown, G.E. & Brown, J.A. (1996) Does kin-biased territorial behavior increase kin-biased foraging in juvenile salmonids? *Behavioral Ecology* **7**, 24–29.

Buoro, M., Prévost, E. & Gimenez, O. (2010) Investigating evolutionary trade-offs in wild populations of Atlantic salmon (*Salmo salar*): incorporating detection probabilities and individual heterogeneity. *Evolution* **64**, 2629–2642.

Cameron, M.F., Frost, K.J., Hoef, J.M.V., Breed, G.A., Whiting, A.V., Goodwin, J. & Boveng, P.L. (2018) Habitat selection and seasonal movements of young bearded seals (*Erignathus barbatus*) in the Bering Sea. *PLOS ONE* **13**, e0192743.

Cody, M.L. (1966) A general theory of clutch size. *Evolution* **20**, 174–184.

Crisp, D.T. (1995) Dispersal and growth rate of O-group salmon (*Salmo salar* L.) from point-stocking together with some information from scatter-stocking. *Ecology of Freshwater Fish* **4**, 1–8.

Cunningham, C., Parra, J.E., Coals, L., Beltrán, M., Zefania, S. & Székely, T. (2018) Social interactions predict genetic diversification: an experimental manipulation in shorebirds. *Behavioral Ecology* **29**, 609–618.

de Gaudemar, B., Schroder, S.L. & Beall, E.P. (2000) Nest placement and egg distribution in Atlantic salmon redds. *Environmental Biology of Fishes* **57**, 37–47.

Dingemanse, N.J., Both, C., Noordwijk, A.J.v., Rutten, A.L. & Drent, P.J. (2003) Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society of London B: Biological Sciences* **270**, 741–747.

Dinkins, J.B., Lawson, K.J., Smith, K.T., Beck, J.L., Kirol, C.P., Pratt, A.C., Conover, M.R. & Blomquist, F.C. (2017) Quantifying overlap and fitness consequences of migration strategy with seasonal habitat use and a conservation policy. *Ecosphere* **8**, e01991.

Dolinsek, I.J., Grant, J.W.A. & Biron, P.M. (2007) The effect of habitat heterogeneity on the population density of juvenile Atlantic salmon *Salmo salar* L. *Journal of Fish Biology* **70**, 206–214.

Einum, S. & Nislow, K.H. (2005) Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. *Oecologia* **143**, 203–210.

Einum, S., Sundt-Hansen, L. & H Nislow, K. (2006) The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos* **113**, 489–496.

Emlen, D.J. (1997) Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behavioral Ecology and Sociobiology* **41**, 335–341.

Finstad, A.G., Okland, F., Thorstad, E.B. & Heggberget, T.G. (2005) Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology* **67**, 919–930.

Fisher, D.O. & Lara, M.C. (1999) Effects of body size and home range on access to mates and paternity in male bridled nailtail wallabies. *Animal Behaviour* **58**, 121–130.

Fleming, I.A. (1996) Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries* **6**, 379–416.

Forchhammer, M.C. & Boomsma, J.J. (1998) Optimal mating strategies in nonterritorial ungulates: a general model tested on muskoxen. *Behavioral Ecology* **9**, 136–143.

Formica, V.A., Augat, M.E., Barnard, M.E., Butterfield, R.E., Wood, C.W. & Brodie, E.D. (2010) Using home range estimates to construct social networks for species with indirect behavioral interactions. *Behavioral Ecology and Sociobiology* **64**, 1199–1208.

Fraser, N.H.C. & Metcalfe, N.B. (1997) The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Functional Ecology* **11**, 385–391.

Fraser, N.H.C., Metcalfe, N.B., Heggenes, J. & Thorpe, J.E. (1995) Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. *Canadian Journal of Zoology* **73**, 446–451.

Fretwell, S.D. & Lucas, H.L.J. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16–36.

Garant, D., Dodson, J.J. & Bernatchez, L. (2001) A genetic evaluation of mating system and determinants of individual reproductive success in Atlantic salmon (*Salmo salar* L.). *Journal of Heredity* **92**, 137–145.

Garant, D., Dodson, J.J. & Bernatchez, L. (2005) Offspring genetic diversity increases fitness of female Atlantic salmon (*Salmo salar*). *Behavioral Ecology and Sociobiology* **57**, 240–244.

Garant, D., Dodson, J.J., Bernatchez, L. & Crespi, B. (2003a) Differential reproductive success and heritability of alternative reproductive tactics in wild atlantic salmon (*Salmo salar* l). *Evolution* **57**, 1133–1141.

Garant, D., Fleming, I.A., Einum, S. & Bernatchez, L. (2003b) Alternative male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. *Ecology Letters* **6**, 541–549.

Garant, D., Fontaine, P.M., Good, S.P., Dodson, J.J. & Bernatchez, L. (2002) The influence of male parental identity on growth and survival of offspring in Atlantic salmon (*Salmo salar*). *Evolutionary Ecology Research* **4**, 537–549.

Garcia de Leaniz, C., Fraser, N. & Huntingford, F.A. (2000) Variability in performance in wild Atlantic salmon, *Salmo salar* L., fry from a single redd. *Fisheries Management and Ecology* **7**, 489–502.

Garcia-Vazquez, E., Moran, P., Martinez, J.L., Perez, J., de Gaudemar, B. & Beall, E. (2001) Alternative Mating Strategies in Atlantic Salmon and Brown Trout. *Journal of Heredity* **92**, 146–149.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A. & Rubin, D.B. (eds.) (2014) *Bayesian data analysis*. Texts in Statistical Science Series, CRC Press/Chapman \& Hall, Boca Raton, Florida, USA., 3. ed edn.

Gelman, A., Jakulin, A., Pittau, M.G. & Su, Y.S. (2008) A weakly informative default prior distribution for logistic and other regression models. *The Annals of Applied Statistics* **2**, 1360–1383.

Gimenez, O., Cam, E. & Gaillard, J.M. (2018) Individual heterogeneity and capture–recapture models: what, why and how? *Oikos* **127**, 664–686.

Griffiths, S.W. & Armstrong, J.D. (2001) The benefits of genetic diversity outweigh those of kin association in a territorial animal. *Proceedings of the Royal Society of London B: Biological Sciences* **268**, 1293–1296.

Griffiths, S.W., Armstrong, J.D. & Metcalfe, N.B. (2003) The cost of aggregation: juvenile salmon avoid sharing winter refuges with siblings. *Behavioral Ecology* **14**, 602–606.

Grimardias, D., Merchermek, N., Manicki, A., Chebaux, J., Gaudin, P., Jarry, M. & Beall, E. (2010a) Effects of habitat on individual reproductive success of mature male parr of Atlantic salmon *Salmo salar*. *Journal of Fish Biology* **77**, 2460–2466.

Grimardias, D., Merchermek, N., Manicki, A., Garnier, J., Gaudin, P., Jarry, M. & Beall, E. (2010b) Reproductive success of Atlantic salmon (*Salmo salar*) mature male parr in a small river, the Nivelle: influence of shelters: Mature male parr success and shelters. *Ecology of Freshwater Fish* **19**, 510–519.

Gustafson-Greenwood, K.I. & Moring, J.R. (1990) Territory size and distribution of newly-emerged Atlantic salmon (*Salmo salar*). *Hydrobiologia* **206**, 125–131.

Hamel, S., Gaillard, J.M. & Yoccoz, N.G. (2018) Introduction to: Individual heterogeneity – the causes and consequences of a fundamental biological process. *Oikos* **127**, 643–647.

Hendry, A.P. & Beall, E. (2004) Energy use in spawning Atlantic salmon. *Ecology of Freshwater Fish* **13**, 185–196.

Hendry, A.P., Berg, O.K. & Quinn, T.P. (2001) Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores). *Oikos* **93**, 407–418.

Hiscock, M.J., Scruton, D.A., Brown, J.A. & Pennell, C.J. (2002) Diel activity pattern of juvenile Atlantic salmon (*Salmo salar*) in early and late winter. *Hydrobiologia* **483**, 161–165.

Hoyos-Padilla, E.M., Klimley, A.P., Galván-Magaña, F. & Antoniou, A. (2016) Contrasts in the movements and habitat use of juvenile and adult white sharks (*Carcharodon carcharias*) at Guadalupe Island, Mexico. *Animal Biotelemetry* **4**.

Humphries, N.E., Queiroz, N., Dyer, J.R.M., Pade, N.G., Musyl, M.K., Schaefer, K.M., Fuller, D.W., Brunnschweiler, J.M., Doyle, T.K., Houghton, J.D.R., Hays, G.C., Jones, C.S., Noble, L.R., Wearmouth, V.J., Southall, E.J. & Sims, D.W. (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature* **465**, 1066–1069.

Hutchings, J.A. & Myers, R.A. (1988) Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. *Oecologia* **75**, 169–174.

Järvi, T. (1990) The effects of male dominance, secondary sexual characteristics and female mate choice on the mating success of male Atlantic salmon *Salmo salar*. *Ethology* **84**, 123–132.

Jones, M.W. & Hutchings, J.A. (2001) The influence of male parr body size and mate competition on fertilization success and effective population size in Atlantic salmon. *Heredity* **86**, 675–684.

Jones, M.W. & Hutchings, J.A. (2002) Individual variation in Atlantic salmon fertilization success: implications for effective population size. *Ecological Applications* **12**, 184–193.

Jonsson, B. & Jonsson, N. (1993) Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* **3**, 348–365.

Jordan, W.C., Fleming, I.A. & Garant, D. (2007) Mating system and social structure. *The Atlantic salmon: genetics, conservation and management*, pp. 167–194, Blackwell Pub, Oxford.

Jordan, W.C. & Youngson, A.F. (1992) The use of genetic marking to assess the reproductive success of mature male Atlantic salmon parr (*Salmo salar*, L.) under natural spawning conditions. *Journal of Fish Biology* **41**, 613–618.

Juanes, F., Perez, J. & Garcia-Vazquez, E. (2007) Reproductive strategies in small populations: using Atlantic salmon as a case study. *Ecology of Freshwater Fish* **16**, 468–475.

Kamath, A. & Losos, J.B. (2018) Estimating encounter rates as the first step of sexual selection in the lizard *Anolis sagrei*. *Proc. R. Soc. B* **285**, 20172244.

Kazakov, R.V. (1981) Peculiarities of sperm production by anadromous and parr Atlantic salmon (*Salmo salar* L.) and fish cultural characteristics of such sperm. *Journal of Fish Biology* **18**, 1–8.

Kim, J.W., Grant, J.W. & Brown, G.E. (2011) Do juvenile Atlantic salmon (*Salmo salar*) use chemosensory cues to detect and avoid risky habitats in the wild? *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 655–662.

Kokko, H. & Rankin, D.J. (2006) Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 319–334.

Kristinsson, J., Saunders, R.L. & Wiggs, A. (1985) Growth dynamics during the development of bimodal length-frequency distribution in juvenile Atlantic salmon (*Salmo salar* L.). *Aquaculture* **45**, 1–20.

Lacroix, G.L., Knox, D. & McCurdy, P. (2004) Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. *Transactions of the American Fisheries Society* **133**, 211–220.

Lepais, O., Manicki, A., Glise, S., Buoro, M. & Bardonnet, A. (2017) Genetic architecture of threshold reaction norms for male alternative reproductive tactics in Atlantic salmon (*Salmo salar* L.). *Scientific Reports* **7**, 43552.

Letcher, B.H. & Terrick, T.D. (1998) Maturation of male age0 Atlantic salmon following a massive, localized flood. *Journal of Fish Biology* **53**, 1243–1252.

Long, R.A., Kie, J.G., Terry Bowyer, R. & Hurley, M.A. (2009) Resource selection and movements by female mule deer *Odocoileus hemionus* : effects of reproductive stage. *Wildlife Biology* **15**, 288–298.

Louhi, P., Mäki-Petäys, A. & Erkinaro, J. (2008) Spawning habitat of Atlantic salmon and brown trout: general criteria and intragravel factors. *River Research and Applications* **24**, 330–339.

Lucifora, L.O., García, V.B., Menni, R.C., Escalante, A.H. & Hozbor, N.M. (2009) Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. *Ecological Research* **24**, 109–118.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *The American Naturalist* **100**, 603–609.

Maldonado-Chaparro, A.A., Montiglio, P.O., Forstmeier, W., Kempenaers, B. & Farine, D.R. (2018) Linking the fine-scale social environment to mating decisions: a future direction for the study of extra-pair paternity. *Biological Reviews* .

Martinez, J.L., Moran, P., Perez, J., De Gaudemar, B., Beall, E. & Garcia-Vazquez, E. (2000) Multiple paternity increases effective size of southern Atlantic salmon populations. *Molecular Ecology* **9**, 293–298.

McDonald, G.C., James, R., Krause, J. & Pizzari, T. (2013) Sexual networks: measuring sexual selection in structured, polyandrous populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20120356–20120356.

McDonald, G.C. & Pizzari, T. (2016) Why patterns of assortative mating are key to study sexual selection and how to measure them. *Behavioral Ecology and Sociobiology* **70**, 209–220.

McDonald, G.C. & Pizzari, T. (2017) Structure of sexual networks determines the operation of sexual selection. *Proceedings of the National Academy of Sciences* p. 201710450.

Metcalfe, N.B., Fraser, N.H.C. & Burns, M.D. (1999) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology* **68**, 371–381.

Moorcroft, P.R. & Barnett, A. (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology* **89**, 1112–1119.

Moorcroft, P.R., Lewis, M.A. & Crabtree, R.L. (2006) Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences* **273**, 1651–1659.

Moore, A., Ives, M.J. & Kell, L.T. (1994) The role of urine in sibling recognition in Atlantic salmon *Salmo salar* (L.) parr. *Proc. R. Soc. Lond. B* **255**, 173–180.

Morris, D.W. (1987) Ecological scale and habitat use. *Ecology* **68**, 362–369.

Myers, R.A. (1984) Demographic consequences of precocious maturation of Atlantic Salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 1349–1353.

Myers, R.A. & Hutchings, J.A. (1987) Mating of anadromous Atlantic salmon, *Salmo salar* L., with mature male parr. *Journal of Fish Biology* **31**, 143–146.

Myers, R.A., Hutchings, J.A. & Gibson, R.J. (1986) Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 1242–1248.

Nislow, K.H., Folt, C.L. & Parrish, D.L. (1999) Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. *Ecological Applications* **9**, 1085–1099.

Pastore, M. (2017) *overlapping: Estimation of Overlapping in Empirical Distributions*. R package version 1.5.0.

Péron, C. & Grémillet, D. (2013) Tracking through life stages: adult, immature and juvenile Autumn migration in a long-lived seabird. *PLOS ONE* **8**, e72713.

Potts, J.R. & Lewis, M.A. (2014) How do animal territories form and change? Lessons from 20 years of mechanistic modelling. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20140231–20140231.

Prevost, E. & Chaput, G. (2001) *Stock, recruitment and reference points: assessment and management of Atlantic salmon*. INRA Editions, Paris, France.

Rich, H.B., Carlson, S.M., Chasco, B.E., Briggs, K.C. & Quinn, T.P. (2006) Movements of male sockeye salmon, *Oncorhynchus nerka*, on spawning grounds: effects of in-stream residency, density and body size. *Animal Behaviour* **71**, 971–981.

Rio-Maior, H., Beja, P., Nakamura, M. & Álvares, F. (2018) Use of space and homesite attendance by Iberian wolves during the breeding season. *Mammalian Biology* **92**, 1–10.

Robertson, M.J., Clarke, K.D., Scruton, D.A. & Brown, J.A. (2003) Interhabitat and instream movements of large Atlantic salmon parr in a Newfoundland watershed in winter. *Journal of Fish Biology* **63**, 1208–1218.

Roy, M.L., Roy, A.G., Grant, J.W. & Bergeron, N.E. (2013a) Individual variability of wild juvenile Atlantic salmon activity patterns: effect of flow stage, temperature, and habitat use. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 1082–1091.

Roy, M.L., Roy, A.G., Grant, J.W. & Bergeron, N.E. (2013b) Individual variability of wild juvenile Atlantic salmon activity patterns: effect of flow stage, temperature, and habitat use. *Canadian Journal of Fisheries and Aquatic Sciences* **70**, 1082–1091.

Sandell, M. & Liberg, O. (1992) Roamers and stayers: a model on male mating tactics and mating systems. *The American Naturalist* **139**, 177–189.

Saura, M., Caballero, A., Caballero, P. & Morán, P. (2008) Impact of precocious male parr on the effective size of a wild population of Atlantic salmon. *Freshwater Biology* **53**, 2375–2384.

Shuster, S.M. & Wade, M.J. (2003) *Mating systems and strategies*. Monographs in behavior and ecology, Princeton University Press, Princeton.

Silk, M.J., Finn, K.R., Porter, M.A. & Pinter-Wollman, N. (2018) Can multilayer networks advance animal behavior research? *Trends in Ecology & Evolution* **33**, 376–378.

Simpson, A.L. (1992) Differences in body size and lipid reserves between maturing and non-maturing Atlantic salmon parr, *Salmo salar* L. *Canadian Journal of Zoology* **70**, 1737–1742.

Simpson, A.L., Metcalfe, N.B., Huntingford, F.A. & Thorpe, J.E. (1996) Pronounced seasonal differences in appetite of Atlantic salmon parr, *Salmo salar*: effects of nutritional state and life-history strategy. *Functional Ecology* **10**, 760.

Sims David W., Humphries Nicolas E., Bradford Russell W. & Bruce Barry D. (2011) Lévy flight and Brownian search patterns of a freeranging predator reflect different prey field characteristics. *Journal of Animal Ecology* **81**, 432–442.

Smith, B.R. & Blumstein, D.T. (2008) Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* **19**, 448–455.

Stan Development Team (2018) RStan: the R interface to Stan. R package version 2.17.3.

Starking-Szymanski, M.D., Yoder-Nowak, T., Rybarczyk, G. & Dawson, H.A. (2018) Movement and habitat use of headstarted Blanding's turtles in Michigan. *Journal of Wildlife Management* **82**, 1516–1527, wOS:000442501700018.

Steingrímsson, S.Ó. & Grant, J.W. (2003) Patterns and correlates of movement and site fidelity in individually tagged young-of-the-year Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 193–202.

Steingrímsson, S.Ó. & Grant, J.W.A. (2008) Multiple central-place territories in wild young-of-the-year Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* **77**, 448–457.

Taborsky, M., Oliveira, R.F. & Brockmann, H.J. (2008) The evolution of alternative reproductive tactics: concepts and questions. *Alternative Reproductive Tactics* (eds. R.F. Oliveira, M. Taborsky & H.J. Brockmann), pp. 1–22, Cambridge University Press, Cambridge.

Tentelier, C., Larranaga, N., Lepais, O., Manicki, A., Rives, J. & Lange, F. (2016a) Space use and its effects on reproductive success of anadromous Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 1461–1471.

Tentelier, C., Lepais, O., Larranaga, N., Manicki, A., Lange, F. & Rives, J. (2016b) Sexual selection leads to a tenfold difference in reproductive success of alternative reproductive tactics in male Atlantic salmon. *The Science of Nature* **103**.

Thomaz, D., Beall, E. & Burke, T. (1997) Alternative reproductive tactics in atlantic salmon: factors affecting mature parr success. *Proceedings of the Royal Society of London B: Biological Sciences* **264**, 219–226.

Thorpe, J.E., Morgan, R.I.G., Pretswell, D. & Higgins, P.J. (1988) Movement rhythms in juvenile Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* **33**, 931–940.

Veilleux, J.P., Whitaker, J.O. & Veilleux, S.L. (2004) Reproductive stage influences roost use by tree roosting female eastern pipistrelles, *Pipistrellus subflavus*. *Écoscience* **11**, 249–256.

Viejou, R., Avgar, T., Brown, G.S., Patterson, B.R., Reid, D.E.B., Rodgers, A.R., Shuter, J., Thompson, I.D. & Fryxell, J.M. (2018) Woodland caribou habitat selection patterns in relation to predation risk and forage abundance depend on reproductive state. *Ecology and Evolution* **8**, 5863–5872, wOS:000435776600056.

Ward, A.J.W. & Hart, P.J.B. (2003) The effects of kin and familiarity on interactions between fish. *Fish and Fisheries* **4**, 348–358.

Webb, J., Fryer, R., Taggart, J., Thompson, C. & Youngson, A. (2001) Dispersion of Atlantic salmon (*Salmo salar*) fry from competing families as revealed by DNA profiling. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 2386–2395.

Webb, P.W., Kostecki, P.T. & Stevens, E.D. (1973) The effect of size and swimming speed on locomotor kinematics of rainbow trout. *Journal of Experimental Biology* **109**, 20.

Weihs, D. (1973) The mechanism of rapid starting of slender fish1. *Biorheology* **10**, 343–350.

Weir, L.K., Grant, J.W.A. & Hutchings, J.A. (2011) The influence of operational sex ratio on the intensity of competition for mates. *The American Naturalist* **177**, 167–176.

Weir, L.K., Hutchings, J.A., Fleming, I.A. & Einum, S. (2005) Spawning behaviour and success of mature male Atlantic salmon (*Salmo salar*) parr of farmed and wild origin. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1153–1160.

Wolf, J.B., Brodie III, E.D. & Moore, A.J. (1999) Interacting phenotypes and the evolutionary process. II. selection resulting from social interactions. *The American Naturalist* **153**, 254–266.

Yano, A., Nicol, B., Jouanno, E., Quillet, E., Fostier, A., Guyomard, R. & Guiguen, Y. (2013) The sexually dimorphic on the Y-chromosome gene (sdY) is a conserved male-specific Y-chromosome sequence in many salmonids. *Evolutionary Applications* **6**, 486–496.

PART V

General discussion

The present thesis aimed to assess the impacts of space use of potential breeders on sexual selection through their participation in reproduction and on population dynamics. How individuals are distributed within available breeding habitats, how individuals move among habitats, how spatiotemporal distribution of individuals affects their encounters, mating system and participation of mature parr, were various underpinning questions. Dealing with the general aim and underlying questions required combining multiple approaches and working at different levels, sometimes combined: from individuals to the population, including river zones and breeding habitats.

I will first discuss the methodology used in the thesis (page 317). I will also discuss the originality and limits of approaches applied. Secondly, I will discuss the findings of the thesis in relation to the different questions raised for this work (page 323). Finally, I will highlight potential implications and perspectives generated by the thesis (page 329) before to conclude (page 333).

Discussion of the methodology used

Contents

A∫ ORIGINALITY OF APPROACHES USED IN THE THESIS

Combining multiple scales. One originality of my thesis was combining different spatio-temporal extents and different grains. Spatial extents of the thesis, namely the overall area encompassed (Wiens 1989), navigated from a 10 m scale (chapter 8) to the whole river (chapter 2), by way of river zones (chapter 3), habitat types (chapter 9) or individual home range (chapters 5 and 6). Temporal extent varied from the day (chapter 8) to a yearly time series (chapters 2 and 3) by way of the breeding season (chapters 5 and 8). Grain defined in the thesis, namely the size of the individual unit (Wiens 1989), also

varied, being either individual (e.g. chapter 5), individuals exhibiting a same alternative reproductive tactic (e.g. chapters 7 or 8), a subpopulation of a river zone (chapter 3), a network of potential breeders (chapter 5), or the whole Nivelle population (chapter 2). Combining different spatial and temporal extents together and with different grains enabled to better understand some processes. Concerning spatial scale, it has clearly been defined as a characteristic of ecological studies since the work of MacArthur & Wilson (1963). Some authors have pointed out the necessary shift between scales to understand unpredictable phenomena (Levin 1992) and the importance of spatial scaling in ecology (Fahrig 2013, Wiens 1989). Lack of consideration of scale differences among studies may lead to erroneous conclusions (Wiens 1989). Same can be said about temporal dimension, temporal scales may differently affect populations (Desharnais *et al.* 2018). Using various scales, in time and space, enabled complementary approaches and findings.

Combining multiple methods as complementary approaches. The choice was made to use different methods and, sometimes, to combine them in order to improve how to respond to the thesis aims. For instance, incorporation of environmental co-variables (here spatial aggregation) in stock-recruitment models is rarely done (Fargo 1994, Iles 1994), whereas it can improve model efficiency (chapter 2— page 65, Fargo 1994, Iles 1994). Probably the most original approach was used in chapter 5 (page 161) when I combined spatial data with parentage ones into a hierarchical Bayesian model in order to infer the sexual network of the population (Eq. 5.1, page 171). The difficulty to obtain true encounters *in natura* motivated this approach to infer the sexual network. The developed model permitted estimating probabilities and, thus, obtaining estimates for all individuals. Using different approaches may, however, also generate difficulties both in linking them and in incorporating them within a general framework. For instance, the model Eq. 5.1 has necessitated considering different data types for all individuals and between two different seasons. Standardising data and defining a hierarchical probabilistic model allowed to deal with such difficulties. Such analyses necessitated taking care when associating different data types to not generate more variability and to have reliable data between individuals and among seasons.

Theory modelling, or experimenting in natura, or both? The latter sentence may correspond to feelings of some scientists. However [1], all models no matter how good they are,

[1] this paragraph is a personal point of view which has been strengthened by doing this thesis

need data either to estimate parameters or to compare models to reality. Confronting model results (e.g. observed phenomena, data, . . .) to reality is necessary even for theoretical models, forecasting models, or explanatory models. At the opposite, statistics are mandatory to explain data except in descriptive studies (which are sadly increasingly rare). The global philosophy of my thesis was to combine descriptive data (e.g. chapter 8), statistical models (most of the chapters), and theoretical simulations when necessary (e.g chapter 1). The difficulty of doing some experiments, especially monitoring in natural populations, may lead scientists to shift to theoretical modelling. Shifting to purely theoretical work may be motivated by the avoidance of ethical or administrative constraints, or field stress, to obtain broader results, or to reduce costs, for instance. Encountering difficulties when doing *in natura* monitoring only add value to these data[2] but also reflect that theoretical models remain simplification. However, simplifications are sometimes required either through theoretical modelling or experiments in laboratories to better understand or isolate phenomena or processes. Combining theoretical models, explanatory models, experiments in laboratories and experiments *in natura* is probably a good way to do science[3], or at least, the way I would like to do science.

B∫ LIMITS OF APPROACHES USED

The temporal dimension was a limit. An important limit of my work was the temporal dimension of chapters 8 and 9. Chapter 8 assessed how maturity affects space use and chapter 9 how maturity affects movement probabilities between habitat types. Both chapters used daily positions with one point per individual per day. Breeding activity mostly occurs at night in salmon (Beall & De Gaudemar 1999) and foraging activity of salmon parr usually also occurs at night (Fraser & Metcalfe 1997, Fraser *et al.* 1995). Discriminating these two activities by using accelerometers (Broell *et al.* 2013, Kawabata *et al.* 2014, Moreau *et al.* 2009) in order to associate each activity to a specific space use under a nycthemeral extent could be a relevant improvement of the work done in chapters 8 and 9. Increasing field presence or establish continuous monitoring over the entire study area could overcome this limit.

Parentage analyses may fail to identify all parents. Chapters 5, 6, and 7 use parentage analyses to infer sperm competition intensity. Sperm competitors were, thus, defined as males that sired juveniles with common mates. Identification of sperm competitors

[2]and sometimes may involve a few or numerous pints of Guinness®, or a thesis on salmon
[3]personal point of view

may have been skewed by the fact that these juveniles were caught during the following spring. A father who sired few juveniles may had not been detected due to mortality of juveniles and catching probability. Thus, all individuals participating in fertilisation of the same batch of eggs were not necessarily detected. Addressing which individuals participate in reproduction at each redd (salmon nest) is a difficult task *in natura*. For example, Mjølnerød *et al.* (1998) used videos and genetic parentage analyses to identify Atlantic salmon in mating at each redd and assess sperm competition in an experimental stream. However, acquiring such data (videos) in rivers remains difficult. One solution could be to combine genetic parentage analysis on eggs sampled just after the spawning season (and not on juveniles) with encounters between individuals. Genetic analyses on eggs could allow having more reliable data on sperm competition compared to those used in the thesis. Encounters could be assessed with proximity loggers (Tentelier *et al.* 2016a) providing more reliable data on encounters. Acquiring such data for the entire sub-population in the Upper Nivelle could enable estimating sperm competition at a finer grain. Such data could also enable disentangling effects of female choices, agonistic competition between males, and fertilisation success on reproductive success of individuals. For instance, Gage *et al.* (2004) found that selection should favour faster sperm and Mjølnerød *et al.* (1998) found that sperm precedence or spawning history may affect fertilisation success and, therefore, reproductive success when sneakers males or sperm competitors are present.

Parentage analyses and encounters at redds: how define reproduction? Genetic analyses provide identification of genetic mates who fertilise eggs, whereas encounters may permit identifying behavioural mates who emit gametes. The definition level of reproduction, between genetic one and behavioural one, to which scientists position the cursor is necessarily dependent on methods employed. In my thesis, reproduction was addressed in multiple ways like recruitment, encounters, sexual selection, and effective breeders. The analysis linking the number of effective breeders to the spatial aggregation of eggs used parentage analysis (chapter 4, page 153). Reproduction was, then, defined as genetic matings. The analysis inferring the sexual network (Eq. 5.1, 171) used genetic matings through mating probability but also potential behavioural matings through encounter probability. The resulting mating probability of the model Eq. 5.1, thus, accounting for the two types of mating (behavioural and genetic) to define reproduction. Combining different data may lead to a contrasting definition of reproduction,

whereas using only one type of data allows having a simple definition of reproduction and of mating. As the model Eq. 5.1, the improvement suggested in the previous paragraph, namely combining genetic analyses and data of proximity loggers, may allow to better identify genetic competitors while accounting for behavioural competitors.

From individual distributions to population dynamics, mating system & sexual selection

Contents

C∫ FEMALES' SPACE USE

Habitat choices of females as a characteristic of their space use. Chapter 2 suggested that females distribute among available habitats according to an Ideal Despotic Distribution (IDD, Fretwell & Lucas 1969). Such IDD has been found in Chinook salmon (Falcy 2015) and seems logical since individuals are phenotypically different and choices of breeding sites are adaptive in salmon (Hendry *et al.* 2001). For instance, body length of females may affect their choices of breeding sites in salmon (Hendry *et al.* 2001) which may, therefore, impact the survival of their juveniles (Gauthey *et al.* 2017a, Steen & Quinn 1999). The arrival time of individuals also affected their choices of breeding habitats (chapter 6) additionally to their phenotype. Competition in females for best-breeding sites happens in other salmonids and occurs in the establishment at breeding sites and during redd digging due to redd superimposition (Dodson *et al.* 2013, Fleming & Gross 1994, Quinn & McPhee 1998). Competition between females may force individuals to go into another breeding site, at least one pool away, modifying the distribution of females on a broader scale. Hence, habitat choices of females determine their spatial distribution and can be influenced by intra-sexual competition.

Specifically, space use of salmon females generated their spatial aggregation. Breeding habitat choice commonly generates such spatial aggregation (Almada *et al.* 1994, Doligez *et al.* 2003, Pomeroy *et al.* 1994). Here, Part II clearly demonstrated that spatial aggregation of females varied among years and independently to the number of individuals. Although spatial aggregation of females was assessed through aggregation of their redds (chapter 2), aggregation of females agreed with weak values of spatial isolations found in chapter 6 from their daily locations. Using spatial distribution of salmon redds appeared, thus, a simple method to assess the spatial aggregation of females, especially because salmon females move less than males (Tentelier *et al.* 2016b).

Other factors than competition and space use impacted aggregation of females. Aggregation of females may also be selected to diminish sexual harassment as advocated for seals (Cassini 2000). Diminishing kinship in further juveniles may also be an explanation of aggregation of females in breeding sites. Aggregation of females could diminish kinship by having a pool of juveniles with different mothers but also because a strong aggregation may favour multiple paternity in a batch of eggs. Chapter 6 highlighted that isolated females tended to have or had a lower number of mates depending on the

number of females. The negative effect of spatial isolation of females on their number of mates may increase kinship in their juveniles. Yet, kinship in salmon juveniles generate either benefits (Brown & Brown 1996) or costs (Griffiths *et al.* 2003). Habitat availability, the timing of arrival, competitive abilities, expected sexual harassment and offspring kinship are factors potentially interacting when females settle at breeding habitats.

D∫ SPATIAL AGGREGATION CAUSED BY FEMALES' SPACE USE MODIFIES POPULATION DYNAMICS AND DIVERSITY

Distribution of females stabilised population dynamics through their aggregation. In their study, Foldvik *et al.* (2010) suggested that females' habitat choice generated spatial heterogeneity in juvenile densities. The theoretical study of Nonaka *et al.* (2013) highlighted that spatial aggregation may stabilise population dynamics and reduce growth rates. My thesis agrees with the findings of Foldvik *et al.* (2010) and of Nonaka *et al.* (2013) because spatial aggregation, stock (number of eggs deposited by females) and recruitment (number of juveniles) varied between zones in the Nivelle population (chapter 3) agreeing also with previous results (Brun 2011). Spatial distribution of females and, especially their spatial aggregation, impacted the recruitment through its variability (chapters 2 and 3). The similar effects of aggregation on recruitment variability at the river zone scale and the population scale suggested that environmental perturbations occur at river scale and impact all river zones. The Upper Nivelle (Figure. I.viii, page 26) seems to be the best suitable zone in the Nivelle (chapters 2 and 3, Brun 2011, Dumas & Haury 1995), its recruitment also being potentially enhanced by the Lurgorrieta (chapter 3). Hence, spatial aggregation of females affected the population dynamics depending on the resulting juvenile densities, environmental quality of breeding sites and connectivity with other breeding sites. Spatial aggregation of females also means the resource of males is aggregated.

Aggregation of females modified the mating system. The spatial aggregation of females either facilitated their monopolisation by guarder males or facilitated participation of satellite males (chapters 4, 5, and 7). For instance, Pérez-González & Carranza (2011) highlighted that ability of a male to monopolise females in its harem decreased as harem size raised in Red Deer. Spatial aggregation of females necessarily impacts the local operational sex ratio influencing the costs of competition between males and, therefore, ability of other males to participate in reproduction (Emlen & Oring 1977, Sandell &

Liberg 1992, Shuster & Wade 2003, Weir *et al.* 2011). Variations in female aggregation modify the number of potential breeders that can access potential mates. Then, aggregation of females affected the number of effective breeders in the population through a U-shaped curve (chapter 4). Among potential breeders, individuals exhibiting an alternative reproductive tactic (sneaker males) also tended to access potential mates according to the aggregation of females (Parts III and IV). Females seemed also affected by their aggregation because their number of mates diminished as their spatial isolation to other females increased (chapter 6). Concerning mature parr, their ability to participate in reproduction also depended on their mobility. Such a relationship between mobility and participation in reproduction was in line with the results obtained for anadromous breeders in salmon (Tentelier *et al.* 2016b) or theoretical predictions (Sandell & Liberg 1992). Space use of females and males whatever their reproductive tactics seemed to interplay together and, probably with environmental factors.

E∫ A LOCAL STRUCTURE IMPACTING SEXUAL SELECTION

Space use of potential breeders brought out a social selection. Tanner & Jackson (2012) highlighted an emerging social structure from individual behaviour and synchronised movements between individuals in the European shore crab (*Carcinus maenas*). In my thesis, the modification of the mating system happened due to the appearance of a local social structure involved by the spatial distribution of breeders (chapters 5 and 6). Encounters between potential mates depended on their displacements (chapters 5, 6, and 8). In chapter 8, space use of mature parr influenced their participation in reproduction. Their participation was assessed from redds' location that indicated by the same potential encounters with females. The local social structure involved potential competitors leading to antagonistic direct or indirect interaction. The result was that the phenotype of neighbours affected the reproductive success of individuals (chapter 5). The social environment of individuals in Atlantic salmon may, thereby, affect reproductive success of individuals.

A local structure as a determinant of sexual selection. Effects of local structure on sexual selection is something well known in birds (McDonald *et al.* 2013, McDonald & Pizzari 2016; 2017, Oh & Badyaev 2010). In my thesis, social environment, and therefore local structure, affected the reproductive success of individuals through the relative attractiveness of individuals (Callander *et al.* 2013, Gasparini *et al.* 2013), but

also through the relative ability to fertilise egg batches (Burness *et al.* 2004, Gage *et al.* 2004). Trait selection operated by sexual selection may, thus, be affected by the local structure as theoretically suggested by McDonald *et al.* (2013). Local structure is necessarily linked to the spatial aggregation of females because local structure depended on the distribution of potential breeders. Participation of sneakers increased the sperm competition intensity faced by guarder males (chapters 5 and 7). The Bateman gradient indicating the mating benefit on the reproductive success also depended on the reproductive success and the participation of sneaker males (chapter 7) and aggregation of females (chapter 5). Hence, local structure affected sexual selection by modifying sexual network of the salmon population.

An alternative tactic modified sexual selection. Participation of mature parr modified sexual selection operating on anadromous salmon (chapter 7). Such effects of sneakers on sexual selection were observed in marine fish such as the sand goby, *Pomatoschistus minutus*, where the presence of sneaky males favours sexual selection of males building small nest-openings. Participation of mature parr also increased the number of effective breeders in the population (chapter 4, Bacles *et al.* 2018, Saura *et al.* 2008) which may raise the genetic diversity in the population (Juanes *et al.* 2007). The effects of mature parr on sexual selection may raise the question of the definition of this tactic as an alternative. The effects of mature parr on the topology of the sexual network, and the sexual selection operating in it is far from anecdotal. Additionally, the early maturation is not homogeneous because mature parr exhibited a broad diversity of space use behaviours (chapter 8 and box Deeper IV.i, page 277). Rather than putting all mature parr in the same bucket, investigating diversity among them and accounting for the effects of such diversity on the population could be further handled. For instance, diversity in their participation in reproduction can be affected by their relatively small size and by habitat complexity (Grimardias *et al.* 2010).

Implications & perspectives

Contents

F∫ CONSTRAINS OF DAMS & HABITAT CHOICES

Dams are obstacles for migration and displacements of potential breeders. Dams constitute obstacles to migration for salmon and other migratory species even if fish passes or ladders are arranged (Antonio *et al.* 2007, Gowans *et al.* 2003, Kareiva *et al.* 2000, Levin & Tolimieri 2001, Meixler *et al.* 2009). Usually, salmon migration or fish passage is associated with large dams (Gowans *et al.* 2003, Levin & Tolimieri 2001). However, small weirs (<5m) equipped with fish passes, such as Uxondoa and Olha dams in the Nivelle, may delay the arrival of breeders (Gowans *et al.* 2003, Newton *et al.* 2017). Arrival date was linked to spatial isolation of females (chapter 6) and to the reproductive

success of males (chapter 5). Delays in arrival due to small weirs may, therefore, affect reproduction and reproductive success of individuals. Such small weirs may also constrain displacements of mature parr whereas they may highly participate in reproduction and have high importance in small populations (Juanes *et al.* 2007, Saura *et al.* 2008, Tentelier *et al.* 2016c). Although it seems not to be the case in the Nivelle, small weirs may prevent accesses of mature parr to some locations where reproduction takes places in some rivers. Small weirs may, thus, generate local structure in sexual networks.

Constraints of dams may also exacerbate female-female competition. Weirs affected reproduction by diminishing availability of breeding sites (II) and displacements of breeders (part IV). The observed weak spatial isolation of females (chapter 6), as well as the low carrying capacities found in chapters 2 and 3 suggested that dam removals could also release competition between females when securing breeding sites, and, therefore, aggregation of females. For instance, in the Selune River (France), a dam removal could allow the return of more than 1,000 anadromous breeders and could decrease redd aggregation in the Oir River, a tributary of the Selune, downstream from the dam.(Forget *et al.* 2018). Chapters 2 and 6 suggested that early arriving females or most competitive ones may secure best breeding sites according to an Ideal Despotic Distribution (Andren 1990, Fretwell & Lucas 1969, Kokko *et al.* 2004, Parker & Sutherland 1986). Dams may, thus, exacerbate competition among females due to the reduced availability of breeding sites and of effects of weirs on arrival time of females at breeding sites. Removal of the upstream dam in the Nivelle could be an adequate management action to raise the surface of breeding habitats available for salmon. However, aggregation of females seemed not to have been affected by the opening of Olha in 1992. After the Olha opening, the number of anadromous salmon also increased and nests distributed in the Upper Nivelle and the Lurgorrieta. To release competition among females, an important part of females should continue to spawn in already available sites. Aggregation and competition among females should remain similar if all females distribute in newly available sites after a dam removal depending on the number of newly available breeding sites.

Habitat restoration is a temporary solution before dam removal. The high aggregation in the Upper Nivelle despite the high surface of available breeding habitats could suggest a poor quality of numerous potential breeding sites (chapter 3). Availability and quality of spawning sites may restrict the density of juveniles (Palm *et al.* 2007) or availability

of favourable foraging habitats for juveniles (Nislow *et al.* 1999). Habitat restoration of breeding habitats and foraging ones could be prioritised as suggested by Fahrig (1997). Battin *et al.* (2007) also shown a benefit in the restoration of habitats used by juveniles and especially to mitigate the effects of climate change. Restoring breeding habitats in the Upper Nivelle and the Lurgorrieta could allow females to select better breeding habitats less subjected to environmental perturbations. Such restoration could also diminish aggregation of nests within each river zone leading to increasing recruitment (chapter 3). Finally, restoration of breeding habitats could release sexual competition between males by diminishing aggregation of females and, thus, monopolisation according to the U-shape relationships found in chapter 4.

G∫ SPACE USE CAUSES MISINTERPRETATION OF SEXUAL SELECTION

Local social structure is a source of raising choosiness. My thesis permitted highlighting that local social structure impacts sexual competition and sexual selection and could be better accounted. Local structure in encounters between potential mates appeared from the spatial use of individuals (chapters 5, 6, and 8). These findings raised the question about how to model the choosiness of individuals in Atlantic salmon. Courtiol *et al.* (2016) found that mutual mate choice only evolves when both females and males exhibit long latency between matings. Anadromous males should not exhibit weak choosiness due to their potentially short latency between matings. The faster life history of mature parr, which may participate in fertilisation of several egg batches, should favour a non-choosiness to capitalise on early mating opportunities. At the opposite, females should exhibit stronger choosiness due to their high parental investment during spawning (i.e. redd digging). High costs of breeding were also pointed out as factors promoting choosiness by Kokko & Johnstone (2002). Authors also suggested that low costs of mate searching and highly variable mate quality can also favour choosiness. The local social structure may, thus, influence choosiness as advocated by Kokko & Rankin (2006) who highlighted density-dependent effects in mating systems. For instance, a female encountering just a few males should be more or less choosy depending on the phenotypic variability between males.

Preferences and choices of females. Additionally to choosiness, preferences exhibited by females should be affected by local social structures. Phenotypic preferences may be modelled through a threshold value from which a male is chosen (Fukui 1995), a

probability according to a male's trait (absolute preference), or a probability according to a male's trait compared to other males encountered (relative preference, Wagner 1998). The difference between the last two possibilities is the accounting for which males are encountered by females in the relative preference. Testing relative preferences remain difficult because preferences may be confounded with female sampling behaviours (Wagner 1998). Because the current thesis highlighted a local social structure (chapter 5), deeply working on females' choosiness in salmon could be interesting. The potential effect of local social structure on females' preferences and choosiness could be assessed. For instance, Gauthey *et al.* (2017b) use parentage analyses and behavioural monitoring with video to infer the effects of phenotypes of both sexes on encounters and matings in Brown trout (*Salmo trutta*). Authors found the body size of females negatively affected their probability of being visited by males, while the body size of males affected neither visit or reproductive success. To go further, encounters between individuals could be monitored with proximity loggers (Tentelier *et al.* 2016a) and mating events with accelerometers detecting "jerking" movements of their body (Broell *et al.* 2013) when gametes are released. Such data could permit to identify the local structure and true mating events. In this way, chosen phenotypes could be compared to encountered ones, the diversity of local structures between females enabling us to identify the effects of density and diversity of males on choosiness. Such work could also permit disentangling females' choosiness to males-males competition to access females.

Conclusion

Habitat availability and quality interplay in shaping the spatial distribution of females. The present thesis highlighted the spatial distribution of potential breeders i) impacted population dynamics by stabilising population recruitment and ii) exacerbated sexual selection by impacting mating system (Figure. V.i). The latter effect reflected that guarder males had difficulties to monopolise several females at a strong aggregation of females, whereas satellite males — anadromous and mature parr — could fertilise egg batches by adopting a sneaky behaviour. The space use of potential breeders either anadromous or mature parr shaped the mating system and the sexual network of the population. In males, consequences at the individual level were notably that competitors' phenotypes influenced reproductive success depending on the aggregation of females. The local structure and the social environment should be accounted for when investigating sexual selection in salmon, especially in wider river systems where sub-structure could be more pronounced. Mature parr should be accounted for in local structure and social environment.

Results of the thesis also suggested that dams and habitat availability were factors impacting the population. Dams and small weirs constrained displacements of anadromous individuals and mature parr during the breeding season. Such constraints may intensified competition for breeding sites — redds aggregated in the Upper Nivelle and the Lurgorrieta —. Small weirs may also exacerbate or produce local structure by aggregating mature parr participation in reproduction at some locations and preventing their participation in other locations. Habitat availability was also highlighted as a factor that can generate aggregation of females increasing the subsequent sexual selection. Aggregation of females also impacted the number of effective breeders. Increasing the number of breeding sites to diminish the spatial aggregation of females could enhance

the genetic diversity in such a small population. Improving habitats to raise the number of breeding sites available and dam removal could be targeted management actions for the Nivelle population.

The local social structure highlighted in the thesis implied that preferences and choosiness of salmon females could be further research questions. Preferences and choosiness of females express for two key processes: habitat choice and mate choice. Mechanisms involved in these choices could be examined. The consequences of environmental perturbations, female density and encountered habitats on habitat choice could be studied rather than to identify the size of pebbles where females dig their nests. The resultant impacts of habitat choices on the spatial distribution of females could then be highlighted. In the case of mate choices, the way of the expression of females' preferences could be assessed. Such preferences could influence their mate choice depending on which males they have in their social environment.

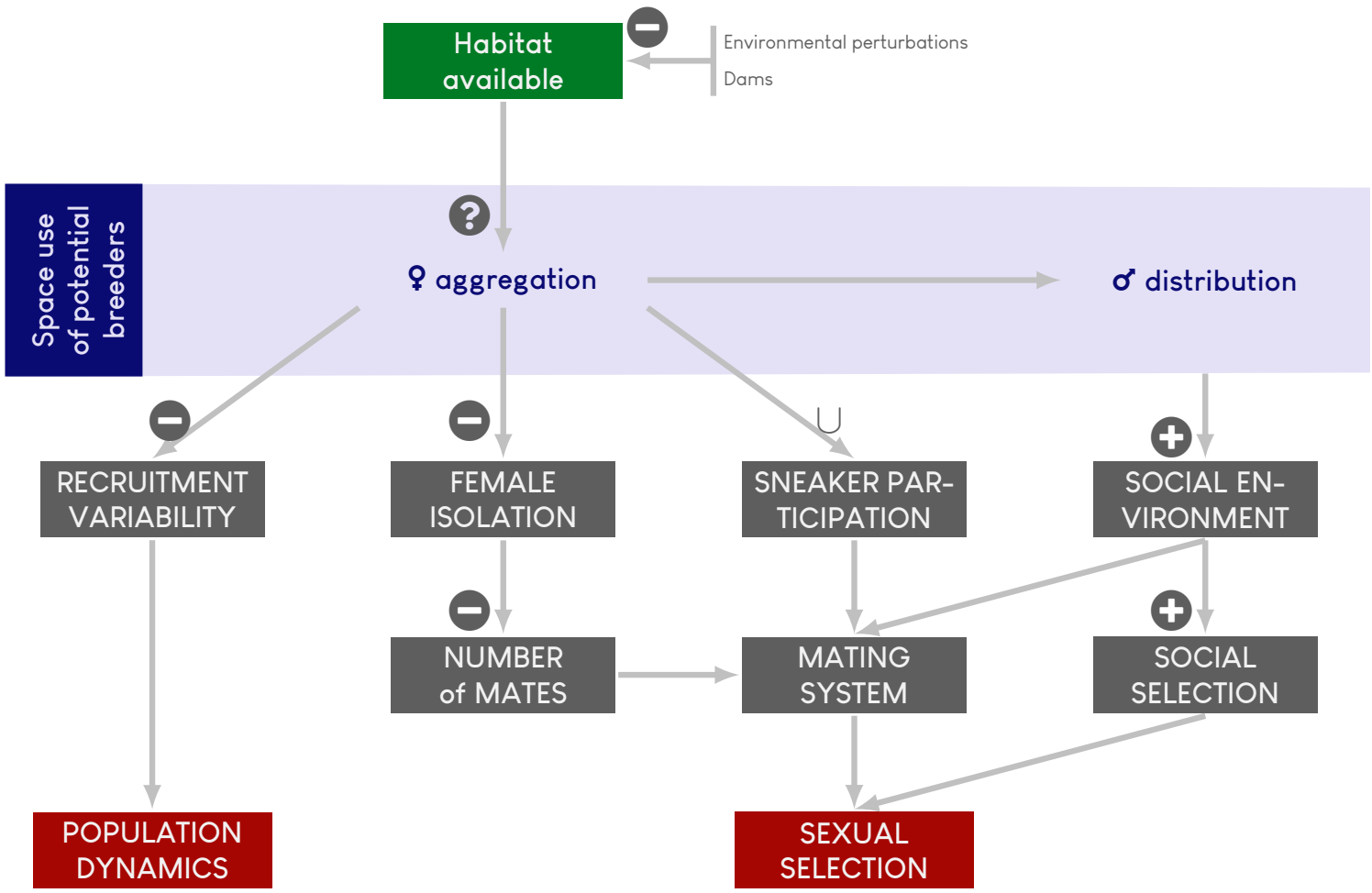

Figure. V.i: Flow chart resuming the different conclusion of the thesis. The "U" characterising the relationship between female aggregation and sneaker participation indicates a U-shaped curve. All effects were not characterised by a way of variations, then, all arrows have not a sign.

Thesis valuing

Are listed published articles, articles in preparation or submitted, talks and posters in scientific conferences.

PART II

- Article --- chapter 2: Bouchard, C., Bardonnet, A., Buoro, M., Tentelier, C. (2018). Effects of spatial aggregation of nests on population recruitment: the case of a small population of Atlantic salmon. Ecosphere, 9 (4), 18 p. , DOI : 10.1002/ecs2.2178
- Talk --- chapter 2: Bouchard, C., Prévost, E., Buoro, M., Bardonnet, A., Tentelier, C. (2017). Impacts of nest spatial aggregation on population productivity: the case of a small population of Atlantic salmon (Salmo salar). In: Understanding fish populations. Symposium handbook (p. 57). Presented at Fisheries Society of the British Isles Annual Symposium, Exeter, GBR (2017-07-03 - 2017-07-07). 162 p.
- Talk --- chapter 2: Bouchard, C., Prévost, E., Buoro, M., Bardonnet, A., Tentelier, C. (2017). Impacts of nest spatial aggregation on population productivity: the case of a small population of Atlantic salmon (Salmo salar). Presented at NowPaS 2017
- Poster --- chapter 2: Bouchard, C., Bardonnet, A., Buoro, M., Tentelier, C. (2018). Effects of spatial aggregation of nests on population recruitment: the case of a small population of Atlantic salmon. In: ISEC 2018 Conference Book (p. 72). Presented at International Statistical Ecology Conference (ISEC 2018), St Andrews, GBR (2018-07-02 - 2018-07-06). 328 p., DOI : 10.13140/RG.2.2.35939.04643

PART III

- Article --- chapter 4: Bacles, C. F., Bouchard, C., Lange, F., Manicki, A., Tentelier, C., Lepais, O. (2018). Estimating the effective number of breeders from single parr samples for conservation monitoring of wild populations of Atlantic salmon Salmo salar . Journal of Fish Biology, online first. , DOI : 10.1111/jfb.13537
- In prep. article: chapter 5

- Submitted article: chapter 8.
- Talk --- chapter 2: Bouchard, C., Rives, J., Lange, F., Tentelier, C. (2018). Heterogeneity of space use in tactics in salmon parr along breeding season in relation to the individual maturity level. In: Program. Presented at EEEF 2018 - Ecology and Evolutionary Ethology of Fishes Conference, Montreal, CAN (2018-06-17 - 2018-06-20). 56 p.

The first 9 months of my thesis were devoted in studying the mating behaviour of Allis shad (*Alosa alosa*). A first breeding season and a too low number of breeders in the population forced me to change my thesis subject. C. Tentelier has continued the work on Allis shad and submitted a paper in *bioRχiv* where I am in co-author.

Photo credits and legends of chapter pages

chapter 1 Uxondo dam — C. Bouchard

chapter 2 Darguy dam — C. Bouchard

chapter 3 Confluence of the Nivelle with the Sorrimenta — C. Bouchard

chapter 4 Part of the Upper Nivelle — C. Bouchard

chapter 5 Part of the Upper Nivelle — C. Bouchard

chapter 6 River mouth of the Nivelle — C. Bouchard

chapter 7 Part of the Upper Nivelle — C. Bouchard

chapter 8 Salmon parr being tagged for the monitoring of chapters 8 and 9 — S. Glise

chapter 9 GPS tablet during electro fishing for the monitoring of chapters 8 and 9 — C. Bouchard

Bibliography

Almada, V.C., Gonçlalves, E.J., Santos, A.J. & Baptista, C. (1994) Breeding ecology and nest aggregations in a population of *Salaria pavo* (Pisces: Blenniidae) in an area where nest sites are very scarce. *Journal of Fish Biology* **45**, 819–830.

Andren, H. (1990) Despotic distribution, unequal reproductive success, and population regulation in the jay *Garrulus Glandarius* L. *Ecology* **71**, 1796–1803.

Antonio, R.R., Agostinho, A.A., Pelicice, F.M., Bailly, D., Okada, E.K. & Dias, J.H.P. (2007) Blockage of migration routes by dam construction: can migratory fish find alternative routes? *Neotropical Ichthyology* **5**, 177–184.

Bacles, C.F.E., Bouchard, C., Lange, F., Manicki, A., Tentelier, C. & Lepais, O. (2018) Estimating the effective number of breeders from single parr samples for conservation monitoring of wild populations of Atlantic salmon *Salmo salar*. *Journal of Fish Biology* **92**, 699–726.

Battin, J., Wiley, M.W., Ruckelshaus, M.H., Palmer, R.N., Korb, E., Bartz, K.K. & Imaki, H. (2007) Projected impacts of climate change on salmon habitat restoration. *Proceedings of the National Academy of Sciences* **104**, 6720–6725.

Beall, E. & De Gaudemar, B. (1999) Plasticité des comportements de reproduction chez le saumon atlantique (*Salmo salar*) en fonction des conditions environnementales. *Cybium* **23**, 9–28.

Broell, F., Noda, T., Wright, S., Domenici, P., Steffensen, J.F., Auclair, J.P. & Taggart, C.T. (2013) Accelerometer tags: detecting and identifying activities in fish and the effect of sampling frequency. *Journal of Experimental Biology* **216**, 1522–1522.

Brown, G.E. & Brown, J.A. (1996) Does kin-biased territorial behavior increase kin-biased foraging in juvenile salmonids? *Behavioral Ecology* **7**, 24–29.

Brun, M. (2011) *Aide à la décision pour la conservation des populations de saumon atlantique (Salmo salar L.)*. Ph.D. thesis, Pau.

Burness, G., Casselman, S.J., Schulte-Hostedde, A.I., Moyes, C.D. & Montgomerie, R. (2004) Sperm swimming speed and energetics vary with sperm competition risk in bluegill (*Lepomis macrochirus*). *Behavioral Ecology and Sociobiology* **56**, 65–70.

Callander, S., Hayes, C.L., Jennions, M.D. & Backwell, P.R.Y. (2013) Experimental evidence that immediate neighbors affect male attractiveness. *Behavioral Ecology* **24**, 730–733.

Cassini, M.H. (2000) A model on female breeding dispersion and the reproductive systems of pinnipeds. *Behavioural Processes* **51**, 93–99.

Courtiol, A., Etienne, L., Feron, R., Godelle, B. & Rousset, F. (2016) The evolution of mutual mate choice under direct benefits. *The American Naturalist* **188**, 521–538.

Desharnais, R.A., Reuman, D.C., Costantino, R.F. & Cohen, J.E. (2018) Temporal scale of environmental correlations affects ecological synchrony. *Ecology Letters* .

Dodson, J.J., Aubin-Horth, N., Thériault, V. & Páez, D.J. (2013) The evolutionary ecology of alternative migratory tactics in salmonid fishes: Alternative migratory tactics as threshold traits. *Biological Reviews* **88**, 602–625.

Doligez, B., Cadet, C., Danchin, E. & Boulinier, T. (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* **66**, 973–988.

Dumas, J. & Haury, J. (1995) Une rivière du Piémont pyrénéen: la Nivelle (Pays basque). *Acta Biologica Montana* **11**, 113–146.

Emlen, S.T. & Oring, L.W. (1977) Ecology, sexual selection, and evolution of mating systems. *Science* **197**, 215–223.

Fahrig, L. (1997) Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management* **61**, 603–610.

Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* **40**, 1649–1663.

Falcy, M.R. (2015) Density-dependent habitat selection of spawning Chinook salmon: broad-scale evidence and implications. *Journal of Animal Ecology* **84**, 545–553.

Fargo, J. (1994) Examining recruitment relationships for hecate strait english sole (*Pleuronectes vetulus*). *Netherlands Journal of Sea Research* **32**, 385–397.

Fleming, I.A. & Gross, M.R. (1994) Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution* **48**, 637–657.

Foldvik, A., Finstad, A.G. & Einum, S. (2010) Relating juvenile spatial distribution to breeding patterns in anadromous salmonid populations. *Journal of Animal Ecology* **79**, 501–509.

Forget, G., Baglinière, J.L., Marchand, F., Richard, A. & Nevoux, M. (2018) A new method to estimate habitat potential for Atlantic salmon (*Salmo salar*): predicting the influence of dam removal on the Sélune River (France) as a case study. *ICES Journal of Marine Science* .

Fraser, N.H.C. & Metcalfe, N.B. (1997) The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Functional Ecology* **11**, 385–391.

Fraser, N.H.C., Metcalfe, N.B., Heggenes, J. & Thorpe, J.E. (1995) Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. *Canadian Journal of Zoology* **73**, 446–451.

Fretwell, S.D. & Lucas, H.L.J. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**, 16–36.

Fukui, Y. (1995) The effects of body size on mate choice in a grapsid crab,*Gaetice depressus* (Crustacea, Decapoda). *Journal of Ethology* **13**, 1–8.

Gage, M.J., Macfarlane, C.P., Yeates, S., Ward, R.G., Searle, J.B. & Parker, G.A. (2004) Spermatozoal traits and sperm competition in Atlantic salmon. *Current Biology* **14**, 44–47.

Gasparini, C., Serena, G. & Pilastro, A. (2013) Do unattractive friends make you look better? Context-dependent male mating preferences in the guppy. *Proceedings of the Royal Society of London B: Biological Sciences* **280**, 20123072.

Gauthey, Z., Lang, M., Elosegi, A., Tentelier, C., Rives, J. & Labonne, J. (2017a) Brown trout spawning habitat selection and its effects on egg survival. *Ecology of Freshwater Fish* **26**, 133–140.

Gauthey, Z., Tentelier, C., Lepais, O., Elosegi, A., Royer, L., Glise, S. & Labonne, J. (2017b) With our powers combined: integrating behavioral and genetic data to estimate mating success and sexual selection. *Rethinking Ecology* **2**, 1–26.

Gowans, A.R.D., Armstrong, J.D., Priede, I.G. & Mckelvey, S. (2003) Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland. *Ecology of Freshwater Fish* **12**, 177–189.

Griffiths, S.W., Armstrong, J.D. & Metcalfe, N.B. (2003) The cost of aggregation: juvenile salmon avoid sharing winter refuges with siblings. *Behavioral Ecology* **14**, 602–606.

Grimardias, D., Merchermek, N., Manicki, A., Garnier, J., Gaudin, P., Jarry, M. & Beall, E. (2010) Reproductive success of Atlantic salmon (*Salmo salar*) mature male parr in a small river, the Nivelle: influence of shelters: Mature male parr success and shelters. *Ecology of Freshwater Fish* **19**, 510–519.

Hendry, A.P., Berg, O.K. & Quinn, T.P. (2001) Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores). *Oikos* **93**, 407–418.

Iles, T.C. (1994) A review of stock-recruitment relationships with reference to flatfish populations. *Netherlands Journal of Sea Research* **32**, 399–420.

Juanes, F., Perez, J. & Garcia-Vazquez, E. (2007) Reproductive strategies in small populations: using Atlantic salmon as a case study. *Ecology of Freshwater Fish* **16**, 468–475.

Kareiva, P., Marvier, M. & McClure, M. (2000) Recovery and management options for Spring/Summer Chinook salmon in the Columbia river basin. *Science* **290**, 977–979.

Kawabata, Y., Noda, T., Nakashima, Y., Nanami, A., Sato, T., Takebe, T., Mitamura, H., Arai, N., Yamaguchi, T. & Soyano, K. (2014) Use of a gyroscope/accelerometer data logger to identify alternative feeding behaviours in fish. *Journal of Experimental Biology* **217**, 3204–3208.

Kokko, H., Harris, M.P. & Wanless, S. (2004) Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. *Journal of Animal Ecology* **73**, 367–376.

Kokko, H. & Johnstone, R.A. (2002) Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philosophical Transactions of the Royal Society B: Biological Sciences* **357**, 319–330.

Kokko, H. & Rankin, D.J. (2006) Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 319–334.

Levin, P.S. & Tolimieri, N. (2001) Differences in the impacts of dams on the dynamics of salmon populations. *Animal Conservation* **4**, 291–299.

Levin, S.A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* **73**, 1943–1967.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogreography. *Evolution* **17**, 373–387.

McDonald, G.C., James, R., Krause, J. & Pizzari, T. (2013) Sexual networks: measuring sexual selection in structured, polyandrous populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20120356–20120356.

McDonald, G.C. & Pizzari, T. (2016) Why patterns of assortative mating are key to study sexual selection and how to measure them. *Behavioral Ecology and Sociobiology* **70**, 209–220.

McDonald, G.C. & Pizzari, T. (2017) Structure of sexual networks determines the operation of sexual selection. *Proceedings of the National Academy of Sciences* p. 9.

Meixler, M.S., Bain, M.B. & Todd Walter, M. (2009) Predicting barrier passage and habitat suitability for migratory fish species. *Ecological Modelling* **220**, 2782–2791.

Mjølnerød, I.B., Fleming, I.A., Refseth, U.H. & Hindar, K. (1998) Mate and sperm competition during multiple-male spawnings of Atlantic salmon. *Canadian Journal of Zoology* **76**, 70–75.

Moreau, M., Siebert, S., Buerkert, A. & Schlecht, E. (2009) Use of a tri-axial accelerometer for automated recording and classification of goats' grazing behaviour. *Applied Animal Behaviour Science* **119**, 158–170.

Newton, M., Dodd, J.A., Barry, J., Boylan, P. & Adams, C.E. (2017) The impact of a small-scale riverine obstacle on the upstream migration of Atlantic Salmon. *Hydrobiologia* pp. 1–14.

Nislow, K.H., Folt, C.L. & Parrish, D.L. (1999) Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. *Ecological Applications* **9**, 1085–1099.

Nonaka, E., Parvinen, K. & Brännström, Å. (2013) Evolutionary suicide as a consequence of runaway selection for greater aggregation tendency. *Journal of Theoretical Biology* **317**, 96–104.

Oh, K.P. & Badyaev, A.V. (2010) Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *The American Naturalist* **176**, E80–E89.

Palm, D., Brännäs, E., Lepori, F., Nilsson, K. & Stridsman, S. (2007) The influence of spawning habitat restoration on juvenile brown trout (*Salmo trutta*) density. *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 509–515.

Parker, G. & Sutherland, W. (1986) Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behaviour* **34**, 1222–1242.

Pérez-González, J. & Carranza, J. (2011) Female aggregation interacts with population structure to influence the degree of polygyny in red deer. *Animal Behaviour* **82**, 957–970.

Pomeroy, P.P., Anderson, S.S., Twiss, S.D. & McConnell, B.J. (1994) Dispersion and site fidelity of breeding female grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology* **233**, 429–447.

Quinn, T.P. & McPhee, M.V. (1998) Effects of senescence and density on the aggression of adult female sockeye salmon. *Journal of Fish Biology* **52**, 1295–1300.

Sandell, M. & Liberg, O. (1992) Roamers and stayers: a model on male mating tactics and mating systems. *The American Naturalist* **139**, 177–189.

Saura, M., Caballero, A., Caballero, P. & Morán, P. (2008) Impact of precocious male parr on the effective size of a wild population of Atlantic salmon. *Freshwater Biology* **53**, 2375–2384.

Shuster, S.M. & Wade, M.J. (2003) *Mating systems and strategies*. Monographs in behavior and ecology, Princeton University Press, Princeton.

Steen, R.P. & Quinn, T.P. (1999) Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. *Canadian Journal of Zoology* **77**, 836–841.

Tanner, C.J. & Jackson, A.L. (2012) Social structure emerges via the interaction between local ecology and individual behaviour: Ecology and behaviour affect social structure. *Journal of Animal Ecology* **81**, 260–267.

Tentelier, C., Aymes, J.C., Spitz, B. & Rives, J. (2016a) Using proximity loggers to describe the sexual network of a freshwater fish. *Environmental Biology of Fishes* **99**, 621–631.

Tentelier, C., Larranaga, N., Lepais, O., Manicki, A., Rives, J. & Lange, F. (2016b) Space use and its effects on reproductive success of anadromous Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 1461–1471.

Tentelier, C., Lepais, O., Larranaga, N., Manicki, A., Lange, F. & Rives, J. (2016c) Sexual selection leads to a tenfold difference in reproductive success of alternative reproductive tactics in male Atlantic salmon. *The Science of Nature* **103**.

Wagner, W.E. (1998) Measuring female mating preferences. *Animal Behaviour* **55**, 1029–1042.

Weir, L.K., Grant, J.W.A. & Hutchings, J.A. (2011) The influence of operational sex ratio on the intensity of competition for mates. *The American Naturalist* **177**, 167–176.

Wiens, J.A. (1989) Spatial Scaling in Ecology. *Functional Ecology* **3**, 385.