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Colin Bouchard, Agnes Bardonnet, Mathieu Buoro, Cédric Tentelier

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Colin Bouchard,† Agnès Bardonnet, Mathieu Buoro, and Cédric Tentelier

ECOBIOP, INRA, University of Pau and Pays Adour, 64310 Saint-Pée-Sur-Nivelle, France

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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.

Key words: Beverton–Holt; breeding site; clustering; density compensation; environmental stochasticity; patchiness; population dynamic; spatial distribution; spatial heterogeneity.

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† **E-mail:** colin.bouchard@icloud.com

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 and 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, that is, the number of neighbors within a habitat unit (Lloyd 1967) or on the distance to the nearest neighbor (Clark and Evans 1954). Assessing whether 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 remain rarely investigated.

Spatial aggregation of individuals may notably arise when they feed or breed in specific habitats (Tregenza 1995, Danchin and Wagner 1997, Clotfelter and Yasukawa 1999, Sergio et al. 2003,

Wagner and Danchin 2003). Individuals select such habitats by assessing either the habitat quality in terms of resources (Boulinier and 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 (Hendry et al. 2001, Morris 2003, López-Sepulcre et al. 2010, Tentelier and Piou 2011, Falcy 2015). 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; McPeek et al. 2001, Wong et al. 2007; Adkison et al. 2014). 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 (Steingrimsson and Grant 1999, Einum and Nislow 2005, Finstad et al. 2009). However, competition between juveniles, caused by aggregation, may be compensated by habitat quality (Fretwell and 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 and 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 (Gustafson-Greenwood and Moring 1990, Crisp 1995, Nislow et al. 2004, Armstrong and Nislow 2006, Aas et al. 2011). 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 yr) 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 and 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 and Chaput 2001, chap. 2), we also evaluated the influence of nest aggregation on demographic processes using stock–recruitment models (Iles 1994, Prévost and 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 hypotheses. First, we predicted that a strong aggregation should diminish recruitment according to the negative density dependence theory (Steingrimsson and Grant 1999, Einum and Nislow 2005, Finstad et al. 2009, Foldvik et al. 2010). Alternatively, we predicted that aggregation should not modify recruitment level if females aggregated their nests in the best and safest breeding sites (Fretwell and Lucas 1969, Hendry et al. 2001, Schlaepfer et al. 2002), but should lead to steadier recruitment by buffering environmental stochasticity (Kallimanis et al. 2005).

Methods

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 (Fig. 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 (Dumas and 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 (Fig. 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 and 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).

We used a long-term (31 yr: 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; https://www6.inra.fr/diapfc). First, the recruitment, that is, 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 (Marchand et al. 2017; Appendix S1: Table S1). 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, that

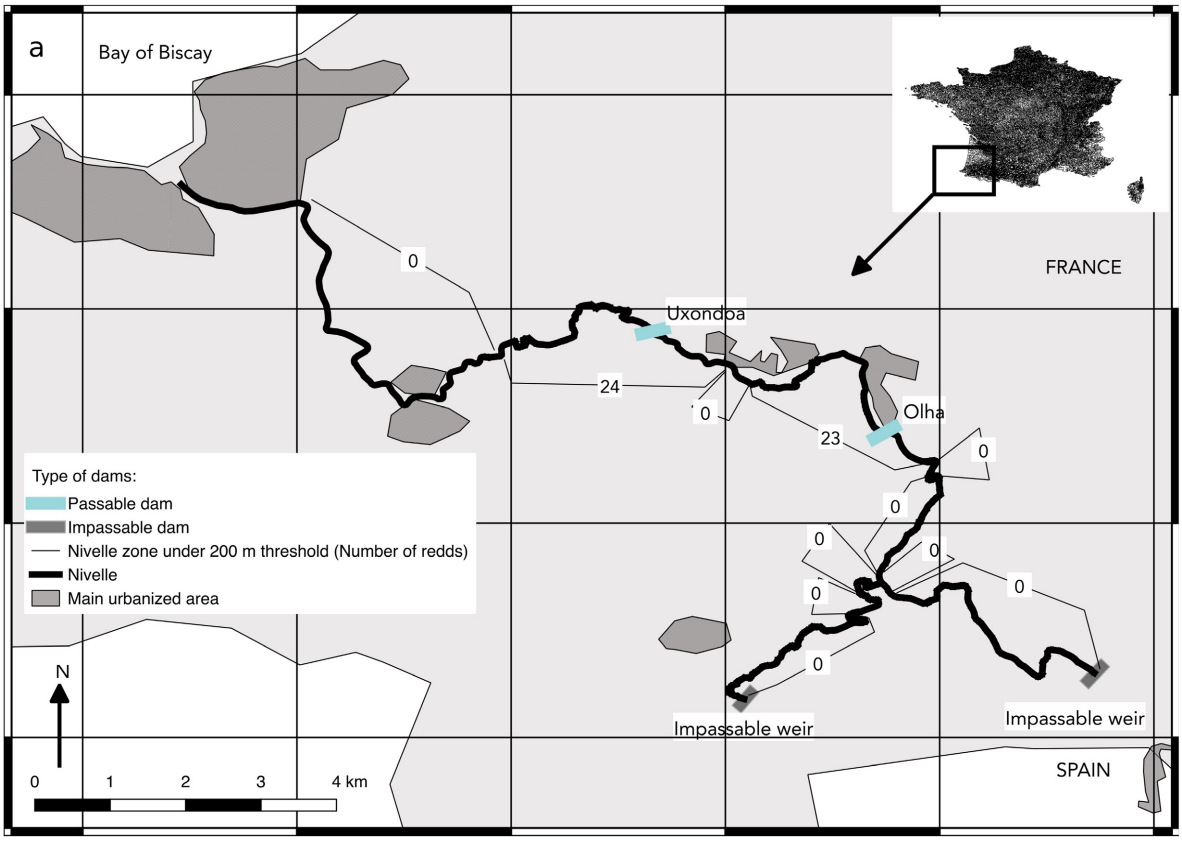
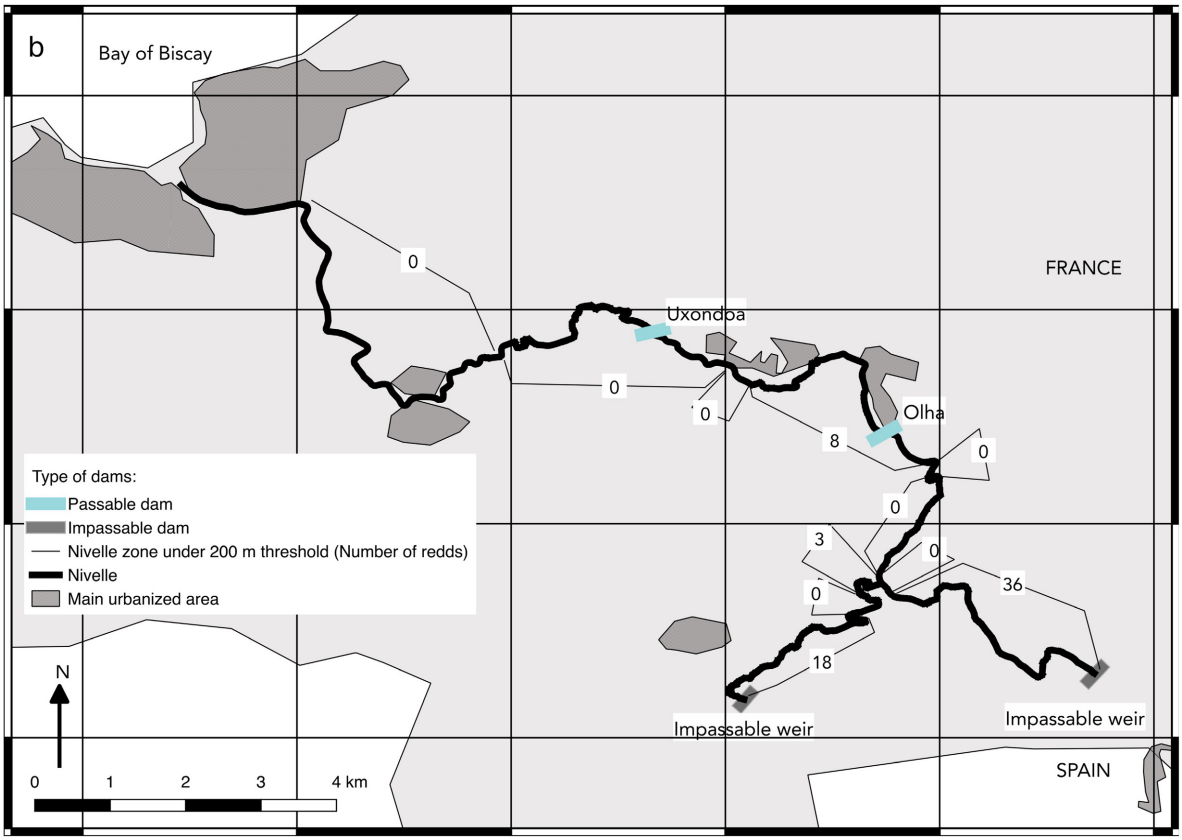


Fig. 1. Maps of the Nivelle river system available for Atlantic salmon. Four dams are indicated, including those equipped with fish passes: Uxondoa and Olha. Gray areas correspond to the major urbanized areas near the Nivelle. (a) Nest distribution in 1986 which corresponds to the year with the lowest aggregation under a 50 m threshold length: 4.20. (b) Nest distribution in 2012, the year with the higher aggregation: 27.46.

is, 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 and Prevost 2016). These estimates of abundance encompass catch probability, which was estimated at 0.9 (Servanty and Prevost 2016; Appendix S1). Then, fecundities were attributed to each age class: 4500 and 7200 eggs/kg for one and two sea winters, respectively (Servanty and Prevost 2016; Appendix S1). 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 (Prévost and Baglinière 1995, Dauphin et al. 2009, Brun et al. 2011, Servanty and 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



(Fig. 1. *Continued*)

same duo of observers after training, experience and training shrinking 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.

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). The mean crowding ($\overset{*}{m}_j$) is defined as the mean number of neighbors per nest in the same patch (Eq. 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):

$$\overset{*}{m}_j = \frac{\sum_{i=1}^{N_j} X_{i,j}}{N_j} \qquad \overset{*}{m}_j = m_j + \left(\frac{\sigma^2}{m_j} - 1\right), \tag{1}$$

$$\text{Patchiness}_j = P_j = \frac{\overset{*}{m}_j}{m_j} \tag{2}$$

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 yr).

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: Fig. S1). We varied the threshold length of unused habitat for separating patches from 20 to 500 m, reflecting the biological low probability that salmon fry cross such a length of unfavorable habitat during their first weeks of life (Gustafson-Greenwood and Moring 1990, Beall 1994, Crisp 1995, Garcia de Leaniz et al. 2000, Einum and Nislow 2005, Einum et al. 2006). Aggregation of nests was computed with patches defined as 624 initial stretches but also patches defined under threshold lengths varying from 20 to 500 m (Appendix S1 for details).

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 1): (1) a null model without effect of aggregation on mean and variance (noted $\mathcal{M}_0$), (2) a model with both simple and quadratic effects of aggregation on the mean μ_j (noted $\mathcal{M}_1$), (3) a heteroscedastic model with an effect of aggregation on variance σ_j (noted $\mathcal{M}_2$), and (4) 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 (Ricker 1954, Beverton and Holt 1957, Cushing 1973). 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 S2). In addition, Beverton–Holt's model is widely used in studies on Atlantic salmon and was therefore chosen to run our analyzes (Prévost and Chaput 2001, Michielsens and McAllister 2004, Brun 2011).

Recruitment was modeled 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:

Table 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).

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

Notes: $\mathcal{M}_0$ 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 $\mathcal{M}_2$.

$$Y_j^* \sim \mathrm{Log}\mathcal{N}\left(\log\left(\mu_j\right), \frac{1}{\tau}\right), \tag{3}$$

A simple Beverton–Holt model was considered as the null model ($\mathcal{BH}_{\mathrm{null}}$) because the question addressed here was whether aggregation affected the stock–recruitment dynamic. Therefore, μ_j in the Eq. 3 corresponded to:

$$\mu_j = \frac{a \times E_j^*}{1 + (E_j^*/K)} \tag{4}$$

where j is the considered year, and a the parameter for density-independent contribution to fish mortality, $1/K$ the density-dependent contribution to fish mortality.

Effects of aggregation were computed in two ways. First, the direct effect of aggregation on recruitment, that is, mean (μ_j), was assessed by elevating yearly aggregation (noted P_j) at power q (Eq. 5):

$$\mu_j = \frac{a \times E_j^*}{1 + (E_j^*/K)} \times P_j^q. \tag{5}$$

Second, the effect of aggregation on recruitment variability, that is, dispersion parameter (τ, inverse of the variance), was estimated by elevating yearly aggregation (noted P_j) at power η (Eq. 6):

$$\tau = \delta \times P_j^\eta, \tag{6}$$

where δ is the intercept of τ calculation. A complete model, noted $\mathcal{BH}_{\mathrm{complete}}$, with effects of aggregation on mean (Eq. 5) and variance (Eq. 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. 5 ($\mathcal{BH}_\mu$) or τ with Eq. 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 (Iles 1994, Aas et al. 2011).

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, Prévost 2003). Gamma distributions, which are more informative, were chosen for scale parameters δ and τ (Prévost 2003, Gelman et al. 2014). For each model, four independent chains were run to save 6400 iterations after a warm-up of 2000 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 and 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 2000 values over the 6400 of each parameter estimates was extracted for each model. From these samples, 2000 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% ($\mathrm{CI}_{95\%}$). Assessment of models was done with the widely applicable information criterion (WAIC, Vehtari et al. 2017), a relevant criterion to rank stock–recruitment models (Wang and Liu 2006, Subbey et al. 2014) under a Bayesian framework.

Table 2. Summary of the main parameters and their prior distributions.

Parameter	Definition	Prior distribution
a	Eqs. 4, 5	$\mathrm{Log}\mathcal{N}(0, 2)$
K	Eqs. 4, 5	$\mathrm{Log}\mathcal{N}(0, 10)$
τ	Eq. 4	$\Gamma(0.01, 100)$
q	Eq. 5	$\mathcal{N}(0, 20)$
δ	Eq. 6	$\Gamma(0.01, 100)$
η	Eq. 6	$\mathcal{N}(0, 20)$

Notes: 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 modelization 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.

Effects of population size on mean density and aggregation of nests

We also tested whether the aggregation of nests (P_j) and the mean density of nests (m_j) was dependent of the anadromous population size ($\mathrm{N}_{\mathrm{pop}}$) using a linear regression (Eq. 7). Aims of this model were to assess (1) 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 (2) to know how aggregation varies with N_{pop}.

$$\mu_j = \text{intercept} + \zeta \times N_{pop},$$
$$m_j \text{ or } P_j \sim \mathcal{N}\left(\mu_j, \sigma\right), \quad (7)$$

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 6400 iterations after a warm-up of 2000 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}").

Results

A total of 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 ~80 nests per year over the last decade (Fig. 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 (Fig. 6). Recruitment was steadier than stock, ranging between 0.04 juveniles/m^2 in 2006 and 0.28 juveniles/m^2 in 2012.

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 and 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 S2).

Aggregation of nests (patchiness) was always higher than the reference value (equals to one)

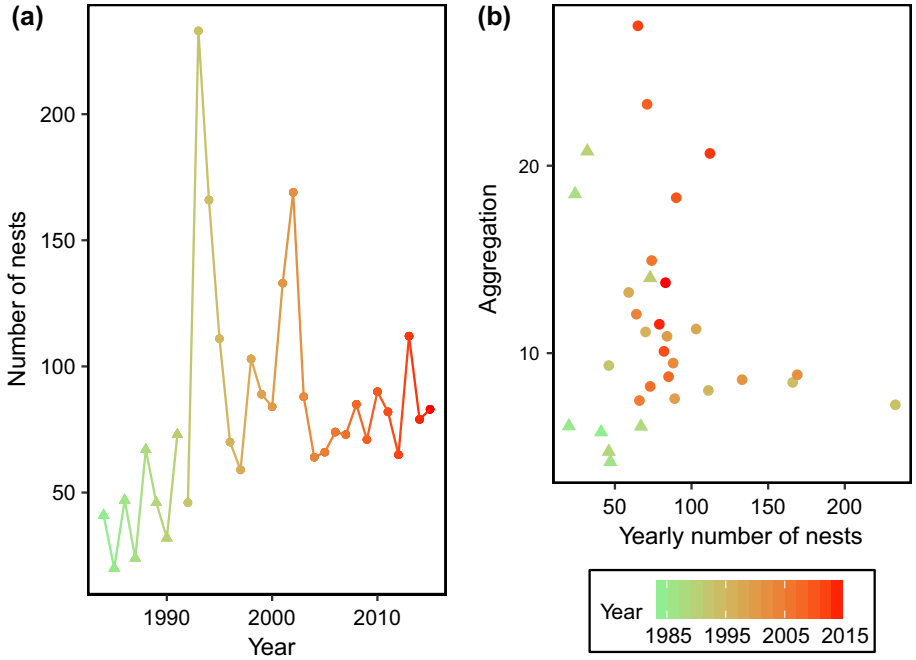


Fig. 2. (a) Plot of the yearly number of nests (N = 32 yr and 2645 nests). (b) Yearly aggregation value (patchiness) as a function of the yearly number of nests (N = 32 yr). Triangles indicate years before the opening of Olha, a dam equipped with a fish pass in 1992, and dots years after the opening.

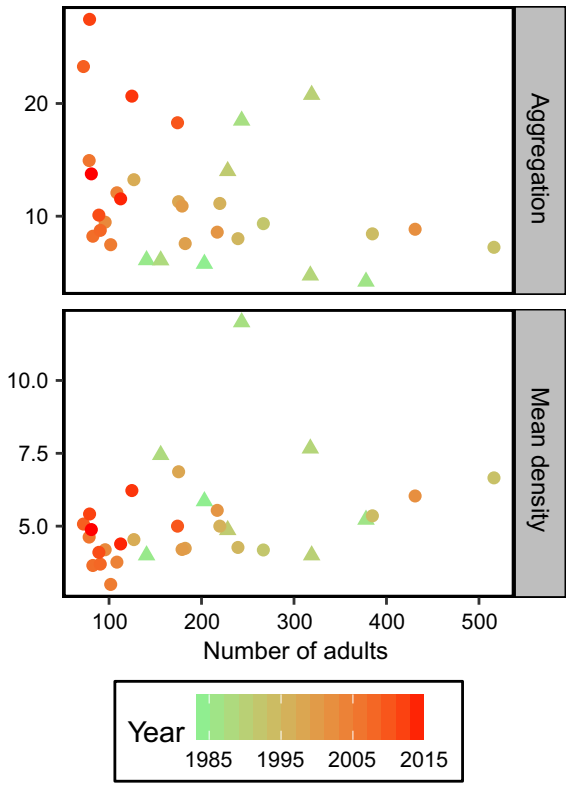


Fig. 3. Aggregation (patchiness) and mean density of nests as a function of the yearly number of anadromous salmon of the Nivelle. Triangles indicate years before the opening of Olha, a dam equipped with a fish pass in 1992, and dots years after the opening.

varying between 4.20 in 1986 and 27.46 in 2012 (Fig. 2). In addition, aggregation value was not linearly dependent of the number of nests (Fig. 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, Fig. 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, Fig. 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 (Fig. 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], Fig. 4).

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 ($\mathcal{BH}_{null}$, $\mathcal{BH}_{\mu}$, $\mathcal{BH}_{\tau}$, and $\mathcal{BH}_{complete}$) had a lower WAIC than models without the stock ($\mathcal{M}_0$, $\mathcal{M}_1$, $\mathcal{M}_2$, $\mathcal{M}_3$—Table 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

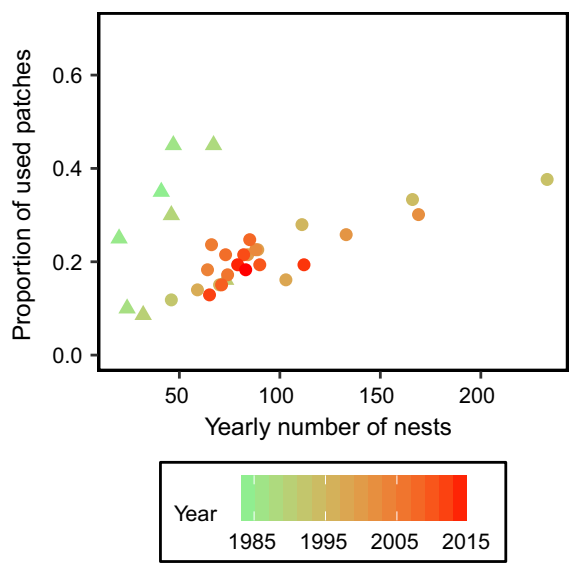


Fig. 4. Yearly proportion of patches used as a function of the yearly number of nests of the Nivelle. The yearly proportion of used patches corresponded to the number of patches where at least one nest was found divided by the number of patches in the available zone. Triangles indicate years before the opening of Olha, a dam equipped with a fish pass in 1992, and dots years after the opening.

Table 3. Summary of the parameter estimates of the four models ($\mathcal{M}_0$, $\mathcal{M}_1$, $\mathcal{M}_2$, and $\mathcal{M}_3$) explaining recruitment by the yearly aggregation of nests (patchiness).

Model	WAIC	m	β	γ	q		η		δ	a	K
					Value	Test ≤ 0	Value	Test ≤ 0	Value	Value	Value
$\mathcal{M}_0$	−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							
$\mathcal{BH}_{\text{null}}$	−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
$\mathcal{BH}_{\text{complete}}$	−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 ($\mathcal{BH}_{\text{null}}$, $\mathcal{BH}_{\mu}$, $\mathcal{BH}_{\tau}$, and $\mathcal{BH}_{\text{complete}}$): the null model with no effect of aggregation, and 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. WAIC, widely applicable information criterion.

aggregation on the mean: $\mathcal{BH}_{\text{complete}}$ ($q = -0.0264$, $\text{CI}_{95\%} = [-0.3657; 0.3522]$, 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 3), we only 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 $\eta = 0.71$ ($\text{CI}_{95\%} = [0.03; 1.37]$ with 2.09% of negative estimates of η over the 6400) 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 (Fig. 5). According to parameters estimated with $\mathcal{BH}_{\tau}$ (best model), a two- or fivefold increase in aggregation did not have a direct effect on recruitment (median = 0.11 for each aggregation values, Table 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 4).

The parameter a of fitted Beverton–Holt models (density-independent mortality) was estimated at $a = 1.23$ ($\text{CI}_{95\%} = [0.08; 46.96]$) for $\mathcal{BH}_{\text{null}}$, and $a = 1.20$ ($\text{CI}_{95\%} = [0.09; 46.79]$) for the best model with aggregation ($\mathcal{BH}_{\tau}$). Parameter K (inverse of the density-dependent mortality) was estimated at $K = 0.26$ ($\text{CI}_{95\%} = [0.00; 1.53]$) for $\mathcal{BH}_{\text{null}}$ and $K = 0.09$ ($\text{CI}_{95\%} = [0.00; 1.39]$) 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 ($\text{CI}_{95\%} = 0.03; 0.26$]) for $\mathcal{BH}_{\text{null}}$ and 0.11 juveniles/m^2 ($\text{CI}_{95\%} = [0.09; 0.13]$) for the best model with aggregation ($\mathcal{BH}_{\tau}$, Fig. 5). There was no significant difference between the two carrying capacities (45% of differences between all the 6400 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 (Fig. 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 ($\mathcal{BH}_{\text{null}}$) and the best one ($\mathcal{BH}_{\tau}$). No particular pattern was graphically detected for residuals of both models before and after 1992 (Fig. 6). In addition, no significant

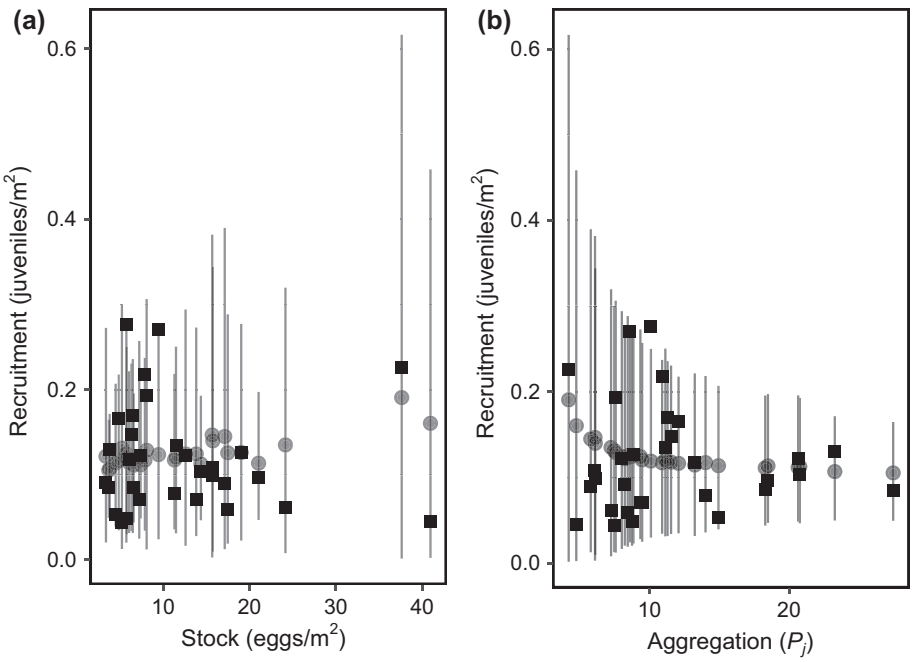


Fig. 5. (a) Stock–recruitment relationship of the Atlantic salmon population of the Nivelle river with the best Beverton–Holt model incorporating the effect of nest aggregation (patchiness) on the recruitment variability. Recruitment was the juvenile density in the river, while the stock was the estimated 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%. (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.

Table 4. Effects of aggregation increase on the recruitment (median with credible interval at 95% and mean) with the best Beverton–Holt model.

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

Notes: 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).

difference in the yearly average residuals before and after the opening of Olha was detected (Wilcoxon: $W = 76$, $P_{\text{value}} = 0.49$, same results for $\mathcal{BH}_{\text{null}}$ and $\mathcal{BH}_{\tau}$).

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 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 (1) aggregation is a way to dampen environmental stochasticity, and (2) salmon females choose their breeding sites on habitat quality and risk of disturbances.

Constraint of dams

The most notable environmental change for the 31 yr, the opening of Olha dam, did not impact stock–recruitment relationships. This

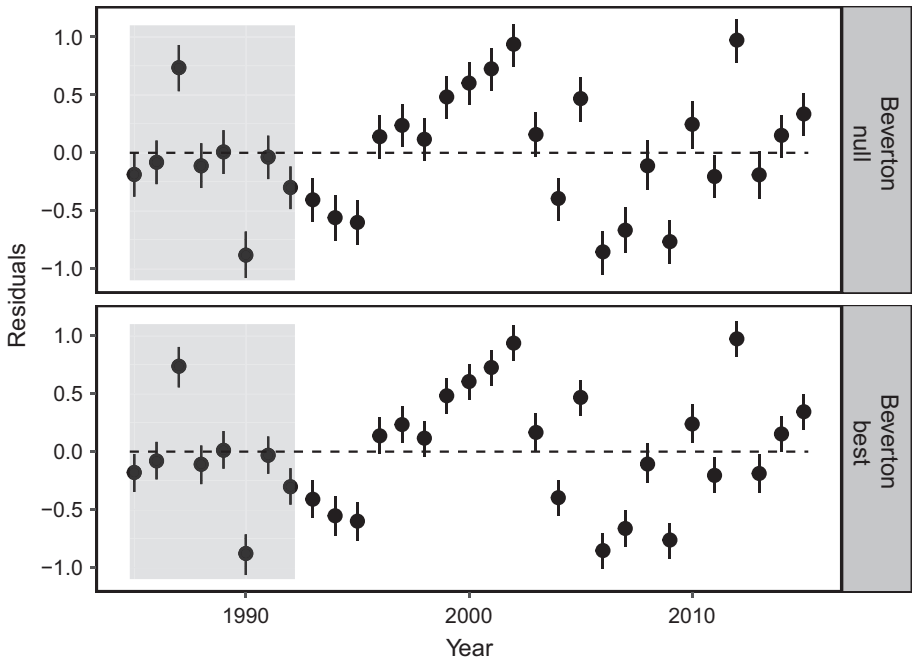


Fig. 6. Plot of the residuals of the stock–recruitment relationship (Beverton–Holt model) of the Atlantic salmon population of the Nivelle. The null model was the model $\mathcal{BH}_{\mu}$, a Beverton–Holt model without aggregation (patchiness). The best model was the model $\mathcal{BH}_{\tau}$, a 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%.

opening in 1992 multiplied the length of river accessible to salmon by 1.5 and the available river habitat for spawning by four (Fig. 3). The surprising lower aggregation before than after 1992 could be explained by the more homogeneous distribution of nests among accessible spawning 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 and 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 (Fig. 1), probably more suitable for salmon (Dumas and 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.

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-yr 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 and Nislow 2005, Einum et al. 2006, 2008, 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 and 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 and McAllister 2004, Rivot et al. 2004, Subbey et al. 2014).

Although the population recruitment is firstly dependent on the stock (Prévost and 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.

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 terms of produced offsprings 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 and 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 (Hendry et al. 2001, Falcy 2015).

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 yr of the time series. In addition, the median of the threshold biomass, $1/K$, 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 threshold 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 (Malcolm et al. 2004, Gauthey et al. 2017). Thus, our results suggest that 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 (Moir et al. 2004, Gauthey et al. 2017), or with high intra-gravel flow (Geist and 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 (Falcy 2015, Lara-Romero et al. 2016, Tentelier et al. 2016, Winandy et al., 2017, Bacles et al. 2018). 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 reproductive success and a low effective number of (Ives 1988, Tilman 1994, Chesson and Neuhauser 2002, Murrell et al. 2002, Rejmánek 2002). 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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