Linking juvenile growth and migration behaviour of brown trout (*Salmo trutta*) using individual PIT-tagging

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Abstract: A study was carried out on the brown trout population of the Oir River (Normandy, France) to understand the relation between juvenile growth and migratory behaviour (i.e. localisation of the growing environment). Thus 5894 0+ brown trout have been PIT-tagged from 1995 to 1999 and monitored using flat bed antennae, permanent trapping and electrofishing to interpret fish movements at a fine spatial and temporal scale as well as growth performances. Data have been analysed to group individuals according to life history traits, including juvenile growth, sex and migration processes in freshwater and to the sea. Results showed that migratory behaviour is variable among year classes and that juvenile growth rates during first and second years play important but different roles on migration determinism.

Résumé. *Relation entre la croissance des juvéniles et le comportement migratoire de la truite (*Salmo trutta*) mise en évidence par la technique de marquage par PIT-tag.* Une étude a été menée sur la population de truite commune de l'Oir (Normandie, France) afin de mettre en évidence les relations entre croissance juvénile et comportement migratoire (i.e. zone de croissance sub-adulte). Ainsi, de 1995 à 1999, 5894 truites d'âge 0+ ont été marquées individuellement à l'aide de PIT-tags (Passive Integrated Transpander) et suivies à l'aide d'antennes fixes, d'un piège de dévalaison et d'échantillonnages par pêche électrique afin de connaître, à fine échelle, leurs déplacements ainsi que l'évolution de certaines caractéristiques biométriques telles que la croissance. Les données ont été analysées afin de regrouper les individus en fonction de leurs traits d'histoire de vie, incluant la croissance juvénile, le sexe et les processus de migration en eau douce et vers la mer. Les résultats montrent que les comportements migratoires sont variables entre les cohortes et que les croissances juvéniles lors de la première et seconde année de vie jouent des rôles importants et différents dans le déterminisme de la migration.

Keywords: Migration; Juvenile growth; PIT-tag; Flat-bed antenna; *Salmo trutta*; Oir River.

Introduction

Salmonids are diadromous species that exploit both fresh-water and marine environments and have to migrate between these environments at least twice during their life history (McDowall, 1988). Nevertheless, some individuals remain during their entire life in the river and exhibit variable patterns of migration within freshwater systems (Baglinière et al., 1989; Gowan et al., 1994). Brown trout is the most ecologically variable salmonid species (Elliot, 1994) and partial migration in brown trout population (i.e. a population that splits into anadromous and freshwater resident individuals) occurred in many coastal streams (Jonsson, 1985; L'Abbée-Lund et al., 1989; Jonsson & Jonsson, 1993). Migration behaviour of brown trout is highly variable and the factors influencing its determination are numerous but growth is certainly the most significant one (Ombredane et al., 1998; Baglinière et al, 2001). Growth parameters are influenced by genetic and environmental factors and their roles in the determination of migration behaviour have already been studied experimentally or in the wild showing that high-growth-rate individuals tend to migrate (e.g. Skrochowska, 1969; Jonsson, 1989). Nevertheless in the wild, growth parameters were estimated by back calculation from scales and this may lead to errors of growth estimation (Berg & Jonsson, 1990; Ombredane & Baglinière, 1992). The use of Passive Integrated Transponder (PIT) tags is a way to measure empirical growth parameters (Vollestad et al., 2002) as well as monitoring fine scale movements in fresh water (e.g. between nursery brook and river: Armstrong et al., 1996; Olsson & Greenberg, 2004). In the present paper, we studied juvenile growth and fine scale and diadromous migrations of 5894 0+ brown trout which were PIT-tagged in their first year of life. Then we analysed the influence of juvenile growth on migration behaviour in a partial migration population, including both freshwater and anadromous movements. This work focused on the qualitative relation between juvenile growth and migration behaviour as part of a larger study (Cucherousset et al., 2005) that investigated the overall life history tactics in the population including adult migration and reproductive life history traits.

Materials and methods

The study was carried out on the Oir River watershed (Normandy, France), including five major tributaries (the Moulin du Bois, the Sourvallée, the Roche, the Moulinet and the Pont-Lévêque brooks). The Oir River flows into the Sélune River at eight kilometres from the sea (English Channel) in the Mont-Saint-Michel bay (Fig. 1). The brown trout population includes both freshwater resident and anadromous individuals. These two forms have been described as sympatric and no genetic differentiation using 15 microsatellites markers was found between anadromous and non-anadromous individuals (Charles et al., 2005). The study consisted in the monitoring of 5894 PIT-tagged young-of-the-year brown trout belonging to five consecutive year classes (1995-1999). Fish were first captured by electrofishing, anaesthetized, measured and then the PIT-tag (11.5 mm long and 2.12 mm diameter) was injected using a sterilized needle in the peritoneal cavity. After recovering, fish were released in the river section in which they were caught. The average PIT-tag loss is low (3.38% on average) and tagging does not show any significant effect on growth and mortality of age 0 juveniles (see details in Ombredane et al., 1998). The survey was operated using three methods: (1) brown trout were recaptured once a year in October by electrofishing; (2) fish emigrating from the Oir River watershed were captured in the Cerisel mill trapping system that was operating continuously during the seven years; (3) fish emigrating from one of the natal brooks were recorded by flat bed antennae disposed at the mouth of each brook and at the Cerisel mill. The study was conducted until December 2002, i.e. once the 1999 year class fish had migrated. Fish migrating in the Sélune River were differentiated from sea migratory individuals based on morphological criteria defined by Baglinière et al. (2000). Nevertheless, fish that were not trapped but recorded by the Cerisel mill antennae were assigned to migrate "out of the Oir River".

Using all data accumulated by the three survey methods during the whole study (1995-2002), we assigned life history traits to investigate the relation between growth, sex and migration of juvenile brown trout. First year of growth was calculated using fork length at age 0 in October divided by the time elapsed between the mean spawning date and the date of tagging. The second year growth was the difference of fork length between the recapture at age 1 in October and the capture at age 0. Juvenile growth parameters were expressed in mm.day^{-1}. Life history traits are listed in Table 1, including the categories in which they have been decomposed. Indeed because of their variability high among year classes (Mann-Whitney U test, $p < 0.01$), first and second year growth were standardized (centred and normalized) to perform the analyses on the whole data set accumulated in seven years. A multiple correspondence analyses (MCA) was performed on life history traits followed by a hierarchical cluster analysis using individual factorial scores of the MCA principal axes to group individuals in relation with their juvenile life history traits. Then, we tested differences in migratory behaviour among year classes using Khi^2 test and in first and second year of growth between groups by performing a series of multiple comparisons using post hoc Tukey procedures for parametric ANOVA.
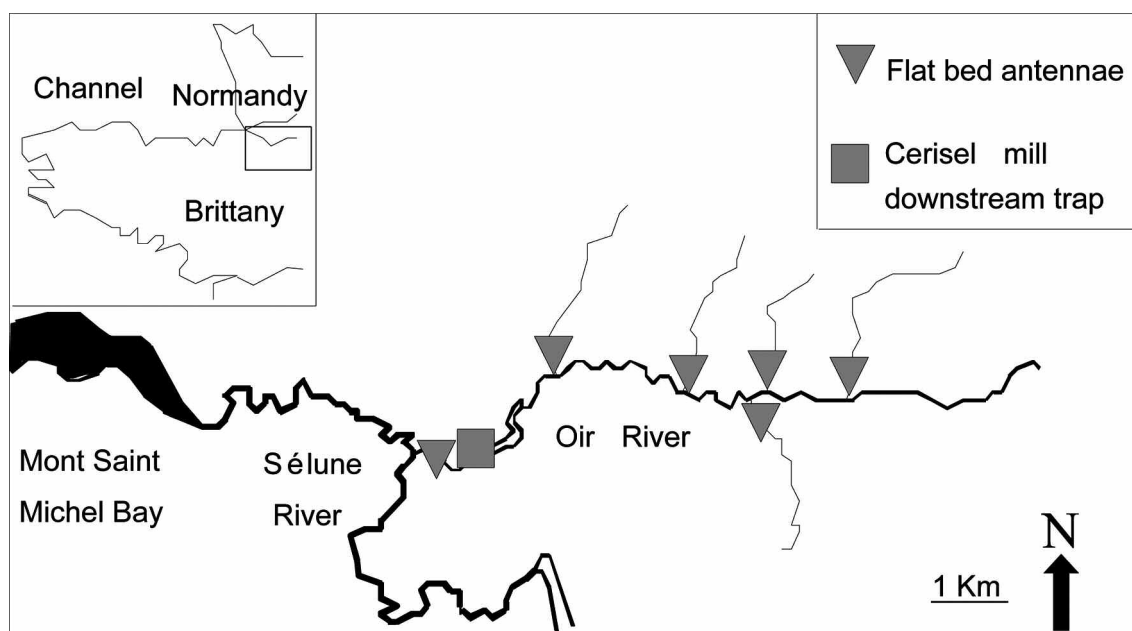
Figure 1. Map of the Oir River watershed including the location of the flat bed antennae and the permanent trapping system of the Cerisel mill.
Figure 1. Carte du bassin versant de l'Oir: localisation des antennes et du système de piégeage du moulin de Cerisel.

Table 1. List of the life history traits and composition of the five groups of brown trout created by the cluster analyses.
**Tableau 1**. Liste des traits d'histoire de vie et composition des cinq groupes de truites communes créés par l'analyse hiérarchique.

Life history traits	Group 1	Group 2	Group 3	Group 4	Group 5
Migration	Brook	Brook	Sea	Oir River	Sélune River
Sex	Male	Male	Female	Male and female	Male and female
1st year growth	Very low	High and very high	Very high	Low and medium	High and very high
2nd year growth	Very low and low	Low and medium	Medium	High and very high	-
Age at emigration from natal brook	-	-	2+	0+ and 1+	1+
Age at emigration from Oir River	-	-	2+	-	1+
Size at emigration from Oir River	-	-	Medium and very high	-	Very low and low

Results

The distribution in the five growing environments (natal brook, Oir River, Sélune, River, Sea and out of the Oir River) was variable among some of the five year classes (Khi^2 test, df = 4, p < 0.05) but did not follow any particular trend during this period (Fig. 2). Using the 1288 individuals monitored until they migrated, five groups of fish were discriminated by the cluster analysis (Table 1 and Fig. 3). Group 1 included trout with a very low first and second year growth that did not migrate out of their natal brook. This group was composed of males. Group 2 was also composed of males that spent their life in their natal brook

with a high to very high first year growth and a low and medium second year growth. Group 3 included females with a very high first year growth and a medium second year growth. At age 2+, they left freshwater (natal brook and Oir River) and migrated to the sea. They left freshwater with a high body size. Group 4 included individuals (males and females) that migrated downstream out of their natal brook to the Oir River during their first winter (age 0+) or their first spring (age 1+). They grew within the Oir River. Group 5 included fish (males and females) with a high first year growth and an indefinable second year growth. These fish migrated downstream at age 1+ to grow in the Sélune river. They left the Oir river system with a
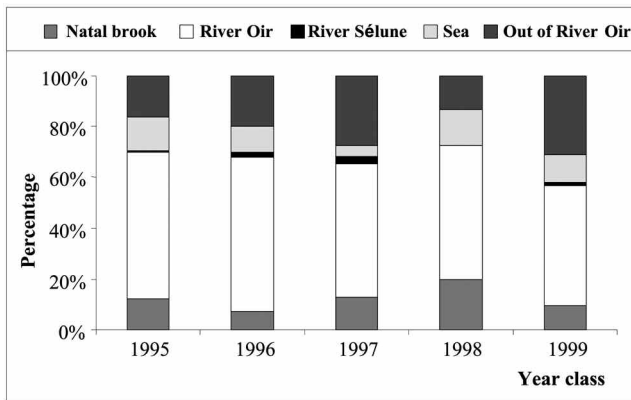
Figure 2. Interannual variability in growing environment of PIT-tagged juvenile brown trout among the five year classes. All pairwise comparisons of year classes were different (Khi^2 test, df = 4, p < 0.05), except 1995 and 1996 (p = 0.134) and 1995 and 1998 (p = 0.518).

Figure 2. Variabilité interannuelle des zones d'engraissement des juvéniles de truites communes marquées par PIT tag pour les cinq cohortes. Toutes les comparaisons appariées des cohortes étaient différentes (Test Khi^2, ddl = 4, p < 0,05), exceptées 1995 and 1996 (p = 0,134) et 1995 et 1998 (p = 0,518).

(calculated using PIT tagging data) allowed distinguishing individuals from the group 2 and 3.

Discussion

Our study showed that the use of life history traits calculated from PIT tagging data enables to demonstrate the variability of migratory behaviour among year classes and to improve understanding of the linkage between juvenile growth parameters and migration behaviour of brown trout. The variability of environmental parameters, such as water flow, fish density or temperature are known to affect juvenile brown trout growth (e.g. Baglinière et al., 2001) and might be a relevant cause to explain the variability of migration behaviour among year classes. Thus their effects on brown-trout life-history-tactics determinism and variability using long term data should be thoroughly investigated in order to understand how they might modulate population functioning. Migration within the freshwater network (Oir and Sélune rivers) and to the sea appeared related to higher growth of fish during their first year of life, as demonstrated in previous studies (Ombredane et al., 1998; Maisse & Baglinière, 1999). Nevertheless, some individuals with high juvenile growth rates remained all their life in their natal brook as the result of a sexual dimorphism in life history due to the higher energetic needs for sexual maturation in females than in males (Baglinière et al., 2001).

Our study showed that the use of PIT-tag technology allows to characterize fine scale movements within the drainage and to emphasize the role of the second year of growth in the determination of migration behaviour. Particularly in a brown trout population where no genetic differences between anadromous and non-anadromous individuals occurred (Charles et al., 2005), migration behaviour appeared to evolve during fish life. Thus, a fish will migrate until satisfying its metabolism needs and finding an adapted trophic condition after a first migration at age 1+ (expressed by a high second year growth), as showed by fish belonging to the group 4. The origins of

smaller size that fish of group 3 (Fig. 3). Nevertheless, few females that spent their entire life in the brook and few males that migrated to the sea were found but not sufficiently to appear in the cluster analyses.

The standardized values of first and second years of growth were assigned to the individuals belonging to the five groups defined by the cluster analysis (Fig. 3). The large overlapping of the growth values showed the need for a use of several life history traits (e.g. sex) to distinguish some migration behaviours. Indeed, some individuals with comparable growth performances during first and second years might demonstrate variable migratory behaviours such as individuals belonging to group 2 and group 5 (Table 3). As well, the use of the second year of growth

Table 2. Results (p values) of ANOVA followed the post hoc Tukey procedures to compare growth parameters assigned to the five groups created by the cluster analysis. NS means no significant.

Tableau 2. Résultats (probabilités p associées) des ANOVA suivis de la procédure de Tukey de comparaison des croissances attribuées aux cinq groupes issus de l'analyse statistique. NS signifie non significatif.

	First year of growth						Second year of growth				
Group	1	2	3	4	5	Group	1	2	3	4	5
1	-					1	-				
2	< 0.01	-				2	< 0.01	-			
3	< 0.01	NS	-			3	< 0.01	0.03	-		
4	< 0.01	< 0.01	< 0.01	-		4	< 0.01	< 0.01	< 0.01	-	
5	< 0.01	NS	NS	< 0.01	-	5	< 0.01	NS	NS	< 0.01	-
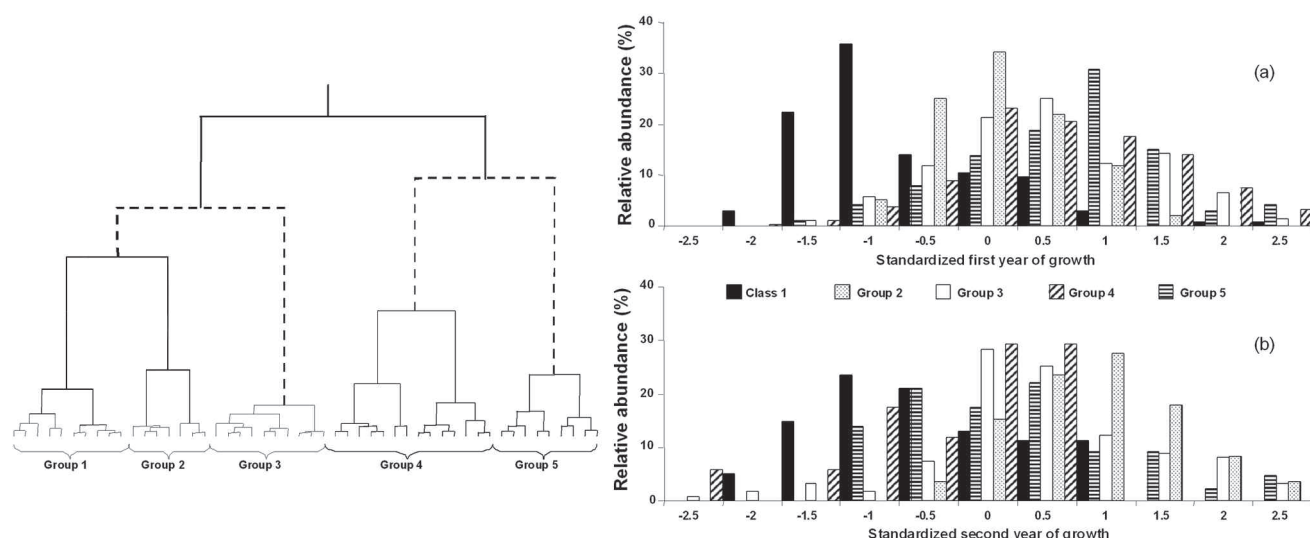
Figure 3: Results of the cluster analysis based on migratory, sex and growth traits (left) and distribution (right, relative abundance in %) of the five brown trout groups from the cluster analysis relatively to (a) their first year growth and (b) their second year growth. Growth data are standardized.

Figure 3. Résultats de l'analyse hiérarchique basée sur les traits migratoires, sexuels et de croissance et distribution (abondance relative en %) des cinq groupes de truites communes issus de l'analyse statistique en fonction de leur première année de croissance (a) et de leur seconde année de croissance (b). Les données de croissance sont centrées et réduites.

metabolic rate and individual need are uncertain (Baglinière & Maisse 1990) but nevertheless they appear to influence displacements and migration behaviour. Migration behaviour appears clearly as a result of a phenotypic plasticity (Stearns, 1992) resulting from the interaction between individual genetic characteristics and environmental conditions, including both biotic and abiotic factors (Jonsson & Jonsson, 1993).

A large proportion of the fish migrating outside of the Oir River drainage were females. Females' fitness is strongly dependent upon their size (Jonsson & Jonsson, 1993) and females have higher energetic needs to mature (Baglinière et al., 1989; Euzenat et al., 1999). Thus, they will attempt to migrate towards more productive environments. Our results confirmed that most males are resident and most migrant are females (Jonsson & Jonsson, 1993) in the sense that females generally migrate the farthest, up to the sea, underscoring the important role of marine ecosystem for the population.

In conclusion, as partial migration in a population evolved in response to resource availability in a changing habitat (Jonsson & Jonsson, 1993), it would be of interest to understand how the evolution of coastal conditions and climatic changes impact the functioning of such a population. Indeed the modifications of estuarine and marine parameters related to population dynamics such as mortality rate or trophic conditions might change the advantages of anadromous migration and so impact the equilibrium of migration behaviour in coastal brown trout population.

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