

Methodological bias in home range and mobility estimates when locating radio-tagged trout, *Salmo trutta*, at different time intervals

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Abstract – Radio tracking has been extensively used to enhance our knowledge on the movement and home range of fish in general and salmonids in particular. However, the use of various temporal sampling protocols is likely to overlook fish movements, and produce experimental artefacts, the amplitude of which is unknown and may compromise comparison of fish behaviours revealed by different protocols. Starting from a day-by-day tracking study of brown trout in Belgian waters (Aisne stream, nine fish, minimum 39 daily locations per fish), we re-examined their home range and mobility, through a subsampling process, as if the fish had been located at longer time intervals (2–14 days). The estimates from subsamples were compared to the original data set in order to quantify the corresponding reduction of accuracy from observed data, and how far this could be predicted on the basis of locating frequency. The results clearly indicate that all intervals longer than one day generally generate substantial biases (reduction of accuracy from 0 to 82% for home range and from 5 to 92% for mobility) but these can be partly corrected through the use of predictive models. This analysis demonstrates that any comparison between studies relying on different locating frequencies can generate some ambiguity when interpreting biological phenomena or geographical differences.
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biotelemetry / locating frequency / home range / mobility / *Salmo trutta*

Résumé – Biais méthodologique dans l'estimation du domaine vital et de la mobilité de *S. trutta* suite à l'adoption de différentes fréquences de localisation. Le radio-pistage est fréquemment utilisé pour étudier l'écologie comportementale de la truite. Cependant, la fréquence des localisations est variable d'une étude à l'autre, ce qui est susceptible d'introduire des artefacts expérimentaux d'amplitude inconnue. Nous avons étudié le domaine vital et la mobilité de truites localisées quotidiennement, puis réexaminé ces variables par sous-échantillonnage, comme si les truites avaient été positionnées à des intervalles plus longs (2–14 jours). Les valeurs générées par sous-échantillonnage ont été comparées aux données originales afin de quantifier la perte de précision résultant de la diminution de la fréquence de positionnement, et d'en déterminer la prévisibilité. Le plus souvent, les fréquences inférieures à une position par jour génèrent des biais substantiels (perte de précision de 0 à 82% pour le domaine vital et de 5 à 92% pour la mobilité) mais qui peuvent être partiellement corrigés par l'utilisation de modèles prédictifs basés sur la fréquence de positionnement. Cette analyse démontre que toutes comparaisons entre des études qui utilisent différentes fréquences de localisation peuvent générer une ambiguïté quant à l'interprétation de phénomènes biologiques ou de différences géographiques.
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télémetrie / fréquence de localisation / espace vital / mobilité / *Salmo trutta*

1. INTRODUCTION

Except for some situations (e.g. Philippart and Baras, 1996), it is now generally accepted that capture–recapture techniques underestimate considerably the actual mobility of fish. By contrast biotelemetry tech-

niques may produce much more accurate estimates (Gowan et al., 1994; Fausch and Young, 1995). However, tracking studies may suffer from several biases, notably with respect to temporal autocorrelation between data points, since the position of one fix is intimately dependent on the previous fix(es). Depend

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ing on the time interval between fixes, and its adequacy to fish mobility, tracking studies may also overlook certain fish movements (Hawkins and Urquhart, 1983; Young et al., 1997). The issues of autocorrelation have been dealt with in a number of papers (e.g. Swihart and Slade, 1985), and are beyond the scope of this article, which focuses essentially on the biases resulting from looser sampling intervals.

To this respect, Baras (1998) modelled the loss of accuracy against locating frequency when estimating the home range and mobility of the cyprinid barbel *Barbus barbus* (L.) by radio tracking. Because the loss of accuracy was intimately dependent on locating frequency and tracking season, and also presumably on habitat structure and individual fish behaviour, Baras concluded that the comparison between home range or mobility estimates arising from different studies using different location frequencies might be biased. Also, in most fish species making day-round trips between resting and feeding places, and homing consistently in these (e.g. Clough and Laddle, 1997; Young et al., 1997; Ovidio, 1999), it is obvious that home range estimates based on daily locations might underestimate considerably the actual movement pattern of the fish.

Interestingly, these relationships have never been investigated in salmonids, which are the most frequently tracked species in Europe and North America. While reviewing the literature on brown trout (*Salmo trutta* L.) tracking, we noticed that most authors used different sampling protocols (Nettles et al., 1987; Haynes and Gerber, 1989; Clapp et al., 1990; Meyers et al., 1992; Schulz and Berg, 1992; Evans, 1994; Young, 1994; Økland et al., 1996; Young et al., 1997; Aarestrup and Jepsen, 1998; Gerlier and Roche, 1998; Ovidio et al., 1998; Ovidio, 1999). Additionally, different protocols had been used during the same study (e.g. Clapp et al., 1990; Meyers et al., 1992; Young, 1994; Økland et al., 1996; Young et al., 1997). If the conclusions of Baras (1998) apply to trout, such discrepancies are likely to produce substantial artefacts while comparing the behaviour of trout between different rivers and streams, or between different times of the year.

This study relies on a day-by-day study of brown trout in the Belgian Ardennes during spring and summer, and re-examines the results simulating trout being positioned at longer time intervals. It addresses the following questions: 1) how much accuracy on home range and mobility do we lose when increasing the time interval between successive locations? and 2) how much of this loss can be predicted on the basis of locating frequency?

2. METHODS

During 1996 to 1998, nine trout were tagged with surgically implanted radio transmitters (ATS Inc; for details on equipment and tagging methods, see Ovidio et al., 1998; Ovidio, 1999). From 21 March to 21

September (or until the end of the transmitter battery), the fish were located daily between 9h00 and 12h00, in a 12-km reach in the Aisne stream (tributary of the river Ourthe, river Meuse basin, southern Belgium) centred in Bomal-sur-Ourthe (49–50°N, 5–6°E). A minimum of 39 daily positions (excluding the initial release point and final location) were collected for each trout. One fish (trout no. 2), which had been tracked over the entire 1996 season, was recaptured in 1997, tagged with an additional transmitter and tracked over a second season in 1997.

Because the stream was narrow, and distances moved along the stream exceeded substantially those moved laterally, the longitudinal component was taken into account for home range and mobility. In order to measure the reduction of accuracy (*RA*, %) resulting from non daily locating, the sets of daily positions in 1996, 1997, and 1998 were sampled as if the fish had been located at 2, 4, 7, and 14 days intervals. For each temporal sampling protocol, the number of data subsets generated by subsampling was equal to the duration (days) of the time interval between consecutive locations (e.g., 14 subsets for a 14-day interval). Positions on the day of release (day 0) and final tracking day (day $n + 1$) were added to each data set.

For each data set and at each locating frequency, two estimates of dispersion and mobility were calculated: the home range (longitudinal distance between the most upstream and downstream locations) and the overall distance travelled or mobility (sum of distances between consecutive locations). The home range and mobility calculated from subsamples were always inferior or equal to those produced by daily locating, enabling to calculate a relative *RA* depending on time interval between consecutive locations. The consistency between different subsamples at the same locating frequency was deduced from the coefficient of variation of the mean reduction of accuracy. We modelled the relative *RA* against the time interval between consecutive locations. For both mobility and home range, the relationships between the *RA* from observed time interval between consecutive locations and consistency among samples were examined by simple and stepwise multiple regression analyses (using raw data and after log-transformation).

The resulting models were later applied to an independent data set (four fish tracked between 32 and 108 days in spring and summer 1996 and 1998) as a test for their reliability.

3. RESULTS

During the study period, trout occupied home ranges from 13 to 354 m long. Their mobility (running sum of net daily journeys) ranged from 97 to 1 967 m (*table I*). These variables were positively correlated ($R^2 = 0.933$; $P < 0.0001$). Daily journeys mainly corresponded to shifts between different residence areas, depending on water temperature and level (for details,

Table I. Home range and mobility data (sum of distances between consecutive locations) of the nine brown trout radio tracked, and reduction of accuracy (*RA*) when increasing the time interval between consecutive locations*.

Trout no.	<i>FL</i> (mm)	Track. days	Size (m)	Home range <i>RA</i> (%) if locating every <i>n</i> days				Total (m)	Distance travelled <i>RA</i> (%) if locating every <i>n</i> days			
				Time between consecutive locations					Time between consecutive locations			
				2d	4d	7d	14d		2d	4d	7d	14d
1	399	140	144	22.2	33.3	38.1	43.3	678	22.7	61.3	65.1	77.9
				40.4	33.3	27.1	22.7		20.0	39.6	46.8	64.1
2a	285	112	32	23.4	60.9	47.3	66.6	213	47.9	78.6	78.4	87.4
				2.9	74.0	38.4	68.5		3.8	65.2	31.4	59.6
2b	325	56	23	19.6	29.3	49.1	59.3	218	42.2	69.5	85.4	91.2
				34.4	27.7	53.7	57.9		7.9	18.3	64.1	65.5
3	279	70	13	3.8	11.5	17.7	18.5	97	44.8	62.9	73.6	81.1
				5.7	11.2	17.6	8.7		19.8	33.5	32.5	22.4
4	428	84	354	21.6	32.6	37.0	53.9	1 967	7.2	42.2	67.0	84.3
				39.0	31.9	26.2	53.4		8.9	14.5	27.0	68.7
5	304	84	327	3.1	4.6	5.2	10.3	1 517	5.0	36.7	57.0	67.1
				4.5	3.2	2.4	5.8		15.5	13.5	32.7	21.1
6	299	70	43	0.0	12.4	28.9	38.8	396	23.7	69.2	80.4	88.0
				0.0	27.8	35.9	42.1		24.1	32.9	36.1	54.4
7	266	39	214	3.0	28.3	56.1	74.9	656	17.7	57.5	68.5	86.2
				4.4	31.4	88.5	138.0		12.0	62.3	91.7	150
8	272	39	90	27.8	38.6	66.6	81.8	405	44.8	66.5	83.0	92.0
				32.6	29.8	90.7	121		38.9	12.7	91.1	121.0
9	280	39	141	8.9	14.2	20.9	39.4	811	31.1	40.0	62.7	73.6
				13.8	12.2	16.4	43.0		3.7	7.5	13.9	40.9
Mean loss of accuracy (%)				13.3	26.6	36.7	48.7		28.7	58.4	72.1	82.9
Models				17.7	28.2	39.7	56.1		15.5	30.0	46.7	60.4
				$RA = 1.071 + 41.804 \log LPF$					$RA = 14.572 + 63.533 \log LPF$			
				$r^2 = 0.370; F = 22.28; df = 39; P < 0.0001$					$r^2 = 0.710; F = 92.81; df = 39; P < 0.0001$			

* For each temporal sampling protocol, the subsampling process produces as many the number of data as the duration (days) of the time interval between consecutive locations. For each locating frequency (*LPF*, every *n* days) the values given are the mean reduction of accuracy (bold) and coefficient of variation (*CV*; %) over the *n* subsets generated by the subsampling process.

see Ovidio, 1999). On some occasions these movements resulted in a permanent change of residence.

3.1. Reduction of accuracy depending on locating frequency

Locating fish less frequently than once a day produced contrasting data sets, depending on fish and parameters considered (*table I*). Because the fish examined here had been tracked over contrasted periods of time and occupied either short or long home ranges, we first tested whether the *RA*, as a result of looser location frequency, was dependent on tracking duration and home range size. No significant correlation was found, either for home range size or distance travelled, suggesting that all data could be pooled into a single analysis.

For fish no. 5, which had a 327-m home range, a locating frequency of once a week would only have caused a *RA* of 5.2% for the home range. The corresponding *RA* for fish no. 8 in 1998, which occupied a smaller range (90 m), would have amounted to

66.6%. By contrast, the *RA* (home range and mobility) was strongly dependent on individual fish behaviour, with maximal underestimation corresponding to individuals moving frequently in between several residences. The comparison between the data sets of 1996 and 1997 for trout no. 2 shows similar losses of accuracy for both parameters, except for the 4-day interval, due to an exceptionally strong summer spate that displaced the fish out of his seasonal range in 1996.

Considering all ten data sets altogether (*table I*), it becomes obvious that locating frequency longer than once a day produced very high losses of accuracy (except for home range at a 2-day intervals, but even 13.8% may probably be unacceptable for some studies, *table I*). The *RA* always was higher when estimating mobility (28.7% to 82.9%, from 2 to 14 days) than when estimating home range (13.3% to 48.7%, respectively). Feeble *RA* for the home range can be associated with high losses of accuracy for the mobility (trout nos. 5 and 6).

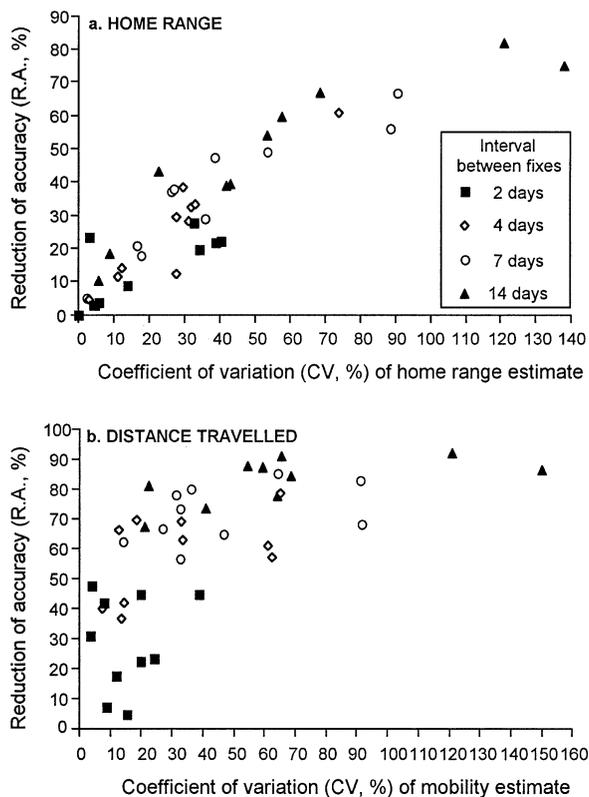


Figure 1. Correspondence between the reduction of accuracy (RA) in estimating trout home range (a) or distance travelled (b) when increasing the locating frequency (LF), and the consistency of the samples, as measured by their coefficient of variation. Different symbols refer to different locating frequencies (intervals of 2 to 14 days between consecutive fixes). The models are generated by stepwise multiple-regression analyses, with the variables (\pm standard error) presented in order of integration into the analysis.

Model a: $RA = 0.278 + 0.534 CV + 16.924 \log LF$ ($R^2 = 0.855$)

Model b: $RA = 0.417 + 16.020 \log CV + 50.785 \log LF$ ($R^2 = 0.749$)

3.2. Predictive models of reduction of accuracy from observed

Both for home range and mobility, RA was significantly correlated with the time interval between successive locations (*table I*). Higher losses of accuracy also corresponded to higher heterogeneity between subsamples at the same locating frequency (*figure 1*). Both variables were significantly retained by a stepwise multiple-regression analysis and improved the resolution of the models, especially for estimating home range (*figure 1*).

These models were evaluated with an independent sample of four trout tracked in summer 1996 and 1998, using time intervals of 2, 4 and 7 days, and a corresponding sample of four sets of weekly intervals to apply the multiple-regression model. Plotting losses of accuracy against locating frequency for these four trout gave results similar to those above (*table II*). Simple predictive models improved the accuracy of

home range estimates by a 15–16% margin at 4 and 7-day intervals, whereas they did not at 2-day intervals. For mobility, simple models always produced better estimates than those obtained from tracking data, whichever the time interval between successive locations (i.e. gain of 20 and 15% of accuracy, for 4 and 7-day intervals, respectively). By contrast, multiple-regression models produced estimates of home range or mobility that were worse than those given by the 2-day interval simple model, and even worse than those estimated from the 2-day interval raw data (*table II*).

4. DISCUSSION

This study showed that locating trout less than once a day indeed could generate some of the disadvantages brought about by capture–recapture techniques, since home range and mobility were systematically, and sometimes strongly, underestimated. The losses of accuracy were further proportional to the interval between successive locations.

The simple predictive models proposed here indeed were less accurate than those produced for *Barbus barbus*, but still reduced substantially the loss of accuracy resulting from longer time intervals between fixes. It is clear that the choice of a locating frequency is intimately dependent on the objective of the study, but our observations suggest that an interval longer than two days would produce excessive losses of accuracy (> 25%) for brown trout during spring and summer. This statement corroborates the conclusions of two previous tracking studies which provided evidence that the spawning migration of trout is ruled by a combination of variations of environmental factors, which apparently act at the daily level (Ovidio et al., 1998; Ovidio, 1999).

In this study, spring and summer were analysed altogether, in view of the similarity between the behaviours of trout during these two seasons (at least in the Aisne stream, Ovidio, 1999). Trout movements during these seasons are not unidirectional, sometimes consisting of short journeys followed by homing, making looser tracking locations more likely to underestimate the actual movement patterns of trout than during autumn, when trout migrate almost unidirectionally to upstream spawning grounds (for Aisne stream, see Ovidio, 1999). Hence, non-daily locating in autumn would cause a much lower loss of accuracy than in summer (< 1% for home range and < 14% for mobility at 28-d intervals; M. Ovidio, unpublished data). This further indicates that losses of accuracy caused by non-daily locating are dependent on season and probably on other factors, such as habitat or fish strain, that both influence the life-history and mobility pattern of trout (Baglinière and Maisse, 1991).

Long time intervals between fixes produced higher losses of accuracy in trout than in *Barbus barbus* (Baras, 1998). This may be due to differences in the social ecology of the two species. Brown trout often

Table II. Relative reduction of accuracy (*RA*) in estimating the home range (longitudinal extension) and distance travelled of *Salmo trutta* depending on locating frequency and use of correcting models*.

	Location	R. Ourthe				Aisne stream			
		Fish 1	Fish 2	Fish 3	Fish 4	Fish 1	Fish 2	Fish 3	Fish 4
		Home range (m)				Distance travelled (m)			
	<i>FL</i> (cm)	48	31	29	28	48	31	29	28
Observed tracking									
1 day		300	4 760	465	70	1 727	19 005	1 335	351
2 days	mean (m)	278	4 733	460	63	972	13 780	1 112	268
	<i>CV</i> (%)	11	1	1.5	17	2	28	8	39
4 days	inaccuracy (%)	-7.2	-0.1	-1.1	-10.5	-43.8	-27.5	-16.7	-23.6
	mean (m)	180	2 620	246	46	588	7 016	547	137
7 days	<i>CV</i> (%)	67	45	103	38	41	106	94	54
	inaccuracy (%)	-40.2	-45.0	-48.0	-34.0	-66.0	-63.1	-59.0	-61.1
7 days	mean (m)	117	2 001	148	37	339	4 014	322	85
	<i>CV</i> (%)	98	111	141	35	69	111	136	41
7 days	inaccuracy (%)	-67.4	-58.0	-68.3	-47.6	-80.4	-78.9	-75.9	-75.7
	Modelled tracking								
2 days	mean (m)	317	5 379	522	71	1 300	18 424	1 487	358.3
	inaccuracy (%)	+5.5	+13.0	+12.3	+1.4	-24.8	-3.1	+11.4	+2.1
4 days (simple model)	mean (m)	22	3 307	305	58	898	10 720	836	209
	inaccuracy (%)	-24.6	-30.5	-34.4	-16.6	-48.0	-43.6	-37.4	-40.6
7 days (simple model)	mean (m)	358	2 729	201	50	572	6 756	542	144
	inaccuracy (%)	+19.9	-42.7	-56.7	-28.5	-66.9	-64.5	-59.4	-59.1
7 days (multiple models)	mean (m)	333	5 602	50	88	543	7 085	575	146
	inaccuracy (%)	+11.1	+17.7	-28.5	+25.6	-68.9	-62.8	-56.9	-58.4

* Observed data give estimates based on observations at 1, 2, 4, and 7 day(s) intervals from four trout radio-tracked in 1996 (fish 1) and 1998 (fish 2, 3 and 4). Modelled data were generated by the correcting models obtained from the 1995–1998 data sets (simple models in *table I*, multiple linear models in *figure 1*). Mean *RA* is the absolute estimate of inaccuracy (under- or overestimation) against the values obtained by daily locating.

are territorial individuals showing a wide range of behaviours and mobility patterns (Baglinière and Maisse, 1991; Elliot, 1994; Ovidio, 1999), whereas barbel usually aggregate in shoals (Baras, 1992, 1997). Hence their behaviour is presumably more stereotyped and predictable (Baras, 1995; Lucas and Batley, 1996), and can thus be more accurately modelled than for trout.

This comparison emphasises further that predictive models can be of similar nature for different species, but no transposition between species or strain, or even populations can be made without a proper calibration. As a corollary, this study indicates further that any comparison between data sets or studies relying on different locating frequencies could generate misleading conclusions and interpretations of biological phenomena or geographical differences. Hence, we recommend that future tracking studies rely on a day-by-day location protocol, in order to provide structured bases for straightforward comparisons. Nevertheless, there already are large amounts of existing information that have been collected during past or ongoing salmonid tracking programmes. Although we do not advocate for extrapolation, it might also be interesting to re-analyse these data at the light of corrective models (to be elaborated on a site-specific basis), and ideally to test for the relevance and predictability of these models in the course of a validation study. This

would permit to make the most of existing data, the compilation of which might contribute to a more thorough analysis of how genetic traits and environmental characteristics shape the mobility patterns and history of trout.

Also, we are particularly aware that a locating frequency of 1-day interval probably generates biases compared to actual movements of trout, and ideally, fish should be monitored continuously to obtain the most accurate results. For practical reasons essentially, this may not be feasible. Hence we recommend, as others did before us, to combine day-by-day tracking with 24-h cycles of observation. As such, the tracking calendar should be adapted to address the broadest possible range of environmental conditions that may influence fish behaviour. Beyond typically season-dependent climates, these should include the potential impact of industries during working days, leisure activity such as kayaking during weekends, and timings of turbine activity in hydropower plants with fixed operational schedules. Eventually, a procedure similar to that presented here could be applied to test for the reduction of accuracy resulting from locating fish at 1-day intervals.

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References

- Aarestrup, K., Jepsen, N., 1998. Spawning migration of sea trout *Salmo trutta* (L.) in a Danish river. *Hydrobiologia* 371/372, 275–282.
- Baglinière, J.L., Maisse, G., 1991. La truite: biologie et écologie. INRA Éditions, Paris.
- Baras, E., 1992. Étude des stratégies d'occupation du temps et de l'espace chez le barbeau fluviatile, *Barbus barbus* (L.). *Cah. Éthol. Appl.* 12, 125–442.
- Baras, E., 1995. Seasonal activities of *Barbus barbus* (L.) – Effect of temperature on time-budgeting. *J. Fish Biol.* 46, 816–828.
- Baras, E., 1997. Environmental determinants of residence area selection and long term utilisation in a shoaling teleost, the common barbel (*Barbus barbus* L.). *Aquat. Living Resour.* 10, 195–206.
- Baras, E., 1998. Selection of optimal positioning intervals in fish tracking: an experimental study on *Barbus barbus*. *Hydrobiologia* 371/372, 19–28.
- Clapp, D.F., Clark, R.D., Diana, J.S., 1990. Range, activity and habitat of large, free-ranging brown trout in a Michigan Stream. *Trans. Am. Fish. Soc.* 119, 1022–1034.
- Clough, S., Ladle, M., 1997. Diel migration and site fidelity in a stream-dwelling cyprinid, *Leuciscus leuciscus*. *J. Fish Biol.* 50, 1117–1119.
- Elliot, J.M., 1994. *Quantitative Ecology and the Brown trout*. Oxford University Press, Eynsham, England.
- Evans, D.M., 1994. Observations on the spawning behaviour of male and female adult sea trout, *Salmo trutta* L., using radio-telemetry. *Fish. Manage. Ecol.* 1, 91–105.
- Fausch, K.D., Young, M.K., 1995. Evolutionarily significant units and movement of resident stream fish: A cautionary tale. *Am. Fish. Soc. Symp.* 17, 360–370.
- Gerlier, M., Roche, P., 1998. A radio telemetry study of the migration of Atlantic Salmon (*Salmo salar* L.) and sea trout (*Salmo trutta trutta* L.) in the upper Rhine. *Hydrobiologia* 371/372, 283–293.
- Gowan, C., Young, M.K., Faush, K., Riley, S., 1994. Restricted movements in resident stream salmonids: a paradigm lost? *Can. J. Fish. Aquat. Sci.* 51, 2626–2637.
- Haynes, J.M., Gerber, G.P., 1989. Movements and temperatures of radiotagged salmonines in lake Ontario and comparisons with other large aquatic systems. *J. Freshwater Ecol.* 5, 197–204.
- Hawkins, A.D., Urquhart, G.G., 1983. Tracking fish at sea. In: McDonald, A.G., Priede, I.G. (Eds.), *Experimental Biology at Sea*. Academic Press, London, pp. 103–166.
- Lucas, M.C., Batley, E., 1996. Seasonal movements and behaviour of adult barbel *Barbus barbus*, a riverine cyprinid fish: implications for river management. *J. Appl. Ecol.* 33, 1345–1358.
- Meyers, L.S., Thuemler, T.F., Kornely, G.W., 1992. Seasonal movements of brown trout in Northeast Wisconsin. *N. Am. J. Fish. Manage.* 12, 433–441.
- Nettles, D.C., Haynes, J.M., Olson, R.A., Winter, J.D., 1987. Seasonal movements and habitats of brown trout (*Salmo trutta*) in Southcentral lake Ontario. *J. Great Lakes Res.* 13, 168–177.
- Økland, F., Jensen, J.A., Johnsen, B.O., 1996. Winter habitat and seaward migration of a Norwegian brown trout population. In: Baras, E., Philippart, J.C. (Eds.), *Underwater Biotelemetry, Proc. 1st conference on fish telemetry in Europe*, University of Liège, Belgium, pp. 161–171.
- Ovidio, M., 1999. Annual activity cycle of adult brown trout (*Salmo trutta* L.): a radio-telemetry study in a small stream of the Belgian Ardenne. *Bull. Fr. Piscic.* 352, 1–18.
- Ovidio, M., Baras, E., Goffaux, D., Birtles, C., Philippart, J.C., 1998. Environmental unpredictability rules the spawning migrations of trout (*Salmo trutta*) in the Belgian Ardennes. *Hydrobiologia* 371/372, 263–274.
- Philippart, J.C., Baras, E., 1996. Comparaison of tagging and tracking studies to estimate mobility patterns and home range in *Barbus barbus*. In: Baras, E., Philippart, J.C. (Eds.), *Underwater Biotelemetry, Proc. 1st conference on fish telemetry in Europe*, University of Liège, Belgium, pp. 3–12.
- Schulz, U., Berg, R., 1992. Movements of ultrasonically tagged brown trout (*Salmo trutta* L.) in Lake Constance. *J. Fish. Biol.* 40, 909–917.
- Swihart, R.K., Slade, N.A., 1985. Testing for independence of observations in animal movements. *Ecology* 66, 1176–1184.
- Young, M.K., 1994. Mobility of brown trout in south-central Wyoming streams. *Can. J. Zool.* 72, 2078–2083.
- Young, M.K., Wilkison, R.A., Phelps, J.M. III, Griffith, J.S., 1997. Contrasting movement and activity of large brown trout and rainbow trout in Silver Creek, Idaho. *Great Basin Nat.* 57, 238–244.