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► **To cite this version:**

Cédric Tentelier, Nicolas Larranaga, Olivier Lepais, Aurélie Manicki, Jacques Rives, et al.. Space use and its effects on reproductive success of anadromous Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 2016, 73 (10), pp.1461-1471. <10.1139/cjfas-2015-0518>. <hal-01901387>

HAL Id: hal-01901387

<https://hal.science/hal-01901387v1>

Submitted on 2 Oct 2024

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Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2015-0518.R1
Manuscript Type:	Article
Date Submitted by the Author:	19-Feb-2016
Complete List of Authors:	Tentelier, Cédric; Univ Pau & Pays Adour, UMR Ecobiop; INRA, UMR Ecobiop Larranaga, Nicolas; Univ Pau & Pays Adour, UMR Ecobiop; INRA, UMR Ecobiop; Hólar University College, Department of Aquaculture and Fish Biology; University of Iceland, Institute of Life and Environmental Science Lepais, Olivier; INRA, UMR Ecobiop; Univ Pau & Pays Adour, UMR Ecobiop Manicki, Aurélie; INRA, UMR Ecobiop; Univ Pau & Pays Adour, UMR Ecobiop Rives, Jacques; INRA, UMR Ecobiop; Univ Pau & Pays Adour, UMR Ecobiop Lange, Frédéric; INRA, UMR Ecobiop; Univ Pau & Pays Adour, UMR Ecobiop
Keyword:	environmental potential for polygamy, home range, sexual selection, TELEMETRY < General, microsatellite

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Manuscripts

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Running headline: Salmon space use and reproductive success

20

Keywords: Environmental potential for polygamy, home range, sexual selection, telemetry, fitness

22 Abstract

We combined habitat mapping, radio tracking of adults, redd mapping and genetic parentage
analysis on juveniles for two consecutive years to test eight predictions on the reproductive payoffs
and individual features associated to space use tactics of anadromous Atlantic salmon in a natural
population. Regarding payoffs, we found that 1) males settled in better habitat visited more redds
and tended to get more mates than males settled in poorer habitat, 2) they also sired more offspring,
and 3) the latter effect was stronger in the first year, when redds were more aggregated, 4) female
reproductive success increased with habitat quality in their home range, especially in the first year.
For individual features, 5) individuals that settled earlier in their home range had better habitat for
juvenile production, but only in the first year, 6) females were less mobile than males especially in
the second year, 7) larger males did not settle in better habitats than smaller males, and 8) smaller
males were not more mobile than larger males.

34 Résumé

Nous combinâmes la cartographie de l'habitat et des frayères, le suivi radio des géniteurs et l'analyse
de parenté sur les alevins pendant deux années pour tester huit prédictions sur les gains et les
caractéristiques individuelles associés aux tactiques spatiales dans une population de saumons de
l'Atlantique. Concernant les gains, nous trouvâmes que 1) les mâles établis dans les meilleurs
habitats visitèrent plus de frayères et eurent plus de partenaires, 2) ils engendrèrent plus de
descendance, 3) ce dernier effet fut plus marqué quand les frayères étaient plus agrégées, et 4) le
succès reproducteur des femelles augmentât avec la qualité d'habitat dans leur domaine vital,
surtout lors de la première année. Pour les caractéristiques individuelles, 5) les individus s'établissant
en premier dans leur domaine vital occupèrent un habitat plus favorable pour la production de
juvéniles, 6) les femelles furent moins mobiles que les mâles, surtout lors de la deuxième année, 7)

les plus grands mâles ne s'établirent pas dans de meilleurs habitats que les petits, 8) qui ne furent
46 pas plus mobiles que les grands.

Draft

48 Introduction

50 The spatio-temporal distribution of resources imposes a selective pressure on many aspects of individual behavior: where to settle (Fretwell and Lucas 1969), how long to stay in a given place (Charnov 1976), and which trajectory to adopt between resource items (Viswanathan et al. 1999).
52 When the resources are potential mates, their spatio-temporal distribution plays a great part in shaping sexual selection and mating strategies (Shuster and Wade 2003). Emlen and Oring's (1977) pioneering work and subsequent theoretical and empirical studies highlighted the role of spatial and temporal distribution of females on the potential for polygyny. Briefly, when females are spatially
54 clumped and do not breed synchronously, males that are able to defend high quality territories can secure many mates throughout the season, possibly resulting in a high reproductive output (Sandell and Liberg 1992). If females are more dispersed, the territory needed to secure them may be too large and too costly to defend, and non-territorial roaming males may be advantaged, resulting in
56 scramble competition between males. If females are dispersed and their breeding activity is highly synchronized, males do not have time to court several females and monogyny arises, associated with
58 restricted space use. Finally, if females are both spatially clumped and synchronous, scramble competition occurs between males on breeding sites.

64 Despite the long lasting attention paid to the mating systems and spawning behaviors of salmonids, especially the *Salmo*, *Salvelinus* and *Oncorhynchus* genera, (reviewed in de Gaudemar 1998, Fleming and Reynolds 2004, Esteve 2005), the mating success and reproductive success associated with space
66 use tactics at the scale of the river has rarely been assessed. On the one hand, because salmon are famous homing migrants and aggregate spawners, their space use during the spawning period has
68 been mostly studied in the context of either upstream migration patterns or factors promoting aggregation, without clear quantification of mating success and reproductive success. On the other
70 hand, because salmon are fierce competitors on spawning grounds, mating success and reproductive
72 success have been addressed using behavioral and genetic tools notwithstanding space use tactics at

the scale of the river. In fact, salmon are renowned for not moving much between spawning grounds
74 (Hendry et al. 1995, Stewart et al. 2004) so the timing of spawning is thought to affect reproductive
success more than movement (Dickerson et al. 2005; Anderson et al. 2010).

76 For the Atlantic salmon (*Salmo salar* L.), the spawning season typically starts with an upstream
migration, characterized by a migratory phase with rapid upstream movements, a transitory search
78 phase with short upstream and downstream movements, and a holding phase with settlement in
spawning grounds (Økland et al. 2001). Upon settlement, females select spawning sites where they
80 dig redds in which to bury their eggs. The physical habitat is very important in the selection of
spawning site (water depth: 20-50cm, water velocity: 35-65cm.s⁻¹, substrate: 16-64mm pebbles;
82 Louhi et al. 2008). Meanwhile, anadromous males both compete fiercely with each other and court
females. When the redd is dug, male and female gametes are simultaneously emitted above the nest
84 depression. Along with the dominant male, subordinate competitors and mature parr (fish that
mature before seaward migration) can sneak into the nest to fertilize eggs, so multiple fertilization is
86 quite common (Garant et al. 2001; Weir et al. 2010). After spawning, the female covers the eggs with
gravel, thereby providing maternal care against predation, while males leave to seek other mates. In
88 up to five days, females can lay up to ten batches of eggs, often but not necessarily at the same site,
and not necessarily with the same mates (Martinez et al. 2000; de Gaudemar et al. 2000). Hence,
90 polygyny is necessarily sequential, whereas polyandry can be both simultaneous and sequential.
Given this mating system, sexual selection is thought to be stronger on males than on females, the
92 former typically increasing their fitness through maximizing the number of mates and the paternity
share within each mate's clutch (Garant et al. 2001) and the latter through judicious mate choice and
94 habitat choice (Järvi 1990; de Gaudemar et al. 2000; Yeates et al. 2009).

In this study, we combined radio tracking of anadromous spawners, redd mapping and parentage
96 analysis on 0+ fry to test eight predictions on the space use tactics of spawning anadromous salmon
and their effects on reproductive success (Table 1). The first four predictions pertain to the effects of

98 space use tactics on reproductive success, and are therefore at the core of this study. According to
sexual selection theory, male reproductive success should be related to their efficiency in finding
100 mates. As a consequence, males which settle in better territories should encounter more females
and obtain higher mating success (Prediction 1), which should translate into higher reproductive
102 success (Prediction 2; Bateman 1948; Tang-Martínez 2010). However, the fitness benefits of spatial
tactics should also depend on the ecological conditions, especially on the spatio-temporal
104 distribution of sexually active females (Prediction 3; Emlen and Oring 1977; Shuster and Wade 2003).
If many females spawn aggregated but asynchronously (high environmental potential for polygyny),
106 large territorial males should get much more mates and sire much more offspring than small roaming
males (Sandell and Liberg 1992). The difference should be smaller if spawning females are few,
108 spaced or synchronous (low environmental potential for polygyny). Because the reproductive success
of females is mostly constrained by their offspring's survival, which depends on the local density
110 (Einum et al. 2006), their reproductive success should increase with the quality of habitat for
juveniles around their nests (Prediction 4; Gibson 1993) rather than with their number of mates. The
112 last four predictions relate to the determinants of space use tactics. Theory and previous empirical
work, especially on Pacific salmon, lead to predict a positive relationship between the quality of
114 habitat within an individual's home range and the date of settlement in this home range, as better
habitats should be preferred and hence colonized first (Prediction 5; Fretwell and Lucas 1969; Hendry
116 et al. 2001). Moreover, females are expected to be less mobile than males because they do not have
to visit several males to increase their mating success and reproductive success (Prediction 6;
118 Anderson and Quinn 2007). From the males' perspective, the advantage of larger males in the
intrasexual competition for local dominance suggests that larger males should secure better
120 territories than smaller males (Prediction 7), and that smaller males, being forced to leave good
territories, should opt for a roaming tactic and be more mobile than larger males (Prediction 8;
122 Baglinière et al. 1991; Finstad et al. 2005). Although the contribution of mature parr to spawning is

one striking feature of salmon mating system, we will not address this topic here, since it is the focus
124 of another study drawn from the same dataset (Tentelier et al. submitted).

Material and methods

126 *Study site and habitat description*

This study was conducted in the 2009-2010 and 2010-2011 spawning seasons in the upper section of
128 the Nivelle, a 39 km long river situated in Northern Basque Country, France, and draining a basin of
238 km² (Fig.1). The study zone consisted of 22.6 km of river situated upstream from an impassable
130 weir equipped with a fish pass and a trap (Olha dam, 43° 20' 41" N, 1° 32' 56" W). On the main stem,
8.5 km are accessible to salmon until the next impassable weir, and 4.5 km on the main tributary
132 (Lurgorrieta). The river is approximately 10 m wide on these two branches. The other small
tributaries (Opalazio and Sorrimenta on the Nivelle; Hauzartia and Lizuniaga on the Lurgorrieta) are
134 on average 5 m wide and do not present impassable weir. Since the fish pass has been installed on
Olha weir in 1992, on average 88 (min. = 13, max. = 262) anadromous Atlantic salmon has entered
136 this zone, with an average sex ratio (number of females/number of males) of 1.3 (min. = 0.76, max. =
2.7).

138 The distribution of sexually active females, which is what sets the environmental potential for
polygyny in Elmen and Oring's (1977) theory may depend on the distribution of spawning habitat in
140 the river. Moreover the test of most predictions implies a quantification of habitat quality for
reproduction. The spawning habitat of Atlantic salmon consists in riffles with pebble substratum, 20
142 to 50 cm water depth and 35 to 65 cm s⁻¹ velocity, while habitat preference for juveniles following
emergence is broader, as they can be found in stretches with lower flows and coarser substratum
144 such as cobbles or boulders (Louhi et al. 2008). Based on the observation that parr density was
highest in rapids and riffles, and one fifth of it in glides, Prévost and Porcher (1996) proposed parr
146 productive surface as an indicator of habitat quality for salmon juveniles:

$P = T \times \left(Ra + Ri + \frac{G}{5} \right)$, with P the productive surface of the stretch, T its total surface area, and Ra ,

148 Ri and G the proportion of its surface classified as rapid, riffle and glide, respectively.

To describe the distribution and quality of reproductive habitat, the whole study zone was covered
150 on foot in summer 2010. River stretches were delimited using conspicuous habitat features (bridge,
confluence, change in morphodynamic or riverbed type). Each stretch was classified as rapid, riffle,
152 glide or pool (Bisson et al., 1982), and we noted the position (GPS coordinates) of its downstream
and upstream limit, its length, width (every 10 m), and substrate composition. This latter variable
154 was recorded by noting the dominant(s) ($\geq 30\%$ of surface covered) and associated ($\geq 5\%$ of surface
covered) size classes of the stretch, taken in a simplified Wentworth scale comprising sand ($< 2\text{mm}$),
156 gravel ($< 16\text{mm}$), pebble ($< 64\text{mm}$), cobble ($< 256\text{mm}$) and boulder ($> 256\text{mm}$). From this, each stretch
was classified as suitable for spawning if it was a riffle with at least some pebbles, and the productive
158 surface of each stretch was computed as above.

Redd distribution

160 Emlen and Oring (1977) assumes that the environmental potential for polygyny arises from the
spatio-temporal distribution of sexually active females. To test the effect of this distribution on the
162 reproductive success of males (Prediction 3) we quantified the spatio-temporal distribution of active
redds. To this end, the 1st of December to the 31st of January of each study year, the whole study
164 site was covered on foot to locate redds. The entire river could not be covered daily but each given
section was visited at least once a week. Redds were detected visually by the typical depression-
166 dome succession and by the contrast of light disturbed substrate on the darker, algae-covered
background. After a few days, the contrast faded and the redds were only detectable by depression-
168 dome successions on the riverbed. Atlantic salmon females sometimes dig their redds on already
existing ones. This superimposition was detected as both the increase of the size of an existing redd
170 and the renewed light color of a redd whose contrast with the surrounding substrate had faded.
When a new redd (or a superimposition) was detected, its GPS coordinates and the date of detection

172 were recorded. Because all portions of the river were not inspected daily, the digging date of a redd
was uncertain and was considered to be uniformly distributed between the day of finding and the
174 last inspection of the portion of river where it was found.

To translate the spatial and temporal distribution of redds into a metric relevant to sexual selection,
176 we computed spatial patchiness P_s (Lloyd 1967) and temporal patchiness P_t , which are directly
related to the environmental potential for polygyny (Shuster and Wade 2003). The spatial patchiness
178 was computed as $P_s = \frac{\sum_{i=1}^N x_i / N}{N/L}$, with N the total number of redds, x_i the number of other redds
situated less than one kilometer from the i^{th} redd, and L the total river length (22.6 km). The
180 numerator of P_s is known as m^* , the spatial mean crowding index, and the denominator is average
redd density. Under random distribution, the mean crowding index is expected to equal average
182 density, hence $P_s = 1$, whereas $P_s > 1$ indicates aggregation and $P_s < 1$ indicates a more uniform
distribution. Temporal patchiness, P_t , was computed likewise, with x_i the number of other redd dug
184 less than two days from the i^{th} redd, and L the duration of spawning season (from 1st December to
31st January = 62 days). Because the date of redd digging was uncertain, we simulated 1000 possible
186 scenarios by randomizing the digging date of each redd among all possible days, according to the first
day on which the redd was found and the last day on which the portion of river had been covered.
188 We then give the average and standard deviation of P_t for each year.

Individual space use tactics

190 The test of all our predictions involved the quantification of individual space use, which was based on
radio tracking. The fish trap at the downstream limit of the study zone was operating all year round,
192 so each anadromous Atlantic salmon entering the study zone (mainly during Spring and Fall runs) was
captured and anaesthetized (eugenol, 0.3 ml/l). We measured its fork length, clipped a piece of
194 pelvic fin (stored in 90% ethanol for further analyses), determined its sex from the relative size of
upper jaw (Maise and Baglinière 1986) and its sea age from body length and subsequent scale
196 examination. Each individual was then tagged with a uniquely coded esophageal radio transmitter

(ATS Inc. F1840 or F1845 according to fish size) and placed upstream from the dam in a releasing
198 cage from which it could freely swim once woken. Thereafter, each fish was located at a 20 m
precision using mobile receiver (ATS Inc. R2100) and a loop antenna. Locations were recorded weekly
200 until the 31st of October, and daily from the 1st of November until the 31st of January. Since the weir
on which we trapped and marked all the individuals was otherwise impassable, our dataset consisted
202 on the daily position of every anadromous salmon of the population throughout the two spawning
seasons.

204 The spawning period of each individual was considered to start one week before the first redd was
found if the fish was already present in the study zone before that day, and on the day it entered the
206 study zone otherwise. The spawning period of each individual was considered to end when the last
redd was found, when the fish died (radio transmitters double their pulse rate when immobile for 8
208 hours) or on the day the fish started to perform only downstream movements until the end of the
study, depending on what occurred first.

210 The spatial strategy of each individual during its spawning period was assessed by computing two
variables. The first one was related to the mobility of the individual. It was computed as the shortest
212 river portion encompassing 50% of a fish's daily positions during its spawning period, and called
UD50 range (Utilization Density 50). The second variable was related to the quality of an individual's
214 UD50 in terms of reproduction, and was computed as the productive surface of the stretches
situated within the individual's UD50. Given that offspring stay in their natal nest until emergence,
216 and hardly disperse more than 400 m downstream from it until summer (Beall et al. 1994), the
quality of an individual's habitat is likely to reflect the habitat experienced by its offspring during
218 their first, critical life stages. Microhabitat variables in nest (e.g. groundwater seeps, resistance to
scouring) greatly affect survival before emergence, and certainly condition the choice of nesting site,
220 but they are very hard to quantify at the scale of an individual's home range. On the other hand,
because juvenile survival and growth after emergence increase with decreasing local density (Einum

222 et al. 2006) the productive surface on a river section may be a good indicator of offspring survival
there and may be used by individuals to decide where to settle during the spawning period. Since
224 having a wide UD50 increases the cumulated productive surface on it, we divided the productive
surface by the range of UD50 to disentangle the size and the quality of the individual's home range.
226 Preliminary observations with fixed radio tracking stations showed that fish detected at a given point
for several consecutive days could wander up to 500 m around this point overnight. Hence we
228 extended the computation of the productive surface 500 m upstream and 500 m downstream from
the boundaries of the 50% kernel home range. To test whether the habitat quality in an individual's
230 home range was positively linked to its date of settlement (Prediction 5), we had to estimate a date
of settlement. This was done by recording the first day, within its spawning period, on which the
232 individual was localized at the central point of its UD50.

Mating success and reproductive success

234 The tests of predictions 1 to 4 imply the quantification of individual mating success and reproductive
success. Several indicators of mating and reproductive success were estimated: number of
236 individuals of the other sex encountered during the spawning season, number of redds visited (for
males only), number of genetic mates, i.e. number of individuals with whom at least one offspring
238 was produced according to parentage analysis based on genetic markers, and total number of
offspring.

240 An encounter between a male and a female was recorded either when the position of the two
individuals on two consecutive days indicated that their trajectories crossed each other, or when the
242 two individuals were localized less than 500 m from each other on a given day. This criterion of 500m
was chosen based on preliminary radio tracking at fine scale showing that males located up to 500m
244 from a redd during the day could spawn on it at night (E. Beall, personal communication).

For a male, encountering a female during the spawning season does not imply that the female is
246 sexually active at the exact moment. To get a more precise picture of how many mating

opportunities were offered to each male, we estimated the number of active redds visited by the
248 male. Because the digging date of redds was uncertain, encounter between a male and an active
redd was recorded if the male was found less than 500 m away from the redd at least once on all the
250 days when the redd may have been dug. Since a redd is typically dug in a few hours, our estimate of
encounters between males and active redds was necessarily overestimated.

252 Going further into the mating process, we also inferred the effect of space use on the number of
offspring and the number of mates of each individual. Both components were estimated with
254 parentage analysis, the number of offspring of an individual being the number of juveniles assigned
to it, and the number of mates being the number of individuals with whom the individual's offspring
256 were produced (mating success *sensu* Bateman 1948). The estimation of individual reproductive and
mating success based on genetic parentage analysis was the same as in Tentelier et al. (submitted).
258 Briefly, 0+ fry were electrofished in riffles and rapids situated up to 200 m downstream and 50 m
upstream from each redd, following a one-sweep open site procedure which covered the whole
260 width of the river stretches. Riffles and rapids are the preferred habitats for salmon juveniles until
their first summer (Mäki-Petäys et al. 2002) and their catchability is the same in both habitats. Even if
262 a stretch was in the sampling zone of several redds (because of redd aggregation), it was sampled
only once. In spring 2010, the sampled summed to 27 114 m², to wit 14% of the total surface of the
264 study zone, and 36% of the surface covered by riffles or rapids. In spring 2011 the sampled surface
was 50 089 m², which represented 26% of the total surface and 67% of the riffle/rapid surface. Under
266 anesthesia (benzocaine 30 mg/l), fin clips were collected and stored in 90% ethanol. DNA was
extracted with a NaCl/Chloroform protocol (Gauthey et al. 2015), and amplified in a single multiplex
268 PCR reaction using nine microsatellite loci: SsaD144, SsaD157, SsaD486 (King et al. 2005), Ssa171
(O'Reilly et al. 1996), SsspG7, Ssp1605 (Paterson et al. 2004), Sssp3016 (Gilbey et al. 2004),
270 Ssa405UOS, Ssa421UOS (Cairney et al. 2000). Fragments were typed using STRand (Toonen and
Hughes 2001) and exported to MsatAllele package (Alberto 2009) in R version 2.13.0 (R Development
272 Core Team 2008) to assign peaks to suitable allele bin range. Using Cervus v3.0.7 (Kalinowski et al.

2007), we preliminarily checked that the multilocus non-exclusion probability computed from
274 parental genotypes was sufficiently low to ensure a powerful parentage assignment. This probability,
which corresponds to the probability that a 0+ fry was assigned to candidate parents that were not
276 its actual parents, was $4.57E-4$ for a single parent and $2.65E-9$ for a parent pair, averaged over the
two years. For each year, parentage analysis was then performed using Colony version 2.0 (Wang
278 and Santure 2009; Jones and Wang 2010) to assign the 0+ fry sampled in May to anadromous
parents. The analysis was performed on the complete pool of offspring, irrespectively of their spatial
280 distribution. Hence, if some 0+ had dispersed away from their natal redd and their sibs, they still
could be assigned to their parents. A sample of 0+ and 1+ parr sampled in September 2009 (125
282 individuals) and 2010 (313 individuals) were added as potential fathers, as they could be precocious
males. Their inclusion as potential fathers reduced the number of offspring assigned to unknown
284 fathers, thereby increasing the power of the analysis (Jones et al. 2010). The analysis was run four
times for each year with different seed numbers, using the pairwise-likelihood score (PLS) method,
286 accounting for typing errors, and assuming dioecious and diploid species, female and male polygamy,
no inbreeding, no sibship structure prior and no update of the allele frequency during the run.
288 Offspring assigned to none of the candidate anadromous mates were considered to be sired by
mature parr.

290 *Statistical analysis*

To test the effect of UD50 range and relative productive surface on the indicators of reproductive
292 success (Predictions 1 to 4), we used generalized linear models, the independent variable being UD50
range, UD50 relative productive surface and their interaction with year of sampling. Data from males
294 and females were analyzed in separate models. For the number of other sex individuals encountered
and for the number of redds visited by males, we used a Poisson distribution, with a Log link
296 function. For the number of offspring and number of mates, which included many zeros, we used
zero-inflated models and tested the effect of each independent variable on both the probability of

298 having at least one offspring or mate (binomial distribution with logit link function) and the number
of offspring and the number of mates (Poisson distribution with log link function). This was done with
300 the *zeroinfl* function in *pscl* package for R (Jackman 2015).

To test the effect of individual covariates on the range of UD50 (sex: Prediction 6; male's body size:
302 Prediction 8) and their possible interaction with sampling year, we used a general linear model with
sex, fork length, year and all their interactions as independent variables. To test the effect of
304 individual covariates on the relative productive surface of UD50 (settlement date: Prediction 5;
male's body size: Prediction 7) and the possible interaction with sampling year, we also used a
306 general linear model with settlement date, sex, fork length, year and their interactions as
independent variables. In both cases, the full model was then reduced using a stepwise selection
308 procedure based on Akaike's criterion (stepAIC function in MASS package for R; Venables and Ripley
2002), and the fit of the final model was assessed by visual check of residuals against fitted values.

310 **Results**

Redd distribution (Environmental Potential for Polygyny)

312 Among the 618 stretches characterized in the Nivelle river, 243 were considered suitable for
spawning, i.e. were riffles with pebbles. Between the 10th of December 2009 and the 7th of January
314 2010, 50 redds were found in 20 different stretches (Fig. 1). Between the 29th of November 2010
and the 14th of January 2011, 100 redds were found in 43 stretches. Redds were aggregated in both
316 years, both spatially and temporally. The spatial patchiness was more pronounced in 2009-2010 ($P_s =$
8714) than in 2010-2011 ($P_s = 4791$). The temporal patchiness was slightly lower in 2009-2010 ($P_t =$
318 750 ± 20) than in 2010-2011 ($P_t = 796 \pm 16$). Together, these results indicate that the environmental
potential for polygamy was higher in 2009-2010 than in 2010-2011, with redds being more spatially
320 aggregated and less synchronous.

Taking both years together, the zero-inflated model showed that, within the 243 suitable stretches,
322 the probability of containing at least one redd (the binomial component) increased with the

productive surface of the stretch ($p = 0.003$), indicating that the quality of the local habitat for
324 offspring survival affected females probability to spawn on it. The number of redds in the stretch (the
Poisson component) also tended to increase with productive surface, although not significantly ($p =$
326 0.059).

Individual space use tactics

328 Fifteen female and 17 male anadromous salmon were tracked in 2009-2010, and 45 females and 46
males in 2010-2011. In both years, females entered the study zone before males, and this difference
330 was due to two-sea-winter salmon (spring salmon) being mainly females. Indeed for both years, 17
females out of 60 were two-sea-winter fish, whereas only 2 males out of 63 were two-sea-winter
332 fish. Males' fork length ranged from 533 to 870 mm (mean = 619 mm), and females' fork length
ranged from 520 to 1020 mm (mean = 651 mm). In relation with predictions 6 (wider UD50 for males
334 than for females) and 8 (wider UD50 for smaller males than for larger males), and from the full model
including the effects of sex, year, fork length and all interactions on the range of the UD50, the
336 stepwise model selection based on Akaike criterion retained the model including sex, year and their
interaction. The interactive term was the only significant one ($p = 0.023$), with males having a wider
338 UD50 than females only in 2010-2011 (Fig. 2). For the relative productive surface of UD50, and in
relation with predictions 5 (better habitat for individuals which settled first) and 7 (better habitat for
340 larger males than smaller males), the AIC-based stepwise selection retained a final model including
the date of settlement ($p = 0.336$), sex ($p = 0.028$), year ($p = 0.748$) and their interactions (date * sex,
342 $p = 0.028$; date * year, $p = 0.698$; sex * year, $p = 0.004$; date * sex * year, $p = 0.004$). According to the
parameter values, habitat quality in the UD50 decreased with increasing settlement date only for
344 males in 2009-2010 and females in 2010-2011 (Fig. 3). Fork length affected neither UD50 range nor
its relative productive surface, for neither males nor females. The UD50 range and its relative
346 productive surface were not related to each other (Pearson's $r = -0.024$; $p = 0.792$).

Effects of space use on mating success and reproductive success

348 The estimates and standard error of all parameters in the generalized linear models, as well as their
statistical significance, are given in Table 2. Plots of data and model predictions are shown in Fig. 4
350 for males and Fig. 5 for females. In both years, almost every male and female encountered each
other. Males encountered on average 11 females (SD = 4, min = 0, max = 15) of the 15 females
352 present in the population in 2009-2010, and 35 females (SD = 7, min = 10, max = 43) of 45 present in
2010-2011. Related to prediction 1, the number of females encountered by males increased with
354 both UD50 range and UD50 relative productive surface.

Males visited on average 15 redds (SD = 13, min = 0, max = 34) out of the 50 that were dug during the
356 2009-2010 reproductive season, and 34 (SD = 19, min = 0, max = 80) out of the 100 redds dug in
2010-2011. In relation with prediction 1, the number of active redds visited by males increased with
358 the range of UD50 and its relative productive surface, and the effect was more pronounced in 2009-
2010 than in 2010-2011.

360 A total number of 1677 0+ fry were caught and genotyped in May 2010 and 1350 in May 2011. A
significant proportion of them (56% in 2009-2010, 24% in 2010-2011) were sired by precocious
362 males. Males produced on average 37.5 offspring (SD = 74, min = 0, max = 303) with 1.9 females (SD=
2.1, min = 0, max = 6) in 2009-2010, and 21.9 offspring (SD = 46.6, min = 0, max = 269) with 1.8
364 females (SD = 2.8, min = 0, max = 10) in 2009-2011. Only 50 % of males (10/17 in 2009-2010, 22/46 in
2010-2011) produced at least one offspring. Related to predictions 1, 2 and 3, the probability of
366 producing at least one offspring, and therefore of having at least one mate (binomial component of
the zero-inflated model) was not affected by the UD50 range but increased with the UD50 relative
368 productive surface, whatever the year. Likewise, the number of offspring produced (Poisson
component of the zero-inflated model) was not affected by the UD50 range but increased with the
370 UD50 relative productive surface. The interaction terms indicated that this effect was weaker in
2010-2011 than in 2009-2010. The number of mates with which the offspring were produced was
372 affected by none of the covariates.

Females encountered on average 12 males (min = 8, max = 16) of the 17 males present in the population in 2009-2010 and 35 males (min = 1, max = 45) of 46 present in 2010-2011. Neither UD50 range nor UD50 relative productive surface affected the number of males encountered by females. Females produced on average 103.3 offspring (SD = 124.2) in 2009-2010, and 30 offspring (SD = 57.7) in 2010-2011. Related to prediction 4, the binomial component of the zero-inflated model indicated no effect of any covariate on the probability that females produced at least one offspring. However, the Poisson component indicated that UD50 range had a negative effect on the number of offspring, and the relative productive surface of the UD50 had a positive effect on the number of offspring. The interaction between year and UD50 relative productive surface indicated that the positive effect of UD50 relative productive surface was stronger in 2009-2010 than in 2010-2011. On average, females had 2.2 anadromous mates (SD = 1.7) in 2009-2010 and 1.9 anadromous mates (SD = 2.3) in 2010-2011. Neither UD50 range nor UD50 relative productive surface affected neither the binomial nor the Poisson component of the zero-inflated model on the number of anadromous mates.

Discussion

Environmental potential for polygyny and the effect of space use on reproductive success

The primary aim of this study was to test the effect of individual space use on the reproductive success of anadromous Atlantic salmon, with specific attention to four theoretical predictions related to the ecology of mating systems (Table 1). A central concept of this theory is the Environmental Potential for Polygyny (EPP; Emlen and Oring 1977). According to this theory, the spatial and temporal distribution of sexually active females constrains the capacity of males to monopolize females in harem, thereby shaping the optimal set of male mating tactics (e.g. territoriality, roaming, sneaking) and the resulting mating system. Since active redds were strongly spatially aggregated and slightly synchronous, the EPP was quite high in both years of this study, as it is probably the case for most populations of Atlantic salmon. Hence, we predicted that males securing the best territories should get more mates (Prediction 1), which should translate in more offspring sired in spring

398 (Prediction 2). Our results globally agreed with these predictions as males that had a relatively large
surface of juvenile-favorable habitat in their UD50 encountered more females, visited more active
400 redds, had a higher probability to have at least one genetic mate and had more offspring genetically
assigned in spring. The range of UD50 also had a positive effect on some components of mating
402 success, as males with larger UD50 encountered more females and visited more active redds.
However, this did not translate into more offspring or more genetic mates. This suggests that the
404 relative productive surface of a male's UD50 confers an advantage in sexual selection and/or
offspring survival, whereas UD50 range only increases the opportunity for mating. In the literature,
406 mating success has several definitions and measurements, such as the number of individuals with
which the focal individual copulated or the number of individuals with which the focal individual
408 shared offspring (Dewsbury 2005). These multiple measurements do not always agree, mainly
because of post-copulatory sexual selection (Pischedda and Rice 2012; Péliissié et al. 2014). In our
410 study, we tried to quantify mating success in different ways which did not give exactly the same
results. Our first indicator of mating success was the number of individuals of the other sex that were
412 encountered. Although it is clear that for salmon males, encountering a female is mandatory to mate
with her, encounter does not necessarily translate into actual mating because chance, female mate
414 choice or male-male competition can prevent some males to be close enough to the female when
she lays her eggs. We did not observe spawning acts directly, and the number of active redds visited
416 by males rather estimated the number of opportunities for mating. Comparing encounters with
females and visits to active redds shows that whereas most males encountered most females, males
418 visited on average one third of the redds dug in each season, and there was more variation, with
some males visiting no redd and some males visiting most of them. Going further in the process of
420 fertilization, mating success measured as the number of females with which a male produced
offspring necessarily comprise copulation, as well as sperm competition, which are known to occur in
422 many species, especially in external fertilizers such as salmon (Mjølnørød et al. 1998; Yeates et al.
2007). Indeed, the average number of genetic mates per male was much lower than the number of

424 redds visited, and the proportion of males with no genetic mate at all was higher, as half of the males
had no progeny sampled, hence no mate. However, it must be noted that when estimated through
426 parentage analysis, mating success may also include post-zygotic effects, such as differential survival
of offspring. Hence combining different measures of mating success, possibly in a common modelling
428 framework (Pélissié et al. 2014; Collet et al. 2014) should be fruitful for understanding sexual
selection and mating systems.

430 The EPP was even higher in the 2009-2010 spawning season than in the 2010-2011 season because
active redds were more aggregated spatially and less synchronous, theoretically giving a higher
432 opportunity for males settled in good territories to monopolize active redds, i.e. active females, in
2009-2010 than in 2010-2011. This third prediction was also partially fulfilled, as the positive effect of
434 habitat quality in the UD50 on the number of redds visited and the number of offspring produced
was stronger in 2009-2010 than in 2010-2011. Such interaction indicates that the “bourgeois” tactic
436 adopted by dominant salmon males becomes less rewarding when the EPP decreases. A similar
effect was already observed at the scale of spawning groups (de Gaudemar 1998). For instance, the
438 ability of large coho and sockeye salmon males to monopolize females decreased at higher group
density and operational sex ratio (Fleming and Gross 1994; Quinn et al. 1996). Likewise, small masu
440 salmon males, which are poorer competitors than larger males, had more opportunity to release
sperm when the OSR was high and females spawned synchronously (Yamamoto and Edo 2006). Here,
442 we showed that female aggregation, through EPP, could affect not only the access of males to active
females (indicated by active redds) but also the number of offspring assigned on following spring.
444 This was done at the scale of the whole population, which, when individuals are mobile, is more
comprehensive than observations at the scale of the spawning group. However, replication is more
446 difficult at this scale, and even though it represents a lot of field and laboratory work, our data set
only consists of two years, which could differ by factors other than EPP, such as total salmon
448 numbers or river flow.

In the theory of sexual selection, the number of offspring produced by females is generally expected
450 to be linked more with the quality of their habitat (which conditions offspring survival) than with
their number of mates. This led to our fourth prediction, that the number of offspring produced by
452 females should increase with local habitat quality. In our data, the number of offspring produced by
females, but not the number of males which sired them, indeed increased with the relative
454 productive surface of their UD50, but only in the 2009-2010 spawning season. The difference of
results between years can be viewed through the lens of density-dependent survival of juveniles. On
456 the one hand, the 2009-2010 spawning season was the one with the least spawners and redds.
Hence, at such a low density (50 redds for 22.6 km of river), competition between clutches may seem
458 so low that the females spawning in the better habitat should get more offspring, whereas at higher
density the number of females and redds in the best habitats would increase, levelling reproductive
460 success across habitats of unequal intrinsic quality (Ideal Free Distribution; Fretwell and Lucas 1969).
On the other hand, 2009-2010 was the year when redds were the most aggregated. Given that
462 juvenile survival is more driven by local than by average density (Einum and Nislow 2005; Einum et al.
2008) the advantage of good habitat quality could have faded because of strong redd aggregation,
464 but it was not the case, probably because even with strong aggregation, the absolute number of
redds in the best reaches was still low.

466 *Determinants of space use tactics*

While the primary aim of this study was to test the effect of space use tactics on mating success and
468 reproductive success, it lay on the variability of space use tactics. Because the costs and benefits
associated to different tactics may depend on individual phenotype, we tested four more predictions
470 on the individual determinants of space use (Table 1).

The fifth prediction we tested was that the individuals should settle first in portions of river with the
472 best habitat for juvenile production. This relationship was linked to the ideal free distribution theory
(Fretwell and Lucas 1969), and had already been observed in sockeye salmon, where spawning

474 aggregations are huge compared to our study system (Foote 1990; Hendry et al. 2001). In our data,
the negative effect of settlement date on the habitat quality in individual home range was observed
476 only for males in the first year and for females in the second year. Such an interaction with sex and
year was unexpected. A basic assumption behind our first prediction is competition for space,
478 because without competition all individuals would settle in the best site, whatever their settlement
date. In 2009-2010, the density of fish was lower and redds were more aggregated than in 2010-
480 2011. This suggests that the 15 females were few enough to share the best sites and even late
settlers did not have to go to poor sites. For males, the lack of effect in 2010-2011 is more puzzling.
482 This year was also the one when males had wider UD50 so one hypothesis is that at high density,
males gave up territoriality and all dwelt in an average habitat.

484 The sixth prediction was that males should be more mobile than females. This prediction lay on the
hypothesis that females would maximize their reproductive success through judicious habitat choice,
486 whereas males would maximize theirs by increasing their number of mates, which may require them
to move more. Indeed, such pattern of higher mobility for males than for females during the
488 breeding season is widespread in polygamous animals (Tew and Macdonald 1994; Perry and Garland
2002; Croft et al. 2003; Anderson and Quinn 2007; Glaudas and Rodríguez-Robles 2011). Our results
490 indicate that although males tended to have a wider UD50 than females in both years, it was only
significant in the 2010-2011 spawning season, when fish density was higher and EPP was lower. This
492 interaction with year may be due to the higher density of fish in 2010-2011. If males tended to be
territorial, the higher number of males in 2010-2011 than in 2009-2010 may have saturated the
494 habitat and driven more males to adopt a roaming tactic, although we did not actually observe
discrete tactics such as Sandell and Liberg's (1992) roamers and stayers. If females can take
496 aggregation more easily, which is suggested by the strong aggregation of redds in suitable reaches,
high density would not cause them to spread their home range.

498 The seventh and eighth predictions were that larger males should settle in better territories than
smaller males, and that the latter should be more mobile. These predictions came from the
500 hypothesis that larger males, being superior competitors, should be able to chase smaller males from
good habitat, forcing them to adopt a roaming tactic. Such effect of body size on space use,
502 supposedly via dominance, has been observed in several species, including Atlantic salmon
(Baglinière et al. 1991). However, in our data, male body size influenced neither the range nor the
504 relative productive surface of UD50, for none of the two spawning seasons. This lack of effect may be
due to either no effect of body size on dominance or no effect of dominance on space use as we
506 measured it. In favor of the first option, (Höjesjö et al. 2007) found that dominant brown trout had a
narrower home range and a privileged access to spawning site compared to subordinates, but that
508 dominance rank was independent from body size. Likewise, and in relation to our prediction 1
discussed above, Rich et al. (2006) found that territory ownership was inversely related to mobility,
510 but was more affected by the date of arrival of sockeye salmon males on spawning grounds than by
their body size. Related to the second option is the hypothesis that the exclusion of small
512 subordinate salmon by larger dominant individuals usually observed at the fine scale of a nest (Foote
1990; Mjølnerød et al. 1998) does not necessarily translate in exclusion at a larger scale. This is for
514 instance what Healey & Prince (1998) found on coho salmon, where small satellite males moved
more than large dominants but even smaller sneaker males were as resident as dominant males. In
516 our system, mature parr played the role of sneaker males, but their movement were not recorded.

To summarize, our results on the determinants of space use clearly showed that males moved more
518 than females but failed to find a consistent effect of body size or settlement date on the quality of
the habitat in an individual's home range. Concerning the effects of space use on mating and
520 reproductive success, we globally validated the prediction that male mating success and reproductive
success increase with the quality of habitat in the home range, especially in the year with high EPP.
522 Although working at the scale of the river prevented us from precise observation of the mating
behavior and mating success as it has been done in controlled environments, it allowed us to get new

524 insights about the interplay between space use and environmental factors affecting the mating
system of Atlantic salmon.

526

Acknowledgements

528 We thank all the Ecobiop staff for the electrofishing sessions, Kévin Picoulet for his contribution to
the laboratory work, and the Nivelles Fishermen's association for the authorization to work in the
530 Nivelles. This work was funded by European Commission through the Interreg program on Atlantic
Aquatic Resource Conservation, by the French Office National de l'Eau et des Milieux Aquatiques, and
532 by the Conseil Général des Pyrénées Atlantiques. The research done in this study meets the ethical
guidelines, including adherence to French legal requirements. The authors declare they have no
534 conflict of interest.

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- 720

722 **Table 1.** The eight predictions tested in this study, and the corresponding experimental results. The first four predictions relate to the determinants of space use, while the last four relate to the effects of space use on reproductive success.

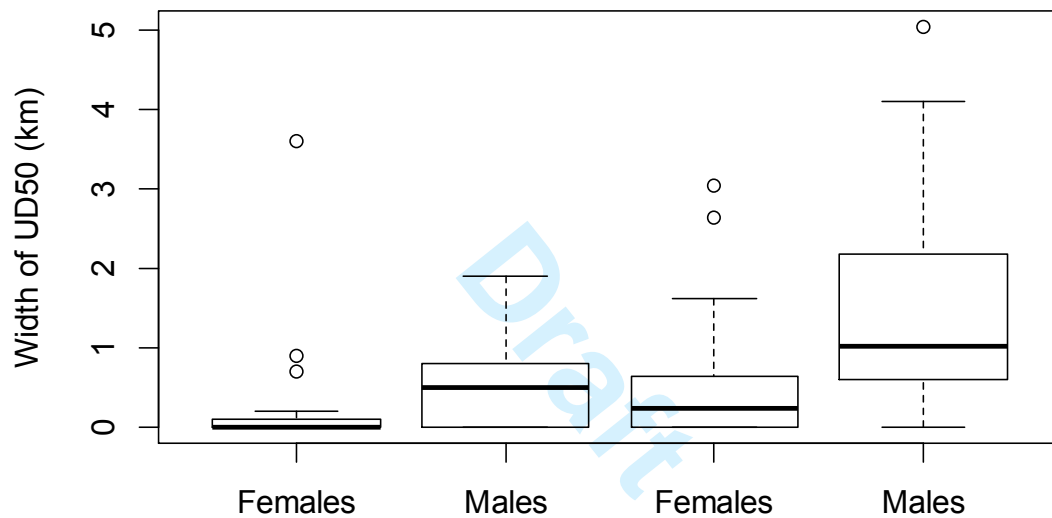
Prediction	Result
1. Males with better habitat in their home range get more mates	Males with broader UD50 and more productive surface on their UD50 encountered more females, visited more active redds but did not have more genetic mates.
2. Males with better habitat in their home range get more offspring	Males with more productive surface on their UD50 had more offspring assigned in May.
3. Positive effect of habitat quality on males' mating success and reproductive success is stronger when sexually active females are clumped and asynchronous	The positive effect of UD50 productive surface on number of offspring was stronger in 2009-2010, when active redds were more aggregated and less synchronous.
4. Females with better habitat in their home range get more offspring Females with relatively more productive surface on their UD50 had more offspring assigned in May.	Females with more productive surface on their UD50 had more offspring assigned in May.
5. Better sites are colonized first.	Earlier settlement was associated to more productive habitat for juveniles in an individual's UD50 only in 2009-2010 for males and in 2010-2011 for females.
6. Females are less mobile than males.	Males had broader UD50 than females only in 2009-2010.
7. Larger males have better habitat in their home range than smaller males.	Male size did not affect productive surface on UD50.
8. Smaller males are more mobile than larger males.	Male size did not affect UD50 range.

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726 **Table 2.** Parameters associated to the range of UD50, relative productive surface of UD50, year and their interactions in the generalized linear models fitted
 on the number of individuals encountered (Poisson distribution), the number of redds visited (Poisson distribution), the number of mates according to the
 728 parentage analysis and the number of offspring (zero-inflated models with Binomial and Poisson distributions). The coefficients are given as partial r
 (Nakagawa and Cuthill 2007). Figures in bold are statistically different from zero, asterisks indicate levels of significance (*p < 0.05, ***p < 0.001). Hyphen
 730 indicates that the associated independent variable was not kept in the AIC-based selection procedure.

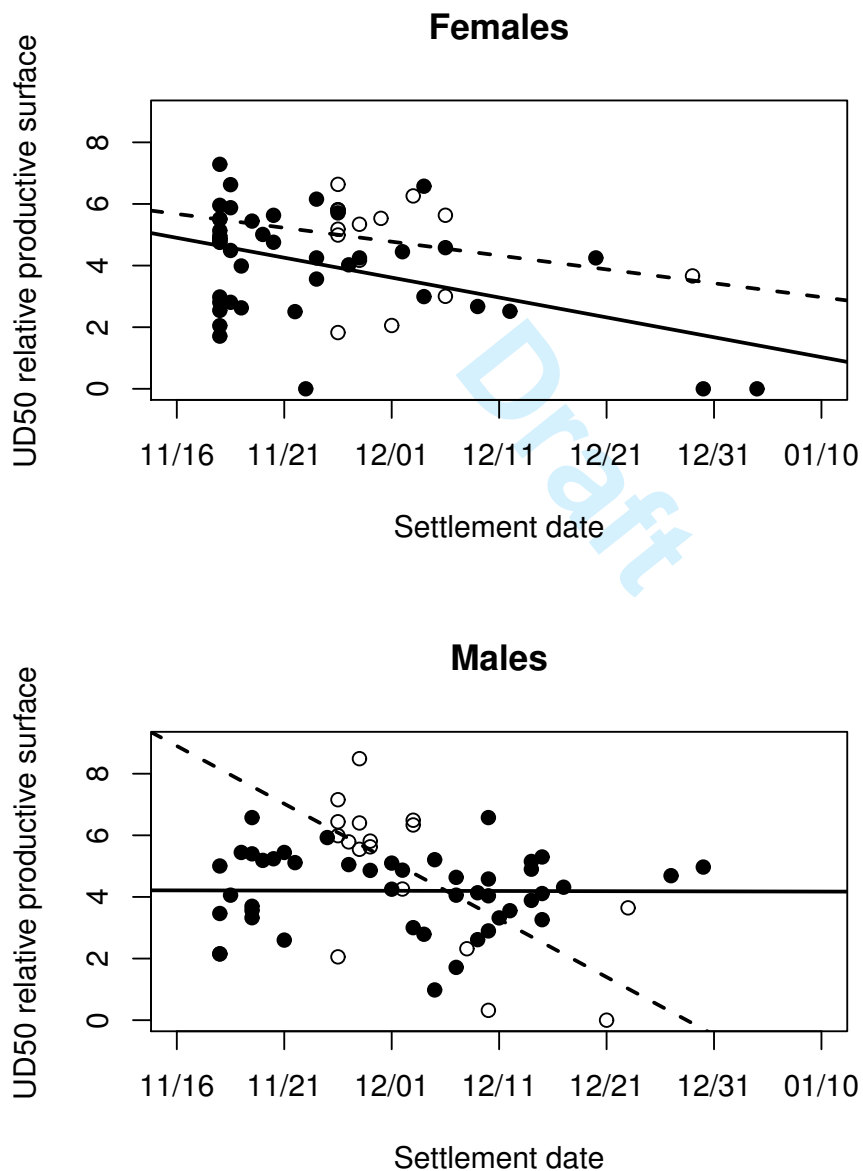
Dependent variable	Independent variables: effect size (Nakagawa & Cuthill, 2007)				
	UD50 range	UD50 relative productive surface	Year	Range x year	Productive surface x year
Number of other-sex individuals encountered					
Males	0.25*	0.283*	0.646***	-0.202	-0.213
Females	-0.13	0.086	0.305*	0.235	0.199
Number of redds visited by males	0.755***	0.719***	0.687***	-0.703***	-0.435***
Number of genetic mates					
Males					
Binomial process	-0.208	0.304*	-0.086	0.186	-
Poisson process	0.128	0.002	0.194	-0.188	-
Females					
Binomial process	-0.022	-	-0.013	0.023	-
Poisson process	0.213	-	0.248	-0.221	-
Number of offspring					
Males					
Binomial process	-0.2	0.218	-0.048	0.18	0.005
Poisson process	0.863	0.559***	0.552***	-0.894***	-0.436***
Females					
Binomial process	-0.113	-0.008	-0.061	-	-0.009
Poisson process	-0.848***	0.947***	0.882***	-	-0.93***

Figure 2. Range of UD50 (shortest portion of river comprising 50% of an individual's daily position during the spawning season) for both male and female Atlantic salmon in the 2009-2010 and 2010-2011 spawning seasons. Different letters above boxes indicate significant differences according to the final linear model following stepwise selection based on Akaike's Information Criterion, and starting from a full model including sex, year, fork length, date of settlement, and their interactions.



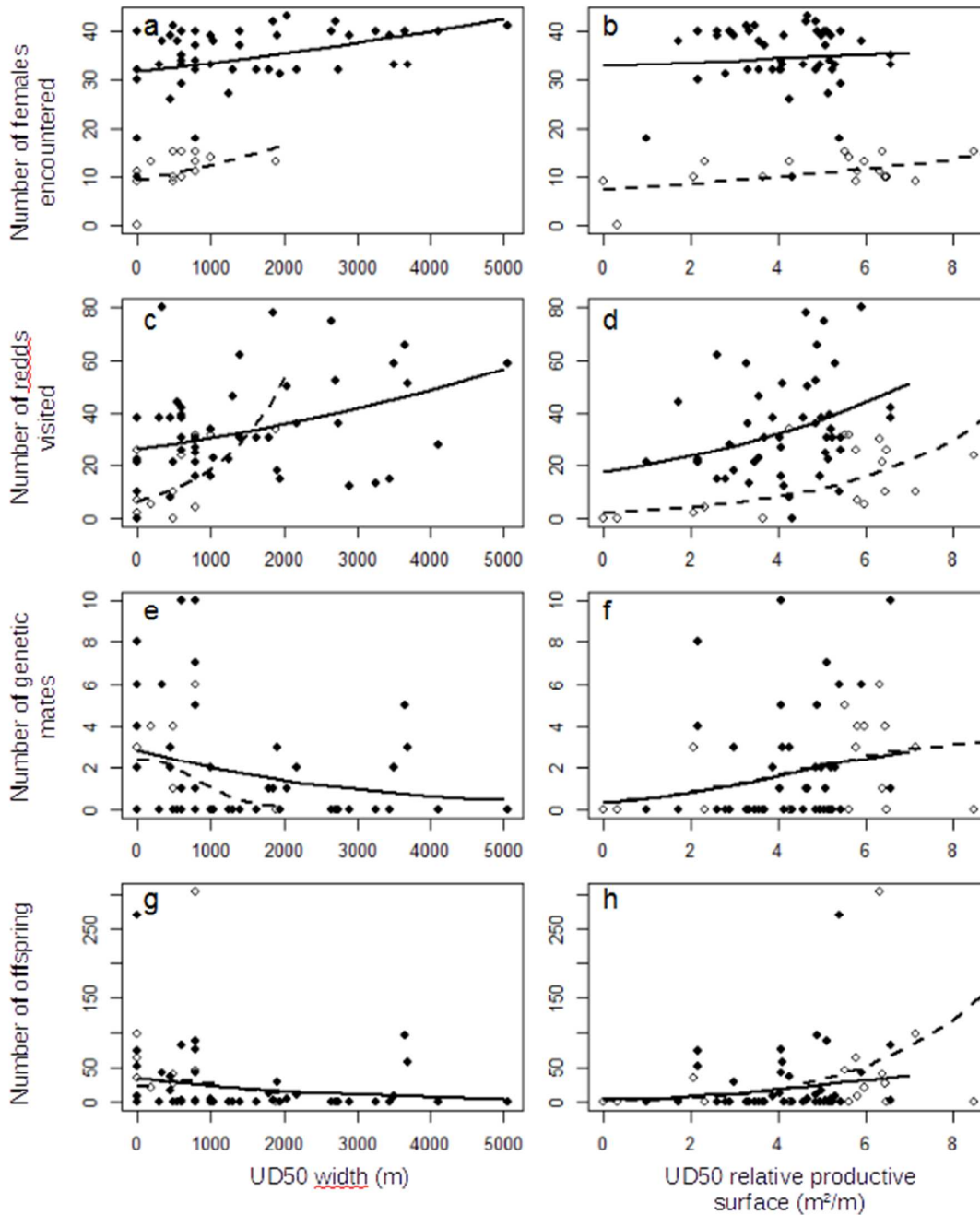
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744 **Figure 3.** Relative parr productive surface within UD50 of female and male Atlantic salmon, as a
746 function of date of settlement in the UD50, for the 2009-2010 (open circles, dashed lines) and 2010-
2011 (filled circles, solid lines) spawning seasons. Lines represent the predictions of the final linear
748 model following stepwise selection based on Akaike's Information Criterion, and starting from a full
model including sex, year, fork length, date of settlement, and their interactions.



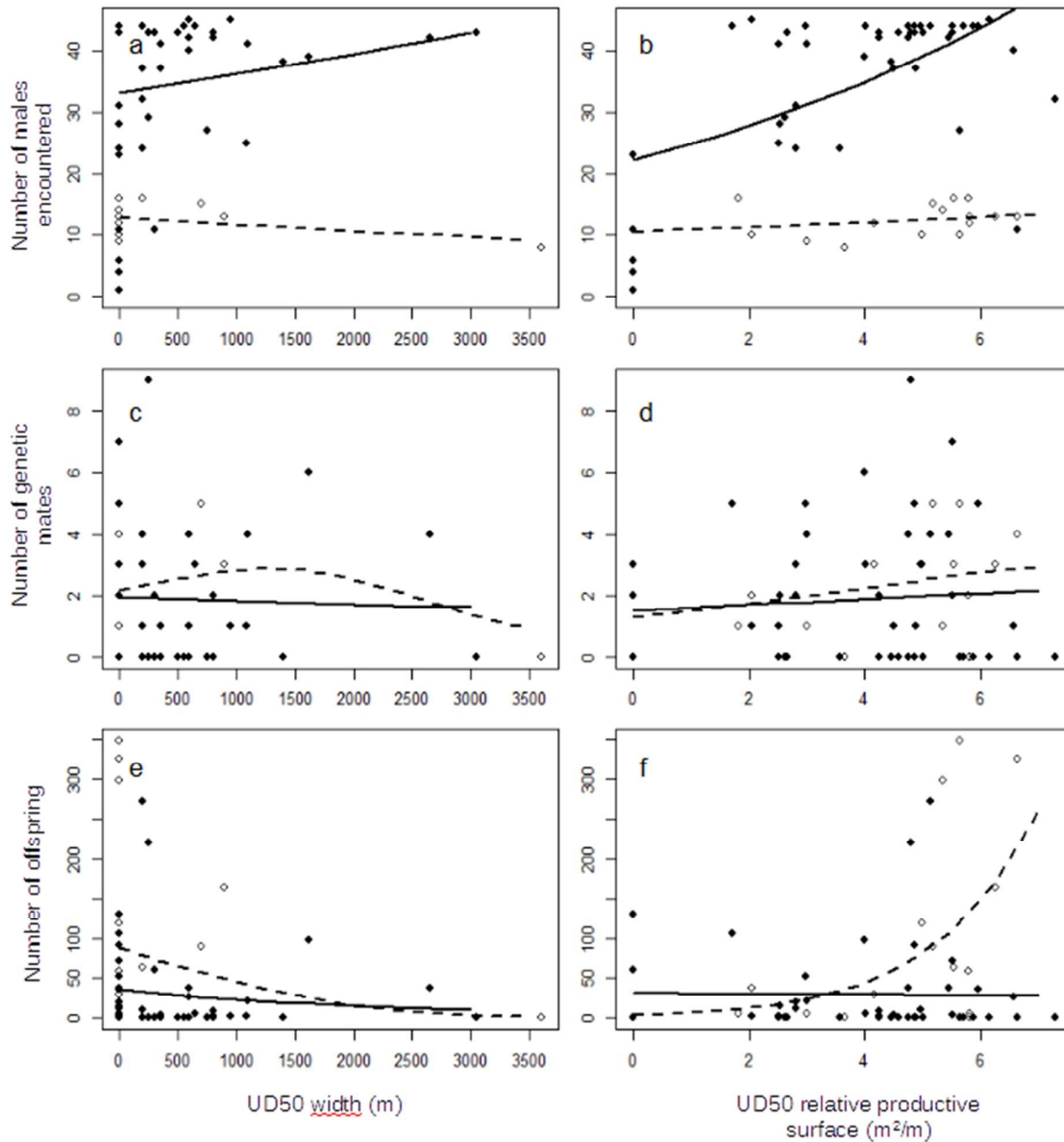
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Figure 4. Effects of UD50 range (a, c, e, g) and relative productive surface (b, d, f, h) on the number of females encountered by males (a, b), the number of redds they visited (c, d), their number of genetic mates (e, f) and their number of offspring (g, h). White and black dots represent data from the 2009-2010 and 2010-2011 spawning seasons, respectively. Dashed and solid lines represent predictions of the statistical models for the 2009-2010 and 2010-2011 spawning seasons, respectively.



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Figure 5. Effects of UD50 range (a, c, e) and relative productive surface (b, d, f) on the number of
 758 males encountered by females (a, b), their number of genetic anadromous mates (c, d) and their
 760 number of offspring (e, f). White and black dots represent data from the 2009-2010 and 2010-2011
 spawning seasons, respectively. Dashed and solid lines represent predictions of the statistical models
 for the 2009-2010 and 2010-2011 spawning seasons, respectively.



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