

Habitat selection by juvenile Atlantic salmon: the interaction between physical habitat and abundance

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The effect of physical river habitat variables on the distribution of juvenile Atlantic salmon *Salmo salar* L. in the Rivière de la Trinité, Québec, Canada, was examined using generalized additive modelling. A survey of Atlantic salmon fry and parr densities and habitat variables (flow velocity, water column depth and substratum size) was conducted in the summer months from 1984 to 1992. Clear patterns of habitat use existed: specific ranges of habitat variables were selected, with parr preferring greater velocities, depths and substratum sizes than fry. There was a large variation, however, in juvenile densities for given velocities, depths or substratum sizes, with this variation being greatest in optimal habitats. On examination of an individual year, interaction between the variables was found to explain some of the variation. On a year-to-year basis the juvenile Atlantic salmon population was found to exhibit an 'Ideal Free Distribution', which resulted in greatest variation in optimal habitats with year-to-year changes in population abundance.

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Key words: generalized additive modelling; habitat selection; juvenile Atlantic salmon.

INTRODUCTION

In analysing spatio-temporal distributions of juvenile Atlantic salmon *Salmo salar* L. within rivers, it is necessary to distinguish between habitat preference, which is based on the requirements of the fish, and habitat utilization, which is a compromise between the innate requirements and how these can be met by availability within the habitat (Johnson, 1980). Distributions that are determined from *in-situ* surveys may differ to the distributions that would be expected from the preferences of the Atlantic salmon population (the entire population will not be found in patches of optimal habitat, high densities may be found in patches of sub-optimal habitat, or low densities may be found in patches of optimal

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habitat). Indeed, relationships between densities and habitat are often weak, exhibiting a large variation in density for a given habitat type (Terrell *et al.*, 1996). The majority of research on relationships between fish densities and physical habitat variables, *e.g.* through the construction of preference curves (Baker & Coon, 1997; Gries & Juanes, 1998; Lamouroux *et al.*, 1999), has focussed on the shape of the relationship, and paid less attention to the relationship's strength or the relationship's consistency from year to year. For example, there is often just a statistical test to see if the relationship is significant, and the spread of densities for a given habitat characteristic is ignored.

Railsback *et al.* (2003) has suggested a variety of causes for the weakness of the relationship between habitat density and habitat quality, including: (1) unused habitat resulting from low population abundance, (2) individual fish variability, (3) the discontinuous nature of the habitat and (4), limited habitat knowledge. Firstly, unused habitat may occur if abundance is low: if adults have not spawned enough juveniles, some patches of optimal habitat may remain unoccupied (Tyre *et al.*, 2001). Secondly, different individuals will prefer different habitats (in the same way that fry prefer different habitats to parr), which may add variability to the relationship between densities and habitat. Thirdly, the physical properties of the habitat often have discontinuous boundaries rather than smooth gradients. If the optimal habitat is occupied, less competitive members of the population may be forced into neighbouring sub-optimal habitat regardless of the relative difference in quality (whether there is a slight or a great difference). Thus, relatively high densities may be found in very poor habitat. Finally, individuals lack knowledge of the entire river habitat, may be unaware of patches of optimal habitat, and may remain in patches of sub-optimal habitat.

Patterns of habitat utilization become even more complex in the temporal domain if there is variation in population abundance because this variation may affect intraspecific competition for habitat resources. The response of habitat utilization to a change in abundance is often described by one of two distribution models: (1), the 'Ideal Free Distribution' (IFD), where the distribution of the population remains constant with a change in mean abundance (Fretwell & Lucas, 1970) and (2), the 'Ideal Despotic Distribution' (IDD) (Fretwell, 1972), where an increase in abundance causes increased utilization of sub-optimal habitat. Bult *et al.* (1999) found the IDD to be appropriate for describing habitat utilization by juvenile Atlantic salmon in an experimental riverine enclosure, and it was inferred that this was because juvenile Atlantic salmon are territorial. Territoriality has been established by several authors (Grant & Kramer, 1990; Cutts *et al.*, 1999; Valdimarsson & Metcalfe, 2001): individuals defend specific patches, the size of which is related to the size of the individual (Table I). With an increase in abundance, there is an increased probability of territorial conflict, and less competitive individuals may be forced into sub-optimal habitat, with the optimal habitat being dominated by the dominant individuals.

In this study, the relationships between distributions of juvenile Atlantic salmon and physical habitat variables were examined using a spatially comprehensive and multi-temporal dataset of the Rivière de la Trinité, Québec, Canada. Firstly, for one of the years the juvenile densities and habitat variables were examined, focussing on the shapes of the relationships, their relative strengths and the importance of interaction between different variables. Secondly, the study was extended into the

TABLE I. Territorial area of juvenile Atlantic salmon

Conditions	Territory area (m ²)	L_F (mm)	Source
Field	1.633	130	Stradmeyer & Thorpe (1987)
Field	0.970	100	Stradmeyer & Thorpe (1987)
Stream tank	1.136	114	Symons, 1971
Stream tank	1.120	118	Symons, 1971
Field	0.55 ¹	64 ¹	Keeley & Grant (1995)
	0.02–7.46 ²	29–145 ²	
Stream tank	0.5	55	Cutts <i>et al.</i> (1999)
Stream tank	0.030	45	Kalleberg (1958)
Stream tank	0.011	25	Kalleberg (1958)

¹Mean.

²Range.

L_F , fork length.

temporal domain, and the temporal consistency of these relationships examined, with a particular emphasis on the effect of changes in abundance on habitat use.

MATERIALS AND METHODS

The Rivière de la Trinité (Trinité) is situated on the north shore of the St Lawrence River estuary (Fig. 1) (Caron *et al.*, 1999). From its source at Lake Washamahwun, it flows through a coniferous forest, firstly southward and then south-eastwards for a distance of *c.* 60 km over a Precambrian granite massif. The 'along-river' profile is fragmented into a variety of different link features, including basins, channels, meanders, steps and rapids. Dominant substratum varies according to the flow profile: rocks and stones dominate areas of fast-flowing running water, and sand and gravels dominate areas of slower running waters. The river is noteworthy for its Atlantic salmon runs but a variety of other fish species also occur. Atlantic salmon dominate the fish biomass but brook trout *Salvelinus fontinalis* (Mitchill) (Guay *et al.*, 2000; Mookerji *et al.*, 2004) and American eel *Anguilla rostrata* (Lesueur) (Jessop, 1998) are found in low densities.

A survey of juvenile Atlantic salmon densities was conducted during the summer of each year from 1984 to 1992. Densities of both fry and parr were estimated by electrofishing at 53 stations throughout the length of the Trinité (Fig. 1). Station locations remained fixed throughout the sample period, with locations being chosen to encompass the range of habitat characteristics that were present in the river. At each station, three sample sites of dimensions 20 m in length along the river course and 5 m in width across the river course were selected. Sample sites were chosen to represent the average habitat characteristics of each station, with the caveat that it was necessary for the water column depth to be < *c.* 1 m for the electrofishing to work correctly. Single-pass electrofishing was used for the bulk of measurements to reduce sampling effort. Given that single-pass electrofishing may provide inaccurate estimates, generally underestimating fish densities (Meador, 2003), a three-pass electrofishing survey was conducted in a subset of stations (station positions changing yearly, with an average of 12 sample sites per year) using a block net that encompassed the electrofished sample site. Sampling efficiency and densities in these enclosed sample sites were estimated by a maximum likelihood method (Junge & Libosvsky, 1965; Seber, 1982), and a correction factor was applied to the single-pass data (Caron & Ouellet, 1987; Jones & Stockwell, 1995). From a sub-sample of the juvenile Atlantic salmon, ages were determined from fish scales, and fork lengths (L_F) were measured. Thus it was possible to determine mean L_F at age.

The physical habitat variables of the sample sites were surveyed concurrently with the electrofishing. Measured river habitat variables were mean water column velocity, mean

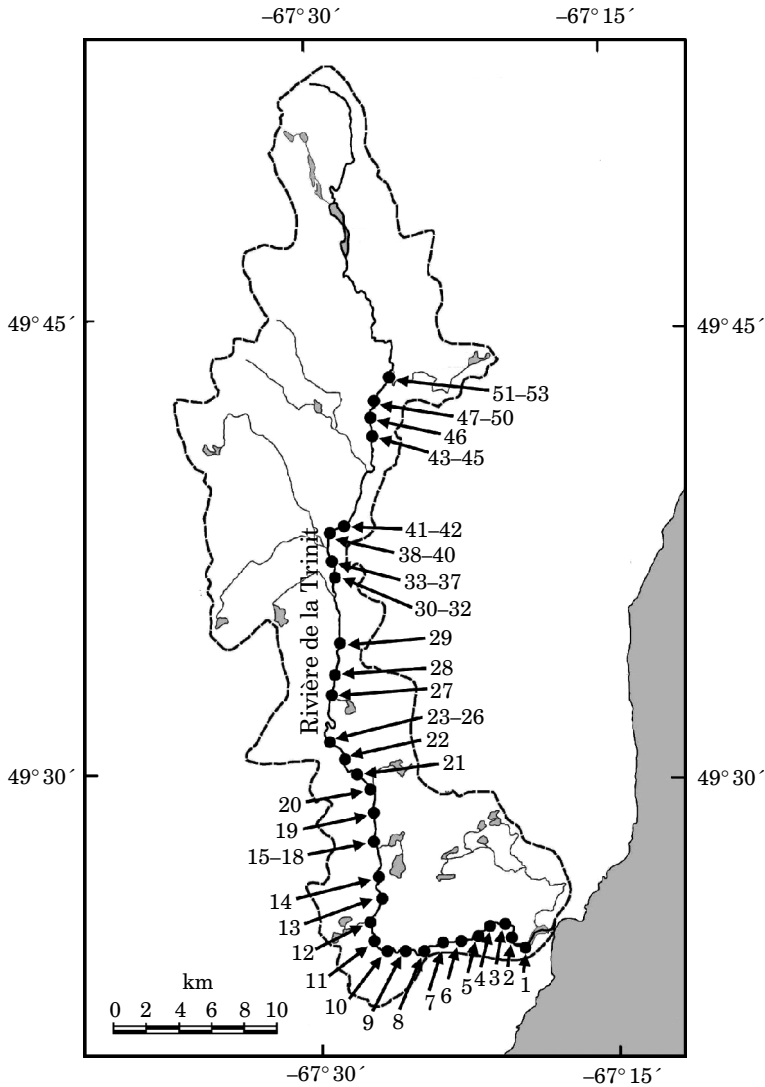


FIG. 1. Study area: the Grande Rivière de la Trinité, Québec, Canada. Station positions are shown along the length of the Trinité.

depth and the proportional substratum composition. Depth and proportional substratum composition were measured in all years; velocity was measured from 1986 to 1990. Velocity was measured to a precision of 0.05 m s^{-1} at a depth of 0.4 m above the bed. Three to 10 measurements were made in each sample site, depending on the velocity variation in the first three measurements (the greater the variation, the greater the number of measurements). Depth was estimated to a precision of 0.05 m using a graduated pole. Five measurements were made in sample sites where the bed elevation was relatively flat, with up to 15 measurements made in sample sites where there was greater variation in bed elevation. Proportional substratum composition was estimated visually by two observers walking along the length of each sample site. When the two independent estimates agreed to within $\pm 5\%$, a consensual estimate was achieved. When the two independent estimates were greater than this, the two observers walked the length

of the sample site again until a new consensual estimate was achieved. Substratum types were then classified according to the scale of Boudreault (1984) into granulometric classes according to size. Granulometric class 1 consisted of sand (<5 mm), class 2 consisted of gravel (5–40 mm), class 3 consisted of pebbles (40–80 mm), class 4 consisted of cobbles (80–250 mm) and class 5 consisted of boulders (250–500 mm). Proportional substratum composition was estimated visually to the nearest 5%, and then combined into a granulometric index as follows: $G_i = \Sigma(G_c G_u)$, where G_i is the granulometric index, G_c is the granulometric class and G_u is the proportion of the substratum composed of that class.

Relationships between densities of juvenile Atlantic salmon and physical habitat variables were determined by generalized additive models (GAMs). GAMs are a type of non-parametric regression (Hastie & Tibshirani, 1990; Venables & Ripley, 1997) which use non-parametric smoothing terms such as splines and lowess filters to identify relationships between predictor (independent) and response (dependent) variables. The general form of a GAM is: $E[y] = g^{-1}(\beta_0 + \Sigma S_k(x_k))$, where $E[y]$ is the expected value of the response variable y (in this study, the density of fry or parr), $g()$ is the link function defining the relationship between the response and the additive predictor, β_0 is the intercept term, S_k is the smooth function of the k predictors and x_k is the value of the k th predictor. GAMs have several advantages for modelling the type of data associated with fish populations and physical habitats. Firstly, it is not necessary for the distribution of the response variable to be homoscedastic. Secondly, there is no assumption of normality for the predictor and response variables. Thirdly, non-linear relationships between the predictor and response variables are permitted. Because of their applicability, GAMs have been used to study habitat preferences of fishes by numerous authors (Knapp & Preisler, 1999; Fox *et al.*, 2000; Maravelias *et al.*, 2000; Stoner *et al.*, 2001; Kupschus, 2003). The relative importance of the predictor variables may be determined by the Akaike information criteria (Boyce *et al.*, 2002).

Analysis followed a two-stage procedure. Firstly, relationships between juvenile densities and physical habitat variables were determined for an individual year (1989 was chosen because it had the largest sample size). This enabled the identification of relationships that were not influenced by inter-year variation in abundance. Secondly, the analysis was extended into the temporal dimension, using data from all the other years, enabling relationships under conditions of changing abundance to be identified. In all cases, analyses for fry were kept separate from analyses for parr.

GAMs were fitted firstly between densities and individual physical habitat variables separately. Splines with 3 d.f. were used as smoothing terms as they identified the non-linear relationship between juvenile Atlantic salmon densities and the physical habitat variables without over-fitting the model to the data. Optimal habitats were identified as being those where juvenile densities for a given value of a habitat variable, predicted by the GAMs, was greater than the juvenile densities that would have occurred if the distribution of the juveniles was equal to that of the habitat variable (that is, if there was no relationship between juvenile densities and the habitat variable). A χ^2 analysis was then used to determine if whether under- or over-estimates of a GAM fitted between juvenile densities and a specific habitat variable were related to whether the sections involved had optimal or sub-optimal characteristics of the other habitat variables. It would be expected, for example, that a GAM fitted between juvenile densities and G_i would over-estimate in sections where velocity and depth were sub-optimal because their sub-optimality would cause a decrease in observed juvenile densities. GAM surfaces were then fitted between juvenile densities and joint-combinations of physical habitat variables, enabling a more complete determination of the interaction between physical habitat variables in determining juvenile habitat use. Lowess smoothing terms were used because of the difficulty of fitting splines in more than one dimension. Despite the use of lowess terms, which may allow for relatively sharp changes in gradient in the relationship between predictor and response variables, negative values of the response variable (juvenile density in this study) may be predicted if values of the predictor variables are near-to or outside the periphery of the data. For example, if most observations of velocity range from 0 to 0.5 m s⁻¹, prediction of juvenile density at a velocity of 1 m s⁻¹ may be negative if there is a strong decline in juvenile density between 0 and 0.5 m s⁻¹.

This problem may be more acute if a GAM is fitted to a combination of predictor variables where data on all combinations are not available. Habitat combinations leading to estimates of negative juvenile densities were noted and excluded from further analysis.

GAMs were then fitted to all other years individually, and to all years together, to determine the temporal consistency of the relative strength of the individual physical habitat variables in affecting habitat utilization. The effect of a change in abundance (abundance being defined here as the mean population density of the sample for any given year) on habitat selection was determined by comparing the observed spatio-temporal distribution of the juveniles with generated spatio-temporal distributions of populations that were distributed according to the IFD based on the proportional density model described by Hilborn & Walters (1992) and Shepherd & Litvak (2004). Each IFD population predicted fry or parr density as a function of a single habitat variable and abundance. Each IFD population was simulated by firstly determining the abundance for each year. For the year with the minimum abundance, the mean density of each particular value of the habitat variable was estimated. Then, for each particular value of the habitat variable in every other year, a mean density was estimated by the product of (1) the mean density of the respective value of the habitat variable in the year of minimum abundance and (2) the ratio of abundances of the years: $\bar{D}_{y,p} = \bar{D}_{mi,p}(A_y A_{mi}^{-1})$, where A_{mi} is the abundance of the year with minimum abundance, and A_y is the abundance of the year, y , for which the densities are to be estimated, $\bar{D}_{mi,p}$ is the mean juvenile density for the value, p , of the habitat variable in the year of minimum abundance, and $\bar{D}_{y,p}$ is the mean density that is to be estimated. IFD populations were estimated for depth and G_i , but were not estimated for velocity because: (1), preliminary analysis showed a weak relationship between juvenile density and velocity, and consequently, IFD populations based on velocity were of dubious quality, and (2), the temporal extent of the data for velocity was less than for depth and G_i . GAMs were then fitted to joint combinations of individual physical habitat variables and yearly abundances for both the observed population and the simulated IFD population. Lowess smoothing terms were used.

RESULTS

SINGLE-PASS AND THREE-PASS DENSITY ESTIMATES

There was generally a strong linear relationship between single and three-pass estimates of fry density. Depending upon the year, estimates from single-pass electrofishing explained between 67 and 96% of the variation in fry density estimated from three-pass electrofishing, and in only 1 year did single-pass electrofishing explain <80% of the variation. Relationships were weaker for parr, with, depending upon the year, single-pass electrofishing explaining between 28 and 88% of the variation in parr density estimated from three-pass electrofishing. In cases where the amount of variation explained was least, however, the bulk of the unexplained variation was caused by an outlying residual, removal of which provided a stronger relationship between the estimates from single- and three-pass electrofishing (single-pass electrofishing estimates explained between 34 and 92% of those of three-pass electrofishing, and only explained <80% in 2 years). Examination of these outliers showed that they occurred when an equal or greater number of juveniles were caught in the third pass than in the second pass, and this may be a limitation of the algorithm used to estimate densities by three-pass electrofishing. Regardless of the ability of the single-pass electrofishing to represent the variation in density shown by the three-pass electrofishing, comparison of single- and three-pass electrofishing estimates showed that single-pass underestimated density (a catch probability

of 0.55 for fry and 0.59 for parr), thus substantiating the need for calibration of the single-pass estimates.

HABITAT SELECTION IN 1989

The relationships between juvenile density and the physical habitat variables for 1989 are shown in Fig. 2. For both fry and parr, GAM relationships between densities and physical habitat variables approximated a Gaussian form. The greatest differences between the relationships of fry and those of parr were in the skew of the distributions. Parr distributions were more positively skewed than fry distributions: that is, the optimal habitats and maximum values occurred at greater values of the habitat variables for parr. Optimal ranges and maximum values for fry were: velocity, 0.04–0.43 m s⁻¹ (maximum of 0.21 m s⁻¹), depth, 0–0.53 m (maximum of 0.30 m) and G_i , 2.1–4 (maximum of 3.05). Optimal ranges and maxima values for parr were: velocity, 0.14–0.79 m s⁻¹ (maximum of 0.53 m s⁻¹), depth, 0.2–0.65 m (maximum of 0.45 m) and G_i , 3–5 (maximum of 4.25).

Variation in observed density around the GAM-predicted density often increased as a positive function of the predicted density. For example, there was little variation in observed parr density at low G_i values where the GAM predicted low parr density, but there was a large variation in observed parr density at high G_i values where the GAM predicted high density. Depth was the most significant variable for fry, and G_i was the most significant variable for parr (Table II). The removal of velocity from the GAM for fry or the removal of depth from the GAM for parr did not cause a statistically significant decrease in the strength of the fit. Under- or over-prediction by the GAM was related to whether the section had optimal or sub-optimal ranges of the other variables. The relationship between under- or over-prediction of the velocity GAM and the presence of optimal or sub-optimal ranges of the other variables was strongly significant (χ^2 , d.f. = 3, $P < 0.001$ for fry; χ^2 , d.f. = 3, $P < 0.001$ for parr): that is, when depth and G_i were optimal, the velocity GAM tended to under-predict, and when depth and G_i were sub-optimal, the velocity GAM tended to over-predict. Relationships between under- or over-prediction and the optimality or sub-optimality of the other variables were weaker for depth (χ^2 , d.f. = 3, $P = 0.049$ for fry; χ^2 , d.f. = 3, $P = 0.031$ for parr) and G_i (χ^2 , d.f. = 3, $P = 0.015$ for fry; χ^2 , d.f. = 3, $P = 0.006$ for parr) but were still significant. The characteristics of the GAM surfaces fitted between juvenile densities and combinations of physical habitat variables (Fig. 3) corroborated the identification of the relative importance of individual habitat variables. For example, for the GAM surface fitted between fry density and velocity and depth, there was more variation in the surface along the depth axis than the velocity axis, so depth was shown to be more important than velocity in determining the habitat utilization of fry. GAM surfaces fitted to joint combinations of variables explained a greater proportion of the variation in juvenile densities than individual variables alone, with the optimal combinations being depth and G_i (explaining 24% of the variation in fry density and 42% of the variation in parr density). When GAMs were fitted between juvenile densities and all three

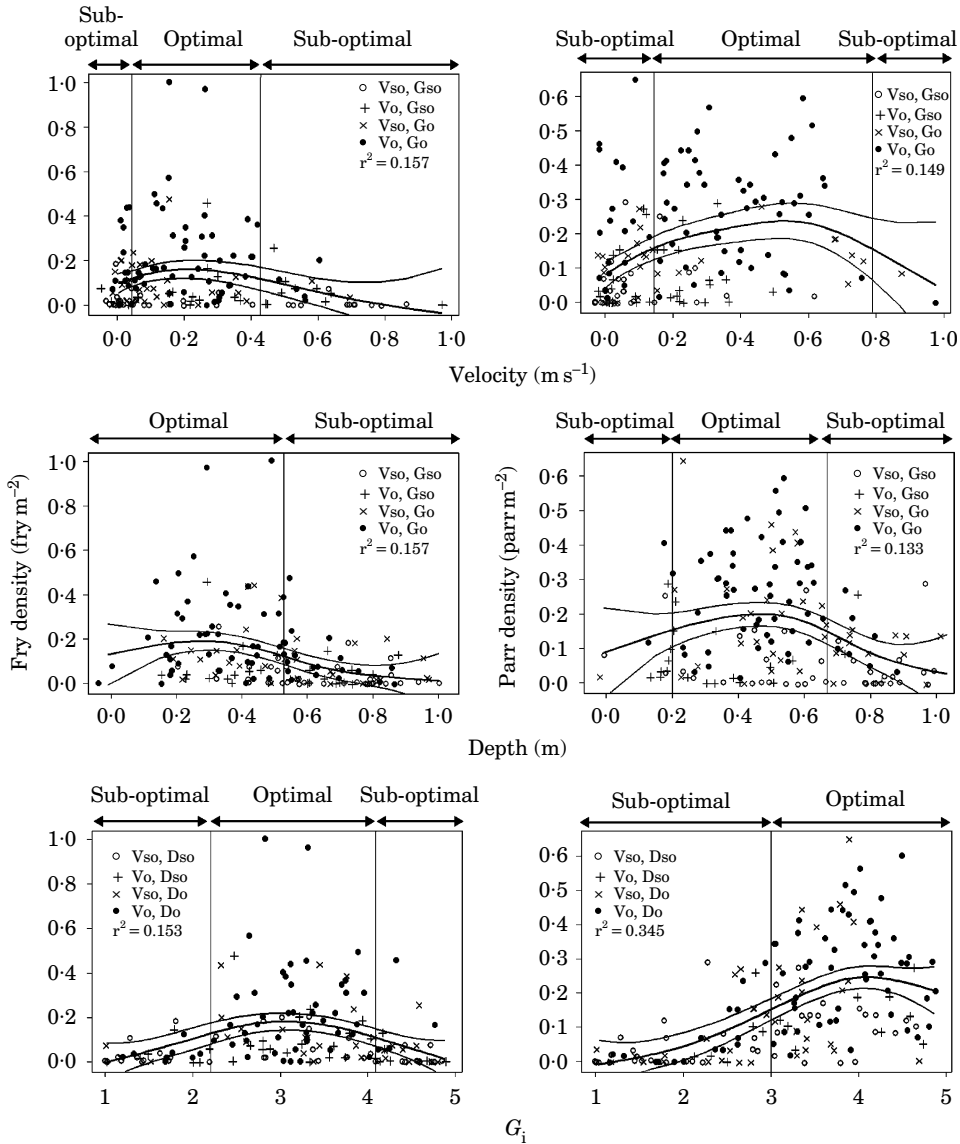


FIG. 2. GAMs showing the relationship between juvenile Atlantic salmon densities and individual physical habitat properties for 1989. Do, occurring in habitat of optimal depth; Dso, occurring in habitat of sub-optimal depth; Vo, occurring in habitat of optimal velocity; Vso, occurring in habitat of sub-optimal velocity; Go, occurring in habitat of optimal granulometric index (G_i); Gso, occurring in habitat of sub-optimal G_i .

habitat variables together, habitat variables explained 28% of the variation in fry density and 47% of the variation in parr density.

INTER-YEAR PATTERNS OF HABITAT SELECTION

Habitat selection by juveniles varied on an inter-year basis (GAMs fitted between juvenile densities and depth and G_i in alternate years are shown in

TABLE II. Analysis of deviance table for the GAMs for juvenile Atlantic salmon density and the physical habitat properties for 1989

	Model	Model		Test		F	Aic	P
		Deviance	d.f.	Deviance	d.f.			
Fry	Full model	4.04	159					
	Null model	2.95	148					
	Full model minus:							
	Depth	3.33	152	0.38	3.0006	6.34	17.34	4.45×10^{-4}
	G_i	3.18	152	0.23	3.0005	3.82	17.19	1.13×10^{-2}
	Velocity	3.06	152	0.10	3.0006	1.69	17.06	1.71×10^{-1}
Parr	Full model	3.54	159					
	Null model	2.01	148					
	Full model - G_i	2.77	152	0.75	3.0005	18.47	16.77	3.04×10^{-10}
	Velocity	2.15	152	0.13	3.0006	3.23	16.15	2.41×10^{-2}
	Depth	2.10	152	0.08	3.0006	2.06	16.11	1.07×10^{-1}

Aic, Akaike information criteria; G_i , granulometric index.

Fig. 4). In most cases, the greatest inter-year variation in juvenile density occurred in the optimal habitat. For example, the inter-year range in mean parr density, as predicted by the GAMs for all individual years, was *c.* 0.5 parr m^{-2} in the optimal G_i for parr (a G_i of 4.25), but only *c.* 0.25 parr m^{-2} in the most sub-optimal habitat (a G_i of 1). The G_i was the most significant physical habitat variable affecting the density of parr in all individual years, whereas the most significant physical habitat variable for fry varied between depth and G_i according to year (Table III). Overall for years 1986–1990, depth was the most significant physical habitat variable affecting the density of fry, followed by G_i and then velocity, and G_i was the most significant physical habitat variable affecting the density of parr, followed by depth and then velocity (Table IV).

Density increased in all habitats with an increase in abundance, but the greatest rate of increase (in absolute terms) occurred in optimal habitats, a pattern of habitat selection corresponding to the IFD (Figs 5 and 6). Correlation between densities that were observed and those that were predicted using the IFD model were statistically significant: fry and depth ($r = 0.88$, t , d.f. = 1276, $P < 0.001$), parr and depth ($r = 0.96$, t , d.f. = 1276, $P < 0.001$), fry and G_i ($r = 0.91$, t , d.f. = 1276, $P = 0.015$) and parr and G_i ($r = 0.96$, t , d.f. = 1276, $P < 0.001$).

DISCUSSION

The habitats favoured by juvenile Atlantic salmon in the Trinité showed the same overall patterns as those identified by other authors (Armstrong *et al.*, 2003; Klemetsen *et al.*, 2003). Depth and substratum size, however, were found to be more important than velocity in determining habitat use, a pattern that conflicts with the findings of DeGraff & Bain (1986) and Morantz *et al.* (1987)

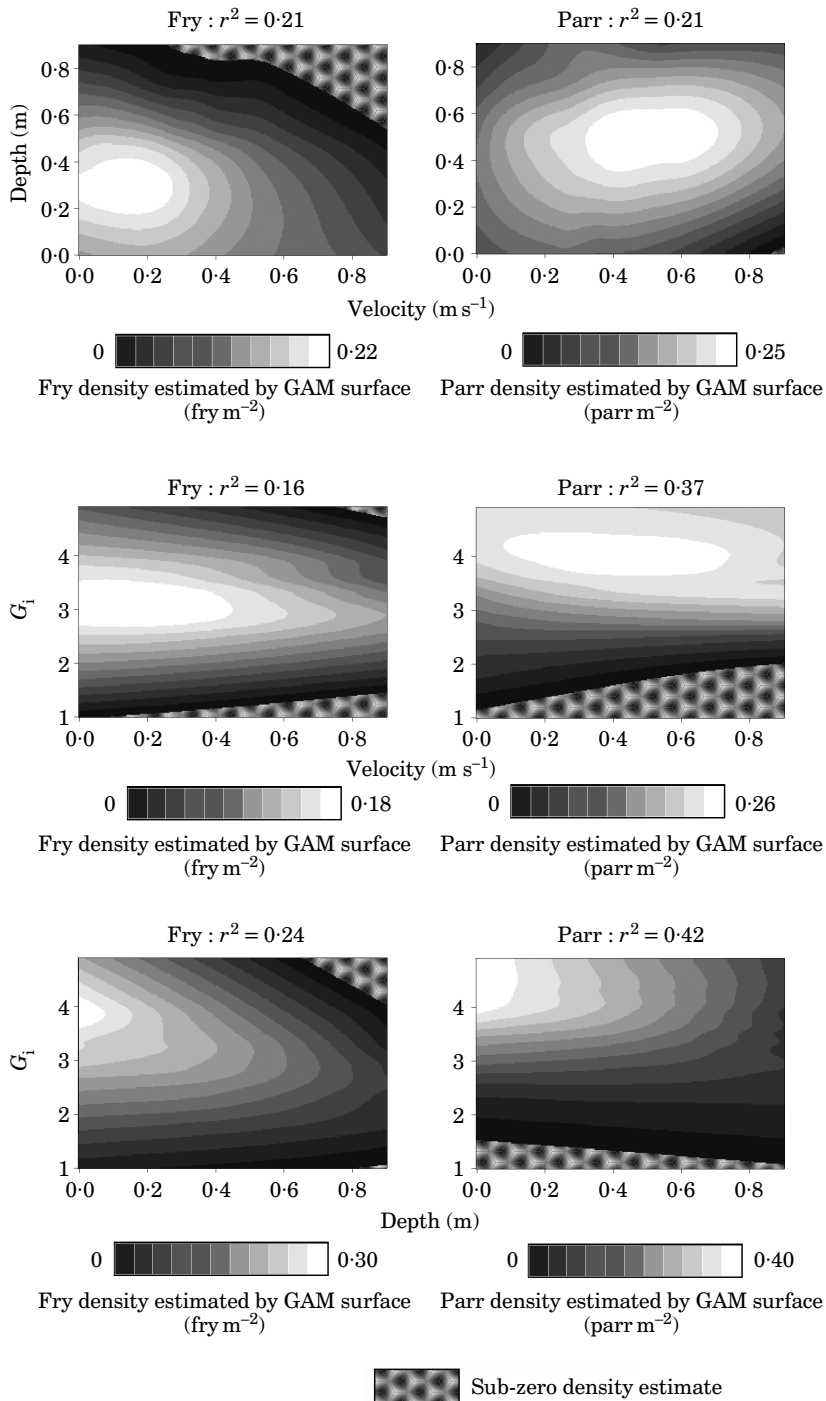


FIG. 3. GAMs showing the relationship between juvenile Atlantic salmon densities and combinations of physical habitat properties for 1989. G_i , granulometric index.

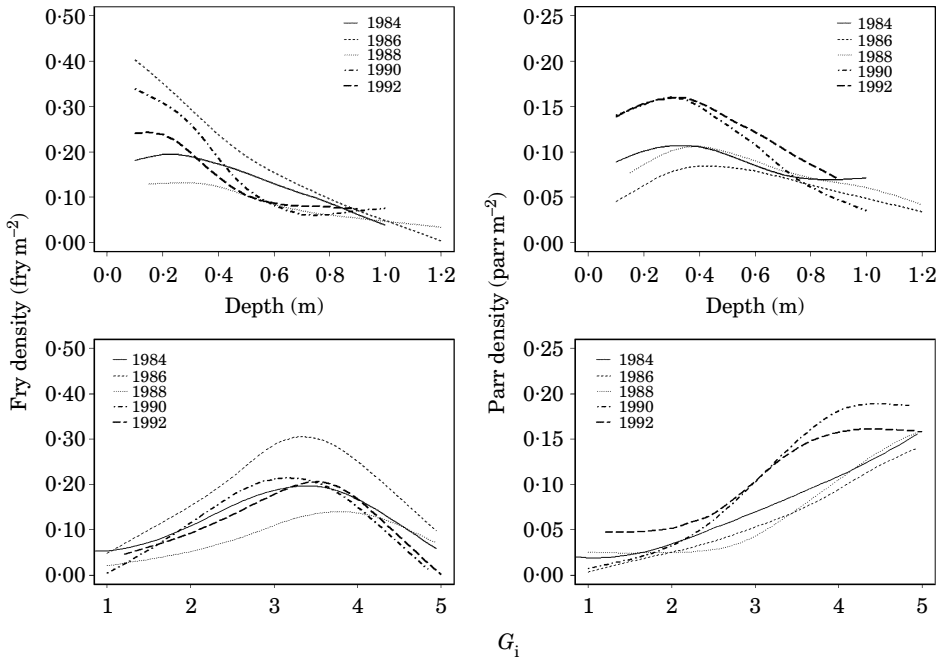


FIG. 4. GAMS showing the relationship between juvenile Atlantic salmon densities and depth and granulometric index (G_i) for individual years.

which suggested that nose velocity was the most important variable. There is no indication that the present measurements of velocity were any less reliable than those of DeGraff & Bain (1986) and Morantz *et al.* (1987) so that the relationship was probably not caused by sampling error. Without more detailed data on the habitat, however, it is difficult to infer the cause of the relative importance of depth and substratum size.

The key finding of this study on juvenile Atlantic salmon habitat use is that, although it is possible to identify habitats broadly selected or avoided by juveniles, there is a high variation in density within these habitats, particularly the ones that are optimal, not all of which can be easily explained. Some of the variation that is apparent when individual habitat variables are being considered can be explained by interaction with other variables. Thus, when authors present preference curves based on individual variables, it is necessary to treat these with some scepticism because an apparent preference for one variable may be strongly influenced by a preference for another variable. In this study, some of the variation in juvenile densities around the GAMS for individual variables, for example, could be explained by the coexistence of optimal or sub-optimal ranges of the other variables. Even when all habitat variables were considered together, allowing for interaction, most of the variation in fry and parr density remained unexplained. It is important not to ignore possible variation induced by the sampling scheme. Firstly, juvenile densities were estimated by single-pass electrofishing (calibrated by three-pass electrofishing in selected stations). Single-pass electrofishing has been used successfully in habitat modelling (Rahel &

TABLE III. Habitat property *P*-values of the year-specific GAMs for juvenile Atlantic salmon density and the physical habitat properties for years 1984–1992

Year	Habitat property affecting fry density			Habitat property affecting parr density		
	Greatest significance	Intermediate significance	Least significance	Greatest significance	Intermediate significance	Least significance
1984	G_i 2.22×10^{-4}	NA	D 1.89×10^{-2}	G_i 1.70×10^{-10}	NA	D 1.63×10^{-3}
1985	D 4.49×10^{-5}	NA	G_i 5.03×10^{-5}	G_i 1.44×10^{-15}	NA	D 8.51×10^{-4}
1986	D 8.09×10^{-6}	G_i 3.80×10^{-5}	V 4.25×10^{-1}	G_i 1.44×10^{-9}	D 9.40×10^{-2}	V 4.10×10^{-1}
1987	G_i 1.04×10^{-4}	V 1.56×10^{-3}	D 4.28×10^{-3}	G_i 1.45×10^{-5}	D 6.36×10^{-2}	V 1.78×10^{-1}
1988	G_i 1.29×10^{-5}	D 3.52×10^{-3}	V 3.16×10^{-2}	G_i 1.07×10^{-13}	D 5.42×10^{-4}	V 1.94×10^{-1}
1989	D 4.44×10^{-4}	G_i 1.13×10^{-2}	V 1.71×10^{-1}	G_i 3.04×10^{-10}	V 2.41×10^{-2}	D 1.07×10^{-1}
1990	D 2.40×10^{-7}	G_i 1.36×10^{-3}	V 8.22×10^{-3}	G_i 1.66×10^{-13}	D 1.31×10^{-4}	V 4.76×10^{-1}
1991	D 1.15×10^{-7}	NA	G_i 2.00×10^{-6}	G_i 1.11×10^{-16}	NA	D 1.23×10^{-3}
1992	G_i 1.11×10^{-3}	NA	D 6.44×10^{-2}	G_i 2.59×10^{-4}	NA	D 2.48×10^{-2}

V, velocity; D, depth; G_i , granulometric index; NA, no available measurement for velocity.

TABLE IV. Analysis of deviance table for GAMs for juvenile Atlantic salmon density and the physical habitat properties for years 1986–1990

	Model	Model		Test		<i>F</i>	Aic	<i>P</i>	
		Deviance	d.f.	Deviance	d.f.				
Fry	Full model	19.93	667						
	Null model	15.37	656						
	Full model less:								
	Depth	17.35	660	1.97	3	3.0005	28.12	31.35	0
	G_i	16.84	660	1.46	3	3.0005	20.81	30.84	6.83×10^{-13}
Velocity	15.57	660	0.20	3	3.0004	2.82	29.57	3.84×10^{-2}	
Parr	Full model	8.25	667						
	Null model	5.91	656						
	Full model less:								
	G_i	7.50	660	1.58	3	3.0005	58.40	21.50	0
	Depth	6.18	660	0.26	3	3.0005	9.71	20.18	2.81×10^{-6}
Velocity	5.98	660	0.03	3	3.0002	2.09	19.98	1.00×10^{-1}	

Aic, Akaike information criteria; G_i , granulometric index.

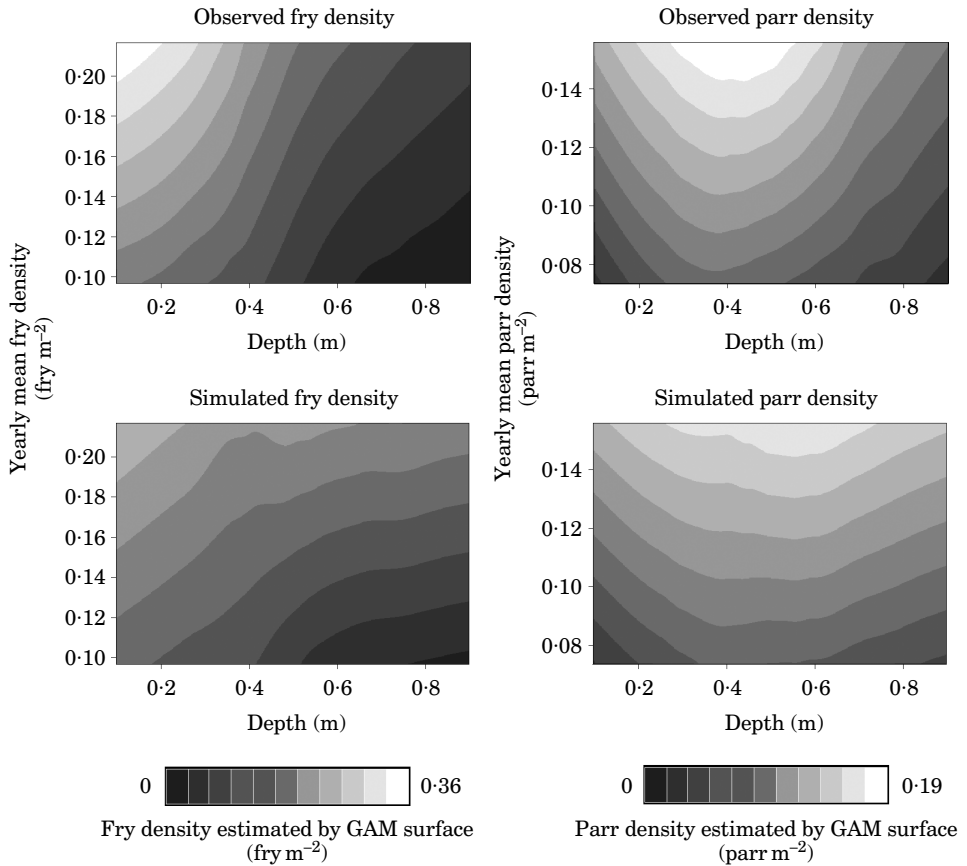


FIG. 5. GAM surfaces showing estimated and observed depth utilization by juvenile Atlantic salmon at different abundances for the years 1984–1992.

Nibbelink, 1999; May & Brown, 2002; Paller, 2002) but it produces less accurate estimates than multi-pass electrofishing (Meador, 2003). In the present study, it was found that single-pass was able to explain a relatively high proportion of the variation in fry and parr density that would be found through three-pass electrofishing. For example, in 1989, single-pass estimates explained 84% of variation in three-pass estimates of fry and 64% of variation in three-pass estimates of parr (92% if one outlier was removed). The relative inaccuracy of single-pass electrofishing does therefore not explain the variation found by the GAMs. It is possible that some of the variation may be attributed to having not sampled enough variables. The sampling scheme in this study was restricted to three habitat variables, but other variables may affect juvenile Atlantic salmon density including food availability and predation (Vehanen, 2003), temperature (Torgersen *et al.*, 1999), light intensity (Heggenes & Dokk, 2001; Girard *et al.*, 2003) and predation (Dionne & Dodson, 2002). Additionally, it is possible that the prevalence of unused habitat resulting from low abundance, the discontinuous nature of the habitat, the variability in individual competitiveness and the lack of knowledge of the habitat could be possible reasons (Railsback *et al.*,

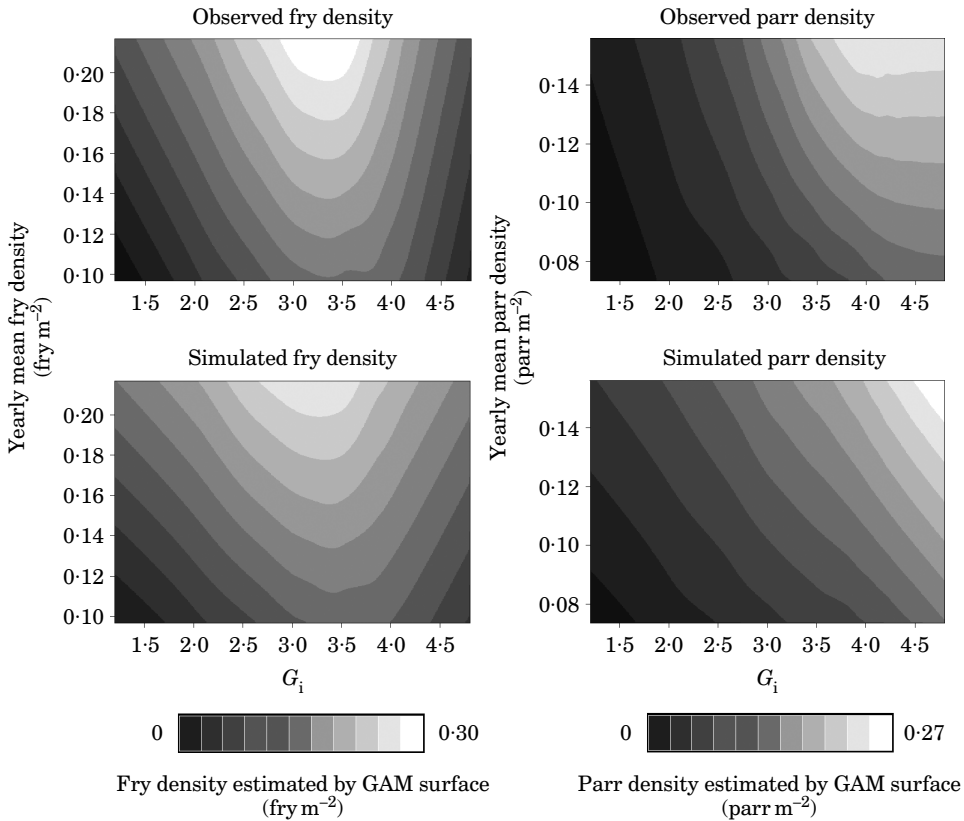


FIG. 6. GAM surfaces showing estimated and observed substratum utilization by juvenile Atlantic salmon at different abundances for the years 1984–1992. G_i , granulometric index.

2003). Spatial heterogeneity in the physical habitat may have had a role. Juvenile Atlantic salmon use a variety of habitats over a range of temporal and spatial scales. On a short-term basis, the spatial distribution of juveniles may respond to ephemeral or transitory events within the environment. For example, if juveniles occupying an optimal habitat detect the presence of a predator, they may temporarily vacate that habitat, possibly to one that is sub-optimal. During this event, low densities would be found in optimal habitats, and high densities would be found in sub-optimal habitats. On a longer-term basis, the proximity of different habitat types may have an effect. For example, juveniles may require coarse substrata for resting, in proximity to fast flows for feeding. If there is no nearby area of fast flows, a patch of coarse substrata may remain unoccupied.

On an inter-year basis, the overall structure of the relationships remained constant, with the spatio-temporal distribution of the juvenile Atlantic salmon population exhibiting an IFD (greatest variation in densities occurred in the optimal habitats, as the proportional utilization of all habitats remained constant regardless of a change in abundance). Firstly, it is possible that the density range within the Trinité was too narrow for density-dependent effects to be enough to cause an IDD. The densities of fry and parr in the Trinité were

relatively low: a mean of 14.2 and a maximum of 110.9 fry per section (of 100 m² in area), and a mean of 10.6 and a maximum of 64.4 parr per section, which is an order of magnitude less than in the study of Bult *et al.* (1999) where an IDD was found. The mean L_F of juveniles in the Trinité were 43 mm (0 + year group), 63 mm (1 + year group), 90 mm (2 + year group) and 113 mm (3 + year group), so it can be inferred that the area of territory defended by an individual Atlantic salmon is in the order of 0.5–1 m² (Table I). Thus, it would be necessary for >100–200 individuals to exist within a section for the territories to overlap and for territorial interactions to have had a larger role. Therefore, it may be inferred that patches of optimal habitat had a carrying capacity that was enough to support increases without competition causing a deviation from the IFD to the IDD. Additionally, it is possible that the traditional view of juvenile Atlantic salmon territoriality, which might lead to the IDD, may not be fully appropriate for all cases. Økland *et al.* (2004), for example, described the situation of flexible habitat use by Atlantic salmon parr, with fish forming hierarchies and shoaling, which would lead to territories overlapping without agonistic behaviour occurring.

Habitat selection of juvenile Atlantic salmon in the Trinité was characterized by a high level of seemingly-stochastic complexity, superimposed on an overall structure. Overall, juveniles selected or avoided clearly delineated habitats. For a given habitat type, there was a large variation in densities, both, within individual years and between different years, with this variation increasing as the optimality of the habitat increased. It was hypothesized in this paper that this variation was caused by: (1), on an individual-year basis, spatial heterogeneity in habitat characteristics and (2), on an inter-year basis, a change in the abundance of a population distributed according to the IFD. Future research on habitat selection by juvenile Atlantic salmon should: (1) focus more on the apparent noise that occurs in the relationships between densities and habitat variables, with emphasis on the interaction between variables and the relative strength of the variables, rather than merely focusing on the shape of the relationships, and (2) take a more comprehensive approach to the analysis of Atlantic salmon territoriality with regards to the type of distribution that this territoriality might create.

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