

## Assessing temporal variation and autocorrelation in fish habitat use

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**A b s t r a c t.** We assessed the extent of temporal variation and autocorrelation in fish habitat use based on an experimental study of individual 0+ juvenile barbel, *Barbus barbus*, in an artificial flume. Five treated and five control fish were individually subjected to an increase in discharge (intervention) halfway through each experiment and kept at baseline discharge throughout, respectively. Preference curves for velocity were generated for each of 60 trials per experiment and for each combination of treated/control (fish) × before/after-intervention. There were large between- and within-individual differences in velocity preference, both in treated and in control fish. Most barbel explored the entire range of velocities, whereas some individuals used a more limited range. Temporal variation in behavioural responses was assessed by a PCA-based methodology. Autocorrelation (i.e. correlation between sequential trials) was diagnosed in most response profiles, supporting recent findings that individuals may have a 'memory' of their past velocity usage. The relevance of the results for numerical habitat models of fish habitat assessment is discussed, as well as the importance of incorporating temporal variability into fish habitat use models (e.g. PHABSIM), not only as ontogenetic intervals but also as longitudinal data of individual behaviours. A warning is also re-issued about the erroneous belief of 'pseudoreplication' simply arising from repeated measurements in time.

**Key words:** PHABSIM, fish behaviour, individual-based models (IBMs), PCA, semi-variogram, log-linear analysis, pseudoreplication

### Introduction

Increasing exploitation of freshwater ecosystems on a worldwide scale has been paralleled by the rapid development and refinement of environmental flow assessment and monitoring techniques aimed at mitigating the extent of human impacts (Downes et al. 2002, Tharme 2003). Riverine fish, in particular, are widely believed to be affected by variations in flow, especially during their early ontogeny (Matthews 1997), so that, in regulated water courses, water allocation policies are required that meet both the economic demands of humans and the ecological requirements of fish (Gibbins & Cornley 2000). These factors have led to implementation both of numerical habitat models (Parasiewicz & Dunbar 2001, Guay et al. 2003) and of fish behaviour and monitoring studies (e.g. Kemp et al. 2003, Scruton et al. 2003a,b).

Among instream flow assessment methods, PHABSIM (Physical HABitat SIMulation) is a widespread technique (Tharme 2003) which has generally relied on a loosely-defined, individual-based approach (Lamouroux & Capra 2002). PHABSIM combines a biological component, hinged on Habitat Suitability Indices (HSI), with a hydraulic model to deliver ultimately Weighted Usable Area (WUA) vs discharge profiles (Ovee et al. 1998).

As part of the modelling process, HSI and suitability/preference curves (HSI's most common graphical format: Parasiewicz & Dunbar 2001), typically are generated for one or more target species, and often separately for their different ontogenetic intervals (e.g. Mallet et al. 2000, Vismara et al. 2001, Armstrong et al. 2004, Booker & Dunbar 2004). Thus, this procedure accounts for the temporal aspects of a fish's ecology only cross-sectionally (*sensu* Diggle et al. 2002) along its ontogenetic trajectory (Kováč 2002); whereas a longitudinal study on individual fish would address the various temporal tiers of the whole spectrum of behavioural responses (Rallsback 2001). Indeed, the main difference between a cross-sectional and a longitudinal study is that in the former only a single outcome is recorded for each individual, whereas in the latter the same individual is repeatedly measured over time (Diggle et al. 2002).

In fish behaviour studies, response to changing flows has often been investigated at the individual level both in laboratory flumes (e.g. Valentin et al. 1994, Huntingford et al. 1999, Vehanen et al. 2000) and in (semi-)natural settings (e.g. Pert & Erman 1994, Valentin et al. 1996, Armstrong et al. 1998, Scruton et al. 2003b); whereas in field studies, radio telemetry has recently been incorporated into PHABSIM predictions (Scruton et al. 2002, Vehanen & Lathi 2003). This is contrary to Bovee et al. (1998, p. 80), who recommended telemetry only "for studying species that are rare, cryptic, or otherwise hard to sample or observe", and who further claimed that "if the time between observations of the same animal is too small, the assumption of independence may be violated, resulting in pseudoreplication", whereas "if the time period is too long [...] the behavior of the animal will likely change".

Since Mather et al.'s (1985) warnings, increasing attention has been drawn on ways to incorporate measures of variability in (PHABSIM-oriented) fish (micro)habitat studies (e.g. Williams 2001). To this end, Vilizzi et al. (2004) implemented a methodology for assessing variation in collections of preference curves and electivity profiles arising from repeated sampling over time and/or space. This methodology was eventually applied to the study of spatial patterns in fish microhabitat use (Copp & Vilizzi 2004). In this perspective, the objectives of the present paper are 1) to extend Vilizzi et al.'s (2004) methodology to temporal variation in collections of individual-based preference curves, 2) to evaluate the degree of autocorrelation in sequential measurements of velocity preference, and 3) to address Bovee et al.'s (1998) concerns about the inapplicability of PHABSIM to repeated measurements and about the issue of pseudoreplication (see also Millar & Anderson 2004).

## Methods

### Experimental set-up

Hatchery-reared 0+ barbel, *Barbus barbus*, from a single cohort were obtained from Calverton Fish Farm (Nottinghamshire, England) in August 1998. In the laboratory, the fish were transferred to 60 l glass tanks (stocking density 0.5 fish l<sup>-1</sup>) and fed 800 µm pellets (Rock Pauls Ltd) *ad libitum* twice daily. Light in the room was determined by natural day length and sun intensity. The room was temperature controlled at 21 ± 1 °C.

Experiments were carried out in an artificial flume (Length × Width × Height = 180 × 50 × 25 cm) made of Perspex™, which was placed on a bench top as part of a recirculating water system. At the upstream end of the flume, the first 20 cm were separated from the experimental

arena (150 cm long, 7,500 cm<sup>2</sup>) by a removable partition, consisting of Perspex™ frames supporting plastic mesh (1 mm). A second, removable partition divided the downstream extent from a 10 cm long out-flow compartment. Water flowing out of the flume was received by an ‘outlet’ reservoir, a 200 l cistern located on the floor that contained large plastic meshing to trap large particles. The outlet reservoir was connected by a 6.6 cm diameter pipe, fitted with a fine (2 mm) mesh screen to trap small debris, to a second 200 l reservoir containing two independent drainage pumps (Oase® Aquadex A8). Water was drawn from the ‘pump’ reservoir into the bottom of an ‘inlet’ reservoir (200 l, containing Canterbury spar as a biofilm substratum as filter), which was located on the bench top at the flume’s upstream end. Water used in the experiment was drawn from domestic water supply and was recirculated through the system for at least two weeks prior to the experiments to ensure thorough de-chlorination and ‘maturation’, which resulted from filtration through the well-established biofilm.

On the bottom of the arena, a reference lattice was drawn consisting of 75 (10 × 10 cm) contiguous quadrats, numbered sequentially from the downstream upper corner to the upstream lower corner. A brick (L × W × H = 20 × 80 × 10 cm) was then placed on one side of the flume to provide a refuge covering quadrats 1–8 and 16–23 (1600 cm<sup>2</sup>). To increase the accuracy of the observations, no substratum was added. Two discharge regimes, supplied by either one ( $Q = 3.7 \text{ l s}^{-1}$ : low discharge) or both pumps ( $Q = 7.4 \text{ l s}^{-1}$ : high discharge), were available. Water velocities were measured with a velocity meter (A.OTT Kempton® Type 02 10.150) at 0.6 of the depth (kept at 20 cm), centred on each of the 75 quadrats.

Ten experiments were conducted, each consisting of 60 series (trials) of continuous 120 s observations on a single fish (i.e. one barbel in the flume per experiment), with each trial consisting of 240 sequential observations (hence, resolution at 0.5 s). Individual fish (mean standard length =  $39.4 \pm 0.6 \text{ SE mm}$ ) were haphazardly selected from the tanks and acclimatised to the flume for about 12 h at low discharge prior to each experiment. The fish were fed before but not during the experiment. There were five treated fish, subjected to an increase in discharge (from low to high) halfway through the experiment, and five control fish, kept at low discharge throughout. During a trial, the position of a fish relative to the reference lattice was visually determined and vocally recorded to a digital tape by a multifunction headset and microphone connected to a laptop computer. Observations were made at 1 m distance from the stream and at an angle of about 30° from the bottom of the arena. The operator stood still during the observations, approaching or leaving discreetly the observation point. This caused no disturbance to the fish, as revealed by a pilot study (unpublished data). A fish was considered to occupy a quadrat when more than half of its body length was within that quadrat’s boundaries. Whenever the movements of a fish were too fast to be recorded discretely over the quadrats traversed, the number of the starting and ending quadrats along the corresponding column (upstream/downstream movements) or row (across-flume movements) were noted. The intermediate quadrats were later included in the analyses without appreciable loss in resolution (further details in *Vilizzi & Copp 2005*).

## Data analysis

Hereafter, the term ‘curves’ will refer to ‘preference curves’ rather than ‘suitability curves’, after *Parasiewicz & Dunbar (2001)* and the caveats by *Rosenfeld (2003)*. For each of the ten individual treated/control fish, curves for velocity were generated for each trial (hence, 60 curves per fish: 30 before and 30 after the actual/null intervention). Available velocities in each quadrat were then arranged into incremental categories at low ( $2\text{--}14 \text{ cm s}^{-1}$ ,

increments of  $2 \text{ cm s}^{-1}$ ) and high discharge ( $5\text{--}35 \text{ cm s}^{-1}$ , increments of  $5 \text{ cm s}^{-1}$ ), and their percent frequency distribution determined (Table 1). Used velocities were then computed relative to the 240 total quadrat positions successively occupied by a fish during a 120 s trial. The frequency distribution of used velocities was then arranged according to the incremental categories, and the ratio used/available velocity calculated after giving the modal value of the corresponding frequency distribution a weighting factor of 1, resulting in a normalised velocity suitability value at each category ranging from 0 (total avoidance) to 1 (maximum preference) (Bovee et al. 1998).

A caveat is in order. Whenever quadrats under a velocity category were used more than those available, the number of used velocities was made equal to the total number of quadrats under that category. As a result, HSI values at certain or all velocity categories would equal 1, providing either a partially- or fully-‘saturated’ curve, respectively. Furthermore, as curves for barbel were computed under experimental settings, the absolute values of their velocity preferences were not of interest, so that the terms ‘low’, ‘medium’ and ‘high’ velocity will be used hereafter relative to the range available under either discharge regime (Table 1).

For display purposes, curves were smoothed by cubic splines; whereas for modelling, third-order polynomials were fitted (Vilizzi 2002). Parametric fits were then analysed by Jones and Rice’s (1992) PCA-based method as implemented in Vilizzi et al. (2004), in order to 1) summarise patterns of variation within each set (‘bundle’) of curves and 2) understand how first component scores for each trial changed over time. Accordingly, for each of the twenty sets (resulting from  $10 \text{ fish} \times 2 \text{ Before/After}$  combinations) of 30 polynomials, the 7 fitted values, corresponding to the velocity categories at low and high discharge, were arranged into a  $30 \times 7$  array and the resulting (unscaled) covariance matrix subjected to PCA. ‘Bundle plots’ were thus obtained for each combination, and variation in first component

**Table 1.** Number of quadrats with a particular velocity category in an artificial flume under low and high discharge. A total of 75 quadrats were available, arranged as a  $5 \times 15$  reference lattice.

Velocity interval ( $\text{cm s}^{-1}$ )	Category ( $\text{cm s}^{-1}$ )	Number of quadrats	Relative velocity
<b>Low discharge</b>			
0.0–2.0	2	35	Low
2.0–4.0	4	8	Low
4.0–6.0	6	10	Medium
6.0–8.0	8	8	Medium
8.0–10.0	10	2	Medium
10.0–12.0	12	7	High
12.0–14.0	14	5	High
<b>High discharge</b>			
0.0–5.0	5	6	Low
5.0–10.0	10	10	Low
10.0–15.0	15	30	Medium
15.0–20.0	20	10	Medium
20.0–25.0	25	8	Medium
25.0–30.0	30	9	High
30.0–35.0	35	2	High

scores over consecutive trials was represented by index plots, in which a greater spread in index scores would correspond to greater among-trial variation. Further, the degree of correlation between consecutive trials was represented by the semi-variogram (Diggle 1990). This method for estimating and displaying the autocorrelation function of a time series is preferable over the correlogram when data, as in the present study, are observed at unequally-spaced times. If the resulting curve shows no 'levelling-off', then the underlying process is non-stationary (i.e. the data are autocorrelated over time). HSI were computed in Windows™ under Microsoft® Excel 2002, curves and PCA with S-PLUS 2000 Professional Release 3.

## Results

There were individual-level differences in velocity preference, as revealed by the distribution of curves in each set (Fig. 1a,b top strips: 'bundle plots'). Thus, amongst treated barbel and before intervention, only fish 5 showed overall preference for low–medium velocities, whereas the other individuals used the entire range. After intervention, fish 3 and 5 preferred overall medium velocities, fish 9 mostly high velocities; whereas fish 1 and 7 still used the entire range. As expected, control barbel showed overall similar within-individual preferences during the first and second half of the trials (i.e. before and after null intervention). Specifically, fish 4 did not show preference for any specific range, whereas fish 2 and, in particular, 6 overall preferred low–medium, and fish 8 either low or high velocities throughout. Notably, in the first set of trials fish 10 showed a shift from no preference to selection of medium velocities, a behaviour that persisted until the end of the experiment.

The above patterns appeared within each set of curves as distinct 'sheaths'. These corresponded to groups of trials, suggesting either similarity in velocity preference over successive trials or consistent preference by fish for certain velocities independent of time of observation. This was assessed by PCA, which showed that first components usually explained most of the variance under each combination (Table 2). However, interpretation of components was generally not clear-cut, and this was likely due to the high 'noise' caused by shifting velocity preferences.

Index plots (Fig. 1a,b middle strips) revealed that, in the first set, fish 5 used (over a short sequence of trials) all available velocities and then returned to low–medium ones. A similar pattern was observed in fish 6, though over a shorter interval. After the increase in discharge, fish 9 selected higher velocities, following a series of alternating shifts between low and high ones. Alternation of velocity preference over successive trials was observed in the remaining fish (index plots with spikes). Finally, the shift in velocity preference by fish 10 was revealed by a drop in component scores.

As indicated by the semi-variograms (Fig. 1a,b bottom strips), amongst treated barbel there was no autocorrelation between sequential component scores (hence, curves) in fish 5 before and in fish 1, 3 and 9 after the intervention, and the same was true of control individuals 6 and 8 throughout. Correlation was instead present in the other combinations, as shown by the rising semi-variogram profiles. Notably, in fish 10 a jump from low to high velocities at trial 16 was highlighted, whereas observations for fish 2 were clearly autocorrelated in the first set of trials, but not in the second.

## Discussion

As revealed in the present study, both between- and within-individual differences in velocity preference would highlight potential bias inherent to time of sampling. As a microhabitat

model, PHABSIM is used to predict fish–habitat associations at a fine spatial scale in the stream channel (Rosenfeld 2003). Microhabitat preference then occurs when a non-random use of space resulting from voluntary movement of fish is observed (Kramer et al. 1997). For non-territorial benthos foragers such as barbel and other stream-dwelling cyprinids, individuals cruise across a wide range of microhabitats to increase their chances of encountering prey. Such behaviour would explain why, in the present study, most 0+ barbel were observed to use the whole range of microhabitat available in the flume. Thus, a single outcome of a fish's position may lead to simplistic graphical formats of their habitat preference, with possible temporal bias in HSI (and, ultimately, WUA projections), which could instead be more effectively encompassed by means of repeated measures.

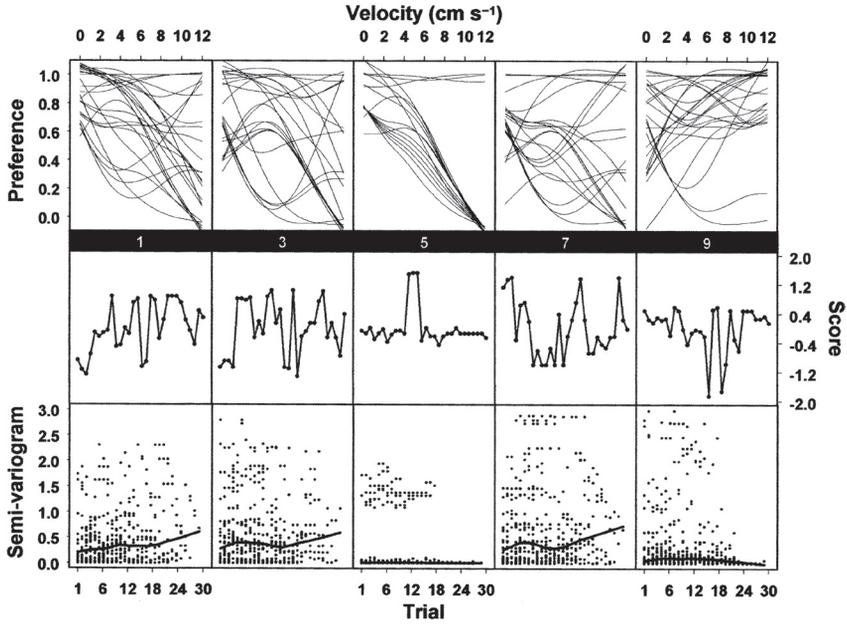
Recently, Booker et al. (2004) developed a physically-based bioenergetic model to predict habitat quality for drift-feeding juvenile salmonids that would overcome some of the limitations with empirical physical habitat models, such as PHABSIM. Specifically, Booker et al. (2004, p. 158) re-stated the importance of incorporating dynamic aspects of fish habitat selection (Matur et al. 1985, Heggnes 1996), but claimed that “repeated measurement would be expensive and lack the predictive capability required for water resource assessment and the spatial and temporal information required for IBMs” (Individual Based Models). In this respect, we argue that recent improvement of monitoring systems, such as those based on passive integrated transponder technology (Armstrong et al. 1996, Rousselet et al. 2000, Riley et al. 2003), now facilitates retrieval of copious amounts of data on the habitat use and behaviour of stream fishes. This would not only allow fast generation of dynamic HSIs (as shown in the present study) but would also be applicable to both territorial and non-territorial foragers (Scruton et al. 2002, Vehanen & Lathi 2003). Finally, we believe that temporal changes in fish behaviour should be of key interest in dynamic habitat assessment studies: this is at variance with Bovee et al.'s (1998) recommendations.

The other concern raised by Bovee et al. (1998) about pseudoreplication looming from repeated observations taken closely over time needs clarification. Pseudoreplication, in its original conception, is concerned with whether “analyses and interpretations of experiments are concordant with the way experiments were designed and conducted” (Hurlbert 2004). In the repeated measurements case, Mead (1988, p. 113) clearly stated that frequent observations “may provide very useful information on the behaviour of the experimental unit which is being monitored. But they do not provide any basis for the comparison of treatments applied to different units”. Accordingly, collection and analysis of longitudinal data on fish habitat use/preference at any (biologically meaningful) time scale is not to be regarded as an error-prone procedure per se, as long as appropriate statistical methods are employed (Diggle et al. 2002). Therefore, it is not ‘pseudoreplication’ that is likely to arise from sequential measures of a fish's activity, but rather autocorrelation, an intrinsic property of time-series data easily handled by means of appropriate statistical techniques (e.g. Diggle 1990). Accordingly, autocorrelation was assessed in the present study by the semi-variogram (Fig. 1a,b bottom), although correlograms could be used with observations taken at regularly-spaced times (Diggle 1990). Further, we believe that our argument carries more than speculative interest. Thus, Kemp et al. (2003) argued that populations of juvenile Atlantic salmon may have an individual-based ‘memory’ of their past habitat-related distribution. To this end, presence or absence of autocorrelation in component scores for barbel in the present study were found to relate to either random or memory-based velocity usage, which in Railsback's (2001) increased potential fitness framework would respectively encompass mechanisms of innate short-term behaviours and movement/exploration (Vilizzi & Copp 2005).

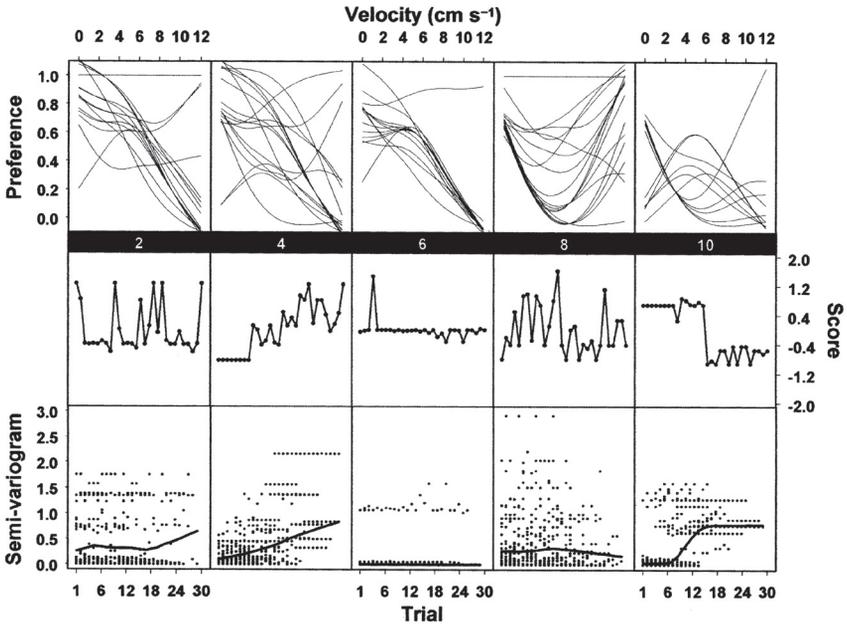
a)

# Before

Treated



Control





**Table 2.** PCA of preference curves for velocity, fitted as third-order polynomials, for 0+ juvenile barbel in an artificial flume. For each Treated/Control  $\times$  Before/After combination, the first component and variance explained are given. Odd numbers: treated individuals; even numbers: control individuals.

	Variance	Velocity category*						
		1	2	3	4	5	6	7
<b>Treated <math>\times</math> Before</b>								
1	0.479	0.000	0.393	0.371	0.162	0.591	0.189	0.544
3	0.435	0.000	0.446	0.500	0.463	0.455	0.125	0.334
5	0.635	0.000	0.574	0.000	0.118	0.475	0.453	0.475
7	0.509	0.000	0.326	0.258	0.403	0.464	0.469	0.478
9	0.398	-0.174	0.522	0.453	0.426	0.384	0.221	0.338
<b>Treated <math>\times</math> After</b>								
1	0.446	-0.201	0.180	0.376	0.484	0.379	0.348	0.536
3	0.451	0.120	0.427	0.000	0.000	0.000	0.579	0.674
5	0.639	0.156	0.000	0.000	0.000	0.500	0.606	0.590
7	0.451	-0.328	0.000	-0.161	-0.156	0.461	0.580	0.451
9	0.419	-0.453	0.000	-0.357	0.413	0.197	0.458	0.498
<b>Control <math>\times</math> Before</b>								
2	0.568	0.000	0.342	0.000	0.000	0.490	0.556	0.575
4	0.431	0.000	0.155	0.534	0.587	0.216	0.433	0.324
6	0.382	0.000	0.000	0.000	-0.956	0.240	0.000	0.000
8	0.488	0.000	0.186	0.482	0.459	0.334	0.358	0.532
10	0.654	0.658	0.000	-0.583	-0.451	0.000	0.143	0.000
<b>Control <math>\times</math> After</b>								
2	0.531	0.000	0.156	0.000	0.000	0.338	0.610	0.633
4	0.726	0.000	0.324	0.578	0.486	0.119	0.392	0.396
6	0.625	0.000	0.978	0.000	0.115	0.000	0.130	0.112
8	0.558	0.000	0.356	0.577	0.533	0.000	0.444	0.240
10	0.611	0.310	0.231	0.918	0.000	0.000	0.000	0.000

\* For Treated  $\times$  Before, Control  $\times$  After: 2, 4, 6, 8, 10, 12, 14 cm s<sup>-1</sup>; for Treated  $\times$  After: 5, 10, 15, 20, 25, 30, 35 cm s<sup>-1</sup> (cf. Table 1)

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## LITERATURE

- ARMSTRONG J.D., BRAITHWAITE V.A. & RYCROFT P. 1996: A flat-bed passive integrated transponder antenna array for monitoring behaviour of Atlantic salmon parr and other fish. *J. Fish Biol.* 48: 539–541.
- ARMSTRONG J.D., BRAITHWAITE V.A. & FOX M. 1998: The response of wild Atlantic salmon, *Salmo salar* L., parr to acute reductions in water flow. *J. Anim. Ecol.* 67: 292–297.
- ARMSTRONG J.D., KEMP P.S., KENNEDY G.J.A., LADLE M. & MILNER N.J. 2004: Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fish Res.* 62: 143–170.
- BOOKER D.J. & DUNBAR M.J. 2004: Application of physical habitat simulation (PHABSIM) modelling to modified urban river channels. *River Res. Appl.* 20: 167–183.
- BOOKER D.J., DUNBAR M.J. & IBBOTSON A. 2004: Predicting juvenile salmonid drift-feeding habitat quality using a three-dimensional hydraulic-bioenergetic model. *Ecol. Model.* 177: 155–177.
- BOVEE K.D., LAMB B.L., BARTHOLOW J.M., STALNAKER C.B., TAYLOR J. & HENRIKSEN J. 1998: Stream habitat analysis using the instream flow incremental methodology. *U.S. Geological Survey, Biological Resources Division Information and Technology Report USGS/BRD-1998-0004*, <http://www.fort.usgs.gov/>.
- COPP G.H. & VILIZZI L. 2004: Spatial and ontogenetic variability in the microhabitat use of stream-dwelling spined loach (*Cobitis taenia*) and stone loach (*Barbatula barbatula*). *J. Appl. Ichthyol.* 20: 440–451.
- DIGGLE P.J. 1990: Time Series: A Biostatistical Introduction. *Clarendon Press, Oxford*.
- DIGGLE P.J., HEAGERTY P., LIANG K.-Y. & ZEGER S.L. 2002: Analysis of Longitudinal Data (2nd edn). *Clarendon Press: Oxford*.
- DOWNES B.J., BARMUTA L.A., FAIRWEATHER P.G., FAITH D.P., KEOUGH M.J., LAKE P.S., MAPSTONE B.D. & QUINN G.P. 2002: Monitoring Ecological Impacts – Concepts and Practice in Flowing Waters. *Cambridge University Press, Cambridge*.
- GIBBINS C.N. & ACORNLEY R.M. 2000: Salmonid habitat modelling studies and their contribution to the development of an ecologically acceptable release policy for Kielder Reservoir, north-east England. *Regul. River.* 16: 203–224.
- GUAY J.C., BOISCLAIR D., LECLERC M. & LAPOINTE M. 2003: Assessment of the transferability of biological habitat models for Atlantic salmon parr (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 60: 1398–1408.
- HEGGENES J. 1996: Habitat selection by brown trout (*Salmo trutta*) and young Atlantic salmon (*S. salar*) in streams: static and dynamic hydraulic modelling. *Regul. River.* 12: 155–169.
- HUNTINGFORD F.A., AIRD D., JOINER P., THORPE K.E., BRAITHWAITE V.A. & ARMSTRONG J.D. 1999: How juvenile Atlantic salmon, *Salmo salar* L., respond to falling water levels: experiments in an artificial stream. *Fisheries Manag. Ecol.* 6: 357–364.
- HURLBERT S.H. 2004: On misinterpretations of pseudoreplication and related matters: a reply to Oksanen. *Oikos* 104: 591–597.
- JONES M.C. & RICE J.A. 1992: Displaying the important features of large collections of similar curves. *Am. Stat.* 46: 140–145.
- KEMP P.S., GILVEAR D.J. & ARMSTRONG J.D. 2003: Do juvenile atlantic salmon parr track local changes in water velocity? *River Res. Appl.* 19: 569–575.
- KOVÁČ V. 2002: Synchrony and heterochrony in ontogeny (of fish). *J. Theor. Biol.* 217: 499–507.
- KRAMER D.L., RANGELEY R.W. & CHAPMAN L.J. 1997: Habitat selection: patterns of spatial distribution from behavioural decisions. In: Godin J.G.J. (ed.), Behavioural Ecology of Teleost Fishes. *Oxford University Press, Oxford*: 37–80.
- LAMOUREUX N. & CAPRA H. 2002: Simple predictions of instream habitat model outputs for target fish populations. *Freshwater Biol.* 47: 1543–1556.

- MALLET J.P., LAMOUREUX N., SAGNES P. & PERSAT H. 2000: Habitat preferences of European grayling in a medium size stream, the Ain river, France. *J. Fish Biol.* 56: 1312–1326.
- MATHUR D., BASON W.H., PURDY E.J. JR & SILVER C.A. 1985: A critique of the Instream Flow Incremental Methodology. *Can. J. Fish. Aquat. Sci.* 42: 825–831.
- MATTHEWS W.J. 1997: Patterns in Freshwater Fish Ecology. *Chapman & Hall, London.*
- MEAD R. 1988: The Design of Experiments: Statistical Principles for Practical Applications. *Cambridge University Press, Cambridge.*
- MILLAR R. B. & ANDERSON M. J. 2004: Remedies for pseudoreplication. *Fisheries Res.* 70: 397–407.
- PARASIEWICZ P. & DUNBAR M.J. 2001: Physical habitat modelling for fish – a developing approach. *Arch. Hydrobiol. Suppl.* 135(2–4): 239–268.
- PERT E.J. & ERMAN D.C. 1994: Habitat use by adult rainbow trout under moderate artificial fluctuations in flow. *T. Am. Fish. Soc.* 123: 913–923.
- RAILSBACK S.F. 2001: Concepts from complex adaptive systems as a framework for individual-based modelling. *Ecol. Model.* 139: 47–62.
- RILEY W.D., EAGLE M.O., IVES M.J., RYCROFT P. & WILKINSON A. 2003: A portable passive integrated transponder multi-point decoder system for monitoring habitat use and behaviour of freshwater fish in small streams. *Fisheries Manag. Ecol.* 10: 265–268.
- ROSENFELD J. 2003: Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. *T. Am. Fish. Soc.* 132: 953–968.
- ROUSSEL J.M., HARO A. & CUNJAK R.A. 2000: Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. *Can. J. Fish. Aquat. Sci.* 57: 1326–1329.
- SCRUTON D.A., CLARKE K.D., OLLERHEAD L.M.N., PERRY D., MCKINLEY R.S., ALFREDSEN K. & HARBY A. 2002: Use of telemetry in the development and application of biological criteria for habitat hydraulic modeling. *Hydrobiologia* 483: 78–82.
- SCRUTON D.A., MCKINLEY R.S., KOUWEN N., EDDY W. & BOOTH R.K. 2003a: Improvement and optimization of fish guidance efficiency (FGE) at a behavioural fish protection system for downstream migrating Atlantic salmon (*Salmo salar*) smolts. *River Res. Appl.* 19: 605–617.
- SCRUTON D.A., OLLERHEAD L.M.N., CLARKE K.D., PENNELL C., ALFREDSEN K., HARBY A. & KELLEY D. 2003b: The behavioural response of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) to experimental hydropeaking on a Newfoundland (Canada) river. *River Res. Appl.* 19: 577–587.
- THARME R.E. 2003: A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. *River Res. Appl.* 19: 397–441.
- VALENTIN S., SEMPEski P., SOUCHON Y. & GAUDIN P. 1994: Short-term habitat use by young grayling, *Thymallus thymallus* L., under variable flow conditions in an experimental stream. *Fisheries Manag. Ecol.* 1: 57–65.
- VALENTIN S., LAUTERS F., SABATON C., BREIL P. & SOUCHON Y. 1996: Modelling temporal variations of physical habitat for brown trout (*Salmo trutta*) in hydropeaking conditions. *Regul. River.* 12: 317–330.
- VEHANEN T. & LATHI M. 2003: Movement and habitat use by pikeperch (*Stizostedion lucioperca* (L.)) in a hydropeaking reservoir. *Ecol. Freshw. Fish* 12: 203–215.
- VEHANEN T., BJERKE P.L., HEGGENES J., HUUSKO A. & MÄKI-PETÄYS A. 2000: Effect of fluctuating flow and temperature on cover type selection and behavior by juvenile brown trout in flumes. *J. Fish Biol.* 56: 923–937.
- VILIZZI L. 2002: Modelling preference curves for the study of fish habitat use. *Arch. Hydrobiol.* 155: 615–626.
- VILIZZI L. & COPP G.H. 2005: An analysis of 0+ barbel (*Barbus barbus*) response to discharge fluctuations in a flume. *River Res. Appl.* 21: 421–438.
- VILIZZI L., COPP G.H. & ROUSSEL J.-M. 2004: Assessing variation in suitability curves and electivity profiles in temporal studies of fish habitat use. *River Res. Appl.* 20: 605–618.
- VISMARA R., AZZELLINO A., BOSI R., CROSA G. & GENTILI G. 2001: Habitat suitability curves for brown trout (*Salmo trutta fario* L.) in the River Adda, Northern Italy: comparing univariate and multivariate approaches. *Regul. River.* 17: 37–50.
- WILLIAMS J.G. 2001: Testing models used for instream flow assessment. *Fisheries* 26: 19–20.