A continuum of life history tactics in a brown trout (*Salmo trutta*) population

Julien Cucherousset, Dominique Ombredane, Katia Charles, Frédéric Marchand, and Jean-Luc Baglinière

Abstract: Life history tactics of the brown trout (*Salmo trutta*) population of the Oir River (Normandy, France) were studied using passive integrated transponder (PIT) tagging data of five consecutive cohorts (5900 individuals) monitored between 1995 and 2002. Results demonstrate that (*i*) life history traits vary among cohorts, chiefly caused by environmental variability, (*ii*) juvenile growth, particularly second-year growth, plays an important role in the determination of the growing environment and trout exhibit variable migratory behaviour (from remaining in the natal brook to migrating in the sea) related to their juvenile growth rate, and (*iii*) the description of life history tactics (including juvenile growth, fine-scale migratory behaviour, and reproduction) can be clarified. Tactics are expressed along a continuum in time (age to reproduce) and space (distance of migration). Flexible life history tactics varying with juvenile growth is consistent with previous studies, but the use of empiric data on growth and migration from PIT tagging allows refining the description of life history tactics, taking into account their continuous distribution in time and space.

Résumé : Les tactiques d'histoire de vie de la population de truite commune (*Salmo trutta*) de l'Oir (Normandie, France) ont été étudiées par le marquage individuel à l'aide de « PIT tag » de cinq cohortes consécutives (5 900 individus) suivies de 1995 à 2002. Les résultats confirment et démontrent que (*i*) les traits d'histoire de vie varient entre les cohortes et que cette variabilité peut être reliée principalement aux fluctuations des conditions environnementales, (*ii*) la croissance juvénile, plus particulièrement celle de la seconde année de vie, est un facteur important dans la détermination de la zone de croissance et les truites possèdent des comportements migratoires variables, allant de la résidence stricte au ruisseau natal jusqu'à la migration en mer, que l'on peut relier à leur taux de croissance juvénile et (*iii*) la description des tactiques d'histoire de vie (en incluant la croissance juvénile, le comportement migratoire à fine échelle et la reproduction) peut être affinée, les tactiques se distribuant le long d'un continuum temporel (age de reproduction) et spatial (distance de migration). La flexibilité des tactiques d'histoire de vie et leurs liens avec la croissance juvéniles sont confirmés dans cette étude. Cependant l'utilisation de données empiriques sur la croissance et la migration issues du marquage individuel par PIT tag a permis d'améliorer la description des tactiques en prenant en compte leur distribution continue dans le temps et l'espace.

Introduction

Salmonids are excellent models for testing predictions from evolutionary theory (global review in Hendry and Stearns 2003), e.g., alternative mating tactics (Gross 1985), evolution of reproductive traits (Kinnison et al. 2001; Olsen and Vøllestad 2003), evolution of migration (Gross 1987; Kinnison et al. 2003), and homing mechanisms (McDowall 2001). They are also particularly interesting because of the polymorphism of their life history tactics and migratory behaviour. This plasticity allows brown trout (*Salmo trutta*) to be the most ecologically variable and successful salmonid species (Jonsson 1989; Elliott 1994; Baglinière 1999). Here, the term "partial migration" is used to describe the phenomenon where a population splits into anadromous and resident individuals (Jonsson and Jonsson 1993). In these brown trout populations, present in coastal rivers (Jonsson 1985; L'Abbée-Lund et al. 1989), anadromous individuals migrate to the sea, whereas residents spend their entire life in fresh water. Migrant and resident adults can spawn successfully together (Jonsson 1985; Pettersson et al. 2001) and juveniles may grow up together and are indistinguishable during ontogeny, i.e., until migrants smoltify (Baglinière et al. 2000). The decision between anadromy and freshwater residence is

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an example of phenotypic plasticity and is influenced by both genetic and environmental factors (Jonsson and Jonsson 1993; Klemetsen et al. 2003).

The relationship between juvenile growth rate and migratory behaviour of brown trout has already been investigated (Jonsson 1985; Jonsson and Gravem 1985) but juvenile growth rate was usually estimated by back-calculation from scales or otoliths (e.g., Jonsson and Hindar 1982; L'Abée-Lund et al. 1989) and this may lead to errors of growth estimation (Berg and Jonsson 1990). The use of passive integrated transponders (PIT) is a method to acquire empiric data on growth (e.g., Vøllestad et al. 2002) because it allows for the individual marking of juveniles and the study of their entire life history (Prentice et al. 1990; Lucas and Baras 2000). As well, many studies on migration behaviour of brown trout have focused on anadromous versus freshwater resident individuals because the two forms were distinguished using morphological criteria (e.g., Jonsson 1985; Jonsson et al. 2001). Nevertheless, some resident fish exhibit freshwater migration (Baglinière et al. 1989; reviewed in Gowan et al. 1994) and these migrations were not integrated in the previous analyses of life histories. Owing to its characteristics, PIT technology allows monitoring of fine-scale movements (Armstrong et al. 1996; Greenberg and Giller 2000; Roussel et al. 2000) and freshwater migratory processes (Olsson and Greenberg 2004).

In the present study, we investigated the relationship between empiric growth rate, migratory behaviour including freshwater migrations, and life history tactics of wild brown trout from five consecutive cohorts of the Oir River population. Thus, we monitored 5900 age-0 PIT-tagged individuals during their entire life (i.e., 8 years of survey) and analysed life history tactics according to the empiric traits calculated from the long-term field survey.

Materials and methods

Studied population

The study was conducted on the Oir River (Normandy, France, 48°37′N, 1°16′W) brown trout population (Fig. 1). Eight kilometres from the sea (Le Mont-Saint-Michel Bay), the Oir River enters the Sélune River. The monitored area was located between Cerisel and Le Buat mills, including 13 km of the Oir River and the five largest tributaries (Moulin du Bois Brook, Sourvallée Brook, Roche Brook, Moulinet Brook (all second order), and Pont-Lévesque brook (third order)), each ranging from 3 to 6 km long.

The Oir River wild brown trout population has been studied since 1985 (e.g., Ombredane et al. 1998; Gouraud et al. 2001; Charles et al. 2004) and is composed of non-anadromous and sea-migratory individuals. The non-anadromous fish are present in the whole drainage from the small tributary to the main stream. The sea migratory part is mainly composed of finnocks (0+ year in the sea). The anadromous trout are mainly females (78.3%) and upstream migration starts in spring, but almost all of the fish enter the Oir River during fall. For both forms, reproduction occurs from the end of November to the middle of February within the tributaries and the upstream part of the Oir River. Furthermore, spawning grounds used by the two forms overlap (Charles et al. 2004).

Fish tagging and data acquisition

Between 1995 and 1999 (five cohorts), 5894 brown trout age-0 parr were captured in October using electrofishing, anaesthetized (phenoxy-2-ethanol), measured (fork length, ±1 mm), and PIT tagged in their natal brook. Tagging consisted of a PIT tag injection in the ventral part of the peritoneal cavity with a modified hypodermic syringe and a 2.7-mm-diameter sterile needle. The PIT tags used were 11.5 mm long and 2.12 mm in diameter and weighed 0.1 g in air (ID 100; EID Aalten B.V., Aalten, Netherlands). These small tags allow for monitoring small-bodied fish, i.e., >51 mm long. All fish were released into the river section from which they were captured (Ombredane et al. 1998). The five cohorts were monitored during 8 years (from 1995 to December 2002). This allowed all 1999 cohort individuals to spawn at least once. Monitoring was performed using three different methods. First, once a year in October, all of the brooks and the Oir River were electrofished by wading using generator-powered electrofishing gear (type Héron; Dream electronique, France). The same sections homogeneously distributed in the drainage basin were sampled every year, totaling 6490 m. Roche Brook and Moulinet Brook (1850 m) were also sampled in May. During the spawning period, adults were electrofished on the spawning areas located in the brooks and the upstream part of the Oir River using a backpack electrofishing unit (type Martin-Pêcheur; Dream electronique, France). Second, an upstream and downstream trapping system was continuously functioning during the entire study at the Cerisel mill (Fig. 1). These traps captured migratory fish that enter or leave the Oir catchment basin. During two winters (1996 and 1997), an upstream trap was placed at the mouth of La Roche Brook to capture spawners. For each trout trapped, PIT tagging was verified and fork length (±1 mm) measured. Scales were removed (age determination, growth patterns, and spawning checks) and a phenotypic description performed (smolting for juveniles, silvering and sexual maturation for adults) (Baglinière et al. 2000). Third, flat-bed antennae (1000 mm × 350 mm × 25 mm) (U.K.I.D. Systems Ltd., Preston, UK) used in conjunction with decoders and data loggers (SPD and HPSPD; U.K.I.D. Systems Ltd.) were placed in each tributary mouth and at the Cerisel mill (Fig. 1). This allowed for the detection of PIT-tagged fish movements and the recording of the day and hour of the displacement (Armstrong et al. 1996; Lucas and Baras 2000). On the brooks, two adjacent antennae were installed to determine displacement direction.

Life history traits and statistical analysis

The data collected during 8 years in the field (tagging, recapture, and antennae recording) were gathered to calculate life history traits for each tagged brown trout (Table 1). From all of the PIT-tagged fish (type 1), some individuals (type 2) were recorded growing either in their natal brook, in the Oir River, in the Sélune River, or in the sea, whereas others (type 3) were monitored until reproduction (i.e., detected as mature, captured in spawning areas, or monitored during an upstream migration to the spawning areas). Indeed, at least 69% of the fish caught before the reproduction in the upstream trap at the mouth of La Roche Brook and 96% of

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Fig. 1. Map of the study site in the Oir River basin, France. Brown trout (*Salmo trutta*) were captured, tagged with passive integrated transponders, and monitored between Le Buat and Cerisel mills, including the five largest tributaries. Thick lines, circles, and triangles indicate impassable dams, traps, and flat-bed antennae, respectively.
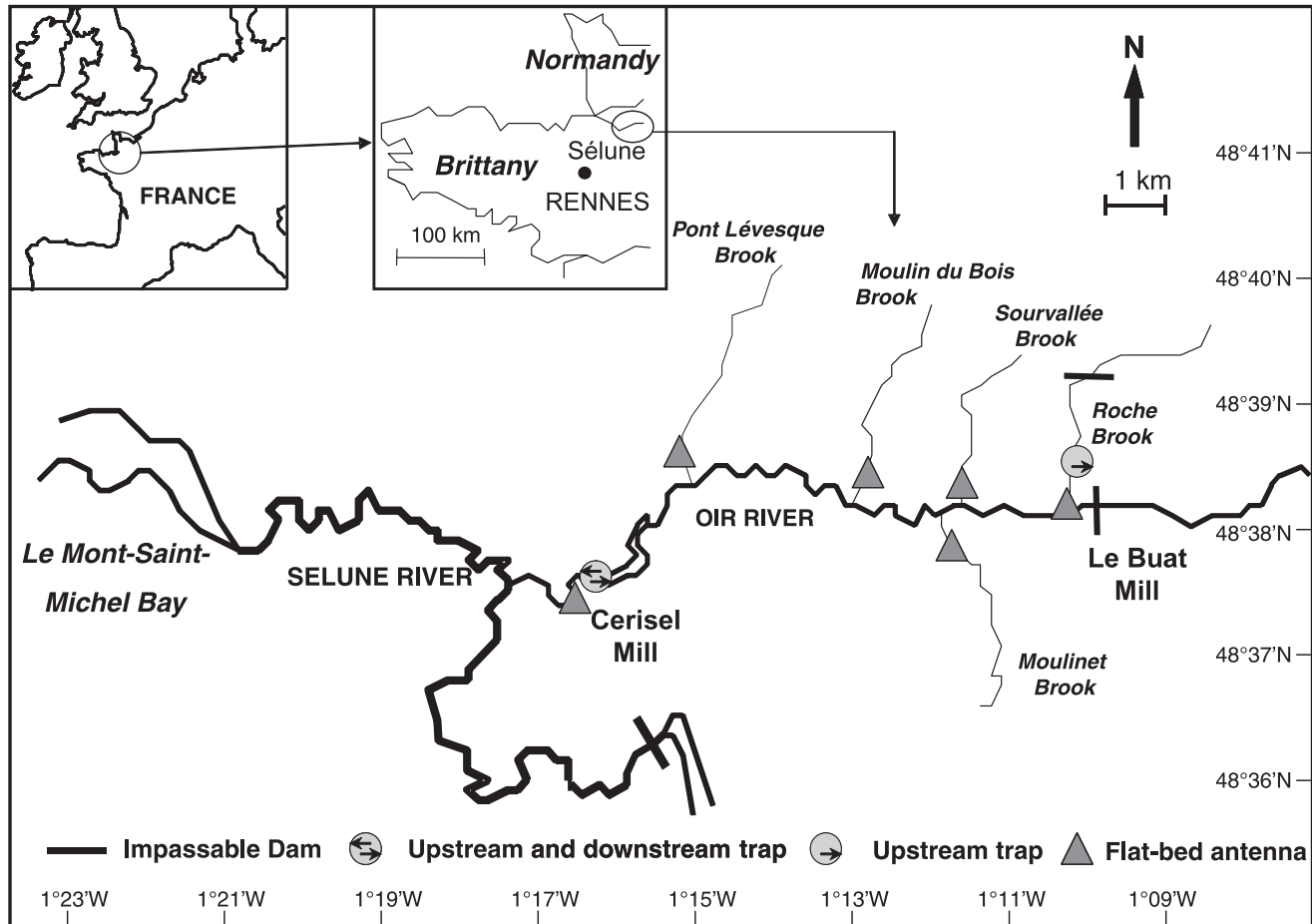
those recaptured in spawning areas were mature. Furthermore, all trapped finnocks were detected as mature.

We tested for differences in life history traits between fish monitored until reproduction and the others (no reproduction observed) and between cohorts for all of the PIT-tagged individuals. Assumptions of normality and homoscedasticity were tested using the Kolmogorov–Smirnov/Lilliefors test (1967) and the Levene test, respectively. A series of one-way analysis of variance (ANOVA) was performed for single comparisons, whereas multiple comparisons were performed using post hoc Tukey pairwise procedures for parametric ANOVA. When deviations from normality were detected, life history trait variability was investigated with the nonparametric Kruskal–Wallis test and Mann–Whitney U test. These statistical analyses were performed using SYSTAT 9 (SPSS Inc., Chicago, Illinois). A rejection level of 0.05 was used in all tests.

An intercohort variability in life history traits was detected. Data were standardized (centred and normalized; Legendre and Legendre 1998) to combine all of the individuals of the five cohorts to investigate of migratory behaviour and life history tactics. Since a majority of life history traits were qualitative (Table 1), quantitative data were converted into qualitative data to homogenize the data set. Five categories (very low, low, intermediate, high, and very high) were

used, each with a similar number of individuals (see details in Escofier and Pages 1988). Multiple correspondence analyses (MCA) were performed on life history traits followed by a hierarchical ascending classification (HAC) using individual factorial scores of the MCA principal axes to create patterns (Lebart et al. 1984; Tenenhaus and Young 1985). The analyses were performed using the empiric traits (Table 1) related to juvenile growth (fork length at age 0 (0+FL) and growth rate between age 0 and age 1 (GR0+1+)), migration (growing environment (GE), age at migration from the natal brook (AMNB), age at migration from the Oir River (AMOR) with the associated fork length (FLMOR), and age at smoltification (AS) with the associated fork length (FLS)), and reproduction (age at maturity (AM), fork length at maturity (FLM), type of reproduction schedule (NR), and sex). The multivariate analyses were performed with SPAD 4.5 (CISIA, Montreuil, France).

Results

Tagging data

During the 8 years of fieldwork (1995–2002), 5894 brown trout parr (type 1) were PIT tagged from 699 to 1759 individuals per cohort. For the entire period of the study, 36.7% of the tagged fish were recaptured at least once (electro-

Table 1. List of the life history traits measured for the study.

Abbreviation	Description	Calculation	Units	Category[a]	Transformation from quantitative to qualitative performed
0+FL	Fork length at age 0	Size in October when the individual was caught for the first time and PIT tagged	mm	JG	Yes
GR0+1+	Growth rate between age 0 and age 1	GR0+1+ = (FLb – FLa)(Db – Da)$^{-1}$; FL, fork length; D, capture date; a, capture at age 0; b, recapture at age 1	mm·day^{-1}	JG	Yes
GE	Growth environment	Environment of subadult growth (brook, Oir River, Sélune River and Sea)	—	M	No
AMNB	Age at migration from the natal brook	Age when migrating downstream and recorded at the antennae of the natal brook	years	M	No
AMOR	Age at migration from the Oir River	Age when trapped and (or) recorded at the Cerisel mill (Oir River mouth)	years	M	No
FLMOR	Fork length at migration from the Oir River	Size when trapped at the Cerisel mill (Oir River mouth)	mm	M	Yes
AS	Age at smoltification	Age when trapped as a smolt or calculated from the scales of anadromous adults	years	M	No
FLS	Fork length at smoltification	Size when trapped as a smolt in Cerisel mill (Oir River mouth)	mm	M	Yes
AM	Age at maturity	Age when migrated upstream or detected as mature for the first time	years	R	No
FLM	Fork length at maturity	Size in October before the first participation in reproduction	mm	R	Yes
NR	Type of reproduction schedule	Split into semelparous (death after spawning) and iteroparous (multispawner)	—	R	No
Sex	Sex	Determined using morphological and physiological criteria for mature fish	—	R	No

[a]JG, juvenile growth; M, migration; R, reproduction. A dash means that the life history trait is expressed without units.

fishing, trapping, or antennae recording), ranging from 21.2% to 41.0% depending on the cohort. Among all tagged fish, 21.9% (n = 1288, type 2) were monitored growing either in their natal brook, in the Oir River, in the Sélune River, or in the sea. Finally, 7.4% (n = 435, type 3) of the tagged fish were monitored until reproduction (Table 2).

Juvenile life history trait variability

Fish that were lost before maturity (reproduction unobserved) grew slowly between age 0 and age 1 (ANOVA, p < 0.05) and moved from the Oir River at an earlier age (Mann–Whitney U test, p < 0.05) than those fish monitored breeding in the system (reproduction confirmed) (Fig. 2). In all life history traits, significant differences (ANOVA and Kruskal–Wallis test, p < 0.05) exist between cohorts (Table 3) but none between brooks. The 1997 cohort had significantly the smallest values, and the 1995 cohort had the largest (ANOVA followed by Tukey's test, p < 0.05).

Relationship between juvenile life history traits and the growing environment

Using the four most informative axes of the MCA (percent inertia = 37.24% cumulated) that was performed with four active variables (0+FL, GR0+1+, GE, and sex) and

three supplementary variables (AMNB, AMOR, and FLMOR), five individual patterns (inter-/intra-inertia ratio = 59%) (Fig. 3) were recognized by HAC. Fish that spent their entire life in their natal brook were chiefly males. They were either (*i*) very small at the end of the first and second year or (*ii*) very fast growers at the end of the first and second year. (*iii*) Many females smolted and moved to grow in the sea at age 2. They grew quickly during the first year but exhibited intermediate growth during the second year in fresh water. (*iv*) Some fish of both sexes with intermediate first-year growth moved downstream to spend the second year as fast growers in the Oir River. (*v*) Some fish of both sexes with high first-year growth moved downstream at age 1 to grow up in the Sélune River.

**Life history tactics in light of reproduction-authenticated fish**

Using the three most informative axes of the MCA (percent inertia = 46.35% cumulated) that was performed with four active variables (GE, sex, AM, and FLM) and seven supplementary variables (AMNB, AMOR, AS, FLS, FLMOR, NR, 0+FL, and GR0+1+), five individual patterns (inter-/intra-inertia ratio = 89%) (Fig. 4) were recognized by the HAC. (*i*) Some trout spent their entire life in the brook;

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Table 2. Data collected per cohort and in total on passive integrated transponder (PIT)-tagged brown trout (*Salmo trutta*) from 1995 to 2002.

Cohort	*n*	0+FL	Recaptured fish	Growing environment documented	Reproduction confirmed
1995	746	88.8 (±15.1)	297 (39.8%)	189 (25.3%)	51 (6.8%)
1996	1619	85.1 (±14.4)	663 (41.0%)	400 (24.7%)	113 (7.0%)
1997	1759	82.7 (±14.7)	601 (34.2%)	339 (19.3%)	143 (8.1%)
1998	699	93.2 (±13.8)	183 (21.2%)	76 (10.9%)	26 (3.7%)
1999	1071	96.1 (±17.5)	419 (39.1%)	284 (26.5%)	102 (9.5%)
Total	5894	87.8 (±15.9)	2163 (36.7%)	1288 (21.9%)	435 (7.4%)

Note: *n* is the number of tagged individuals. Data for fork length at age 0 (0+FL) are means (±SD). The proportion (%) within the number of PIT-tagged fish for recaptured fish (electrofishing, trapping, and (or) antenna recording) and growing-environment-documented and reproduction-authenticated individuals is given in parentheses.

Fig. 2. Comparison of juvenile brown trout (*Salmo trutta*) life history traits between reproduction-confirmed (solid bars) and reproduction-unobserved individuals (open bars). (*a*) Fork length: 0+FL, fork length at age 0; FLMOR, fork length at migration from the Oir River; FLS, fork length at smoltification. (*b*) Age: AMNB, age at migration from the natal brook; AMOR, age at migration from the Oir River; AS, age at smoltification. (*c*) Growth rate: GR0+1+, growth rate between age 0 and age 1. Error bars are standard deviation.
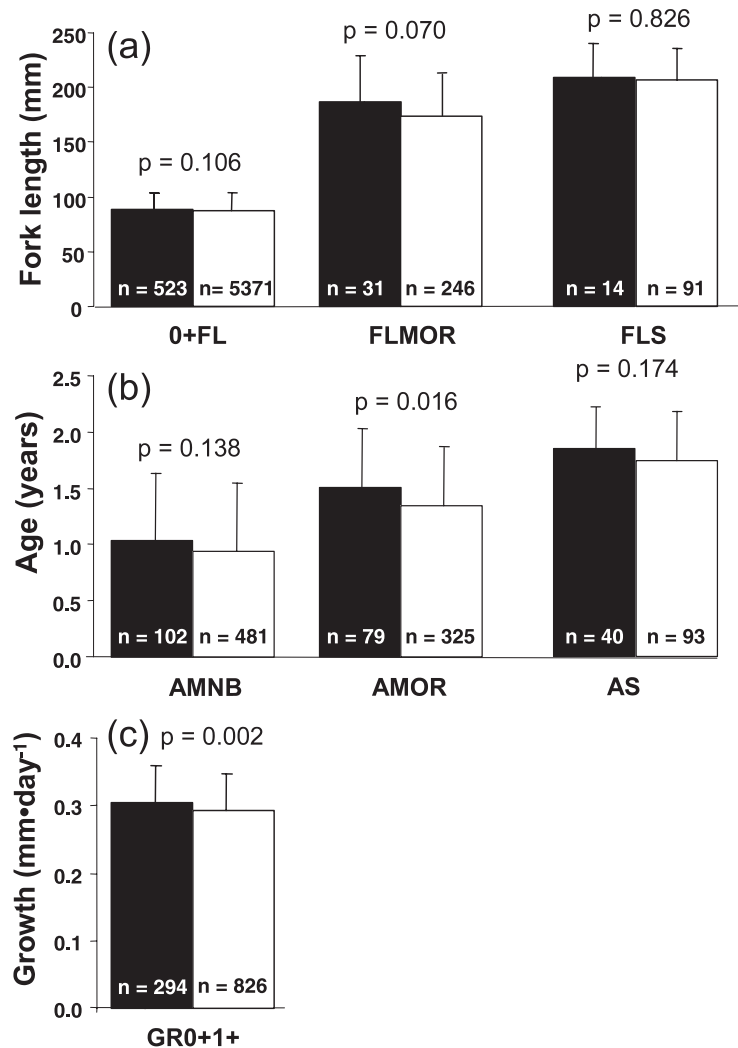
their mean life span was 3 years but few data were available on their reproduction. (*ii*) Other fish migrated downstream from the brook at age 1, grew in the Oir River, and spawned the first time at 3 years old. They had an intermediate and high size and generally died after spawning. (*iii*) Many males grew as subadults in the Oir River and reproduced once at age 2 with an intermediate size. (*iv*) Some females migrated downstream at either age 1 or age 2, grew in the sea, and spawned for the first time at age 3. Usually, these fish had very large size and were multispawners. (*v*) Some

Table 3. Mean (±SD) values of juvenile brown trout (*Salmo trutta*) life history traits used to investigate yearly variability for the five cohorts.

Cohort	Trait								
	0+FL	GR0+1+	FLMOR	FLS	FLM	AMNB	AMOR	AS	AM
1995	88.75 (±15.08)	0.27 (±0.06)	196.21 (±42.06)	215.65 (±27.50)	238.30 (±58.50)	1.74 (±0. 45)	1.68 (±0. 47)	2.00 (±0.00)	2.59 (±0.66)
1996	85.11 (±14.39)	0.28 (±0.05)	179.35 (±38.27)	210.28 (±22.94)	216.29 (±61.64)	0.99 (±0. 53)	1.64 (±0. 48)	1.93 (±0.26)	2.58 (±0.66)
1997	82.68 (±14.67)	0.32 (±0.05)	144.30 (±30.87)	222.00 (±43.50)	212.98 (±90.40)	0.74 (±0. 59)	1.13 (±0. 45)	1.82 (±0.40)	2.32 (±0.85)
1998	93.08 (±13.66)	0.28 (±0.06)	203.18 (±30.10)	213.47 (±23.69)	231.76 (±54.12)	1.07 (±0. 65)	1.62 (±0. 64)	1.94 (±0.24)	2.51 (±0.56)
1999	96.08 (±17.48)	0.33 (±0.05)	166.60 (±29.60)	192.23 (±32.82)	251.29 (±55.56)	1.01 (±0. 59)	1.12 (±0. 33)	1.25 (±0.44)	2.50 (±0.50)

Note: 0+FL, fork length at age 0; GR0+1+, growth rate between age 0 and age 1; FLMOR, fork length at migration from the Oir River; FLS, fork length at smoltification; FLM, fork length at maturity; AMNB, age at migration from the natal brook; AMOR, age at migration from the Oir River; AS, age at smoltification; AM, age at maturity.

fish, staying in the natal brook or migrating downstream from the brook at age 0, reproduced at age 1. They spawned with a very small size and were mainly semelparous individuals.

A diagram representing the principal life history of the Oir River wild brown trout population was formulated using the results of the analyses of empiric life history traits related to juvenile growth, migration, and reproduction (Fig. 5). In light of these results, the overall life history tactics present a continuous gradient in time (life cycle duration) and space (growth from the natal brook until the sea).

Discussion

This approach is novel because it examines empiric life history traits coming from a study using long-term individual data, i.e., from a massive PIT tagging of five cohorts and their monitoring during their entire life. This study confirms and demonstrates that (*i*) juvenile life history traits present a yearly variability and some traits tend to be higher for those fish monitored until reproduction, (*ii*) juvenile growth, particularly GR0+1+, plays an important role in the determination of the growing environment, and (*iii*) life history tactics cannot be classified solely as anadromous and resident individuals and can be described more precisely. We detected that when freshwater migrations are taken into account, life history tactics are expressed along a spatial and temporal continuum.

Juvenile life history trait variability

Juvenile growth tended to be higher for those fish monitored until reproduction in comparison with those fish lost during the survey. With regard to the high recapture effort (electrofishing, antennae, and trapping) and the very low level of PIT tag loss (Ombredane et al. 1998), fish lost during the survey certainly do not survive and never spawn. This result confirms the classical knowledge that early life history traits influence fitness by affecting survival probability later in life (e.g., Chadwick and Claytor 1990; Einum and Fleming 2000; Pakkasmaa and Jones 2002). Nevertheless, the absence of significant differences between groups could be explained with reference to the disproportion between sample sizes. Indeed, the number of fish monitored until reproduction fish is smaller owing to the effect of natural mortality from tagging (age 0) until the individual reaches maturity. As well, the analysis of finer parameters such as energy status or instantaneous growth rate (Forseth et al. 1999) might allow detection of the differences between these individuals.

A yearly variability, particularly in 1995 and 1997 cohorts, was detected for all traits calculated in the present study, highlighting the environmental influence on life history traits, such as growth rate (Näslund 1993). Environmental factors will act at two levels: (*i*) the river basin level, where temperature and water flow will affect the entire population and create intercohort variability (L'Abée-Lund et al. 1989; Jonsson and L'Abée-Lund 1993; Lobón-Cerviá and Rincón 1998), and (*ii*) the river section level, where habitat quality (Heggenes et al. 1999; Roussel and Bardonnet 2002), resource availability (Heggenes et al. 1995), and competition (Heggenes et al. 1999; Nordwall et al. 2001; Harwood et al.

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Fig. 3. Distribution of passive integrated transponder (PIT)-tagged brown trout (*Salmo trutta*) (type 2) within the patterns (*n* individuals) regarding the determination of growing environment in a hierarchical ascending classification. The composition of the patterns can be seen following the tree diagram. Sex was qualified as undefined when both sexes were present in the pattern and as defined when only one sex occurred in the pattern. 0+FL, fork length at age 0; GR0+1+, growth rate between age 0 and age 1.
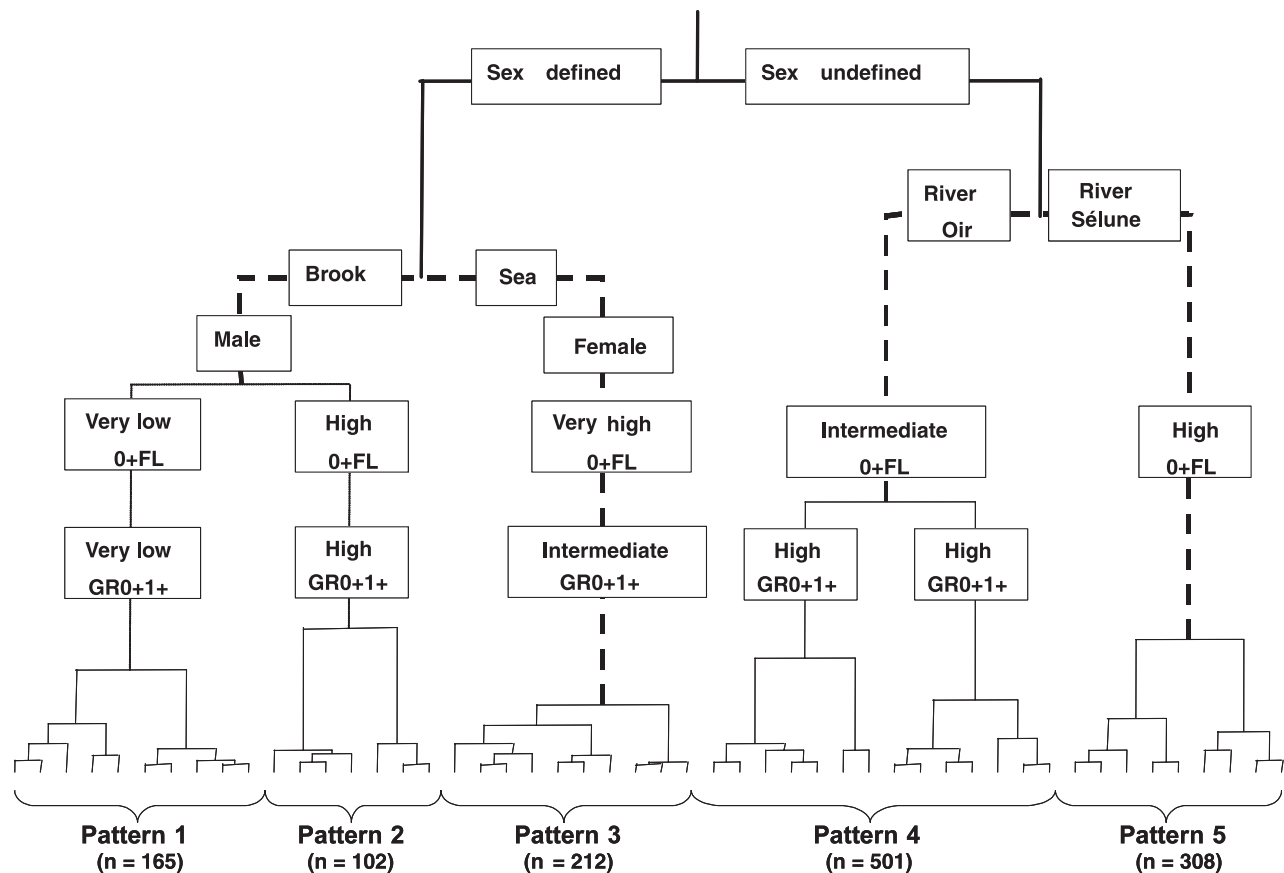
2002) will affect the individual and create intracohort variability. In future studies, the influence of environmental conditions on life history traits should be thoroughly investigated at a finer scale and included in the study of life history tactics.

Migration behaviour and the migration continuum concept

This paper underscores that juvenile growth and metabolic rate play a major role in the determination of the growing environment (Forseth et al. 1999) and demonstrates that GR0+1+, calculated from PIT-tagging data, may allow clarification of this role. Thus, individuals with a low energetic rate remained in the environment in which they were born because it can be sustained in the brook (pattern 1). Trout, whose metabolic needs were higher, left the brook to migrate to the Oir River. If they were able to maintain their growth rate during their second year (expressed by a high GR0+1+), these fish remained in the Oir River (pattern 4). If they did not satisfy their high metabolic rate (expressed by lower GR0+1+), they extended their downstream migration outside the Oir system in the Sélune River (pattern 5) or as far as the sea (pattern 3). There were sexual differences for individuals with very high 0+FL. Males tend to remain in the brook (pattern 2), whereas females migrate to the sea (pattern 3). Juvenile brown trout appear to migrate from one

habitat to another as a phenotypically plastic response to declining growth performance as they reach a threshold in their present habitat owing to environmental conditions. The sources of variation in metabolic rates among individuals are uncertain, but maternal and developmental effects might cause such variation (Forseth et al. 1999).

With regard to our PIT tagging data, fish that migrate in the river were monitored growing from the upper part to the river mouth and clearly grew in a spatial continuum from the natal brook to the sea, including the entire drainage. To understand such complex mechanisms, we should interpret migrations not only with reference to their distance and the salinity of the environment that they traverse but with an ecological and biological viewpoint. The migration continuum concept (Lucas and Baras 2001) is a new way to investigate such complex phenomena. Migration, whatever the distance and environment travelled (Lucas and Baras 2001), is likely to be dependent on a trade-off between benefits and costs of the environment (Jonsson and Jonsson 1993). The access to environment with higher production may have to be balanced by unfavourable conditions, such as an increased mortality rate or osmoregulation changes (Northcote 1992; Jonsson and Jonsson 1993). Thus, the food availability hypothesis (Gross et al. 1988) is a relevant way to understand why fish migrate. As partial migration in a population evolved in response to resource availability in a changing

Fig. 4. Distribution of passive integrated transponder (PIT)-tagged brown trout (*Salmo trutta*) (type 3) within the life history tactic patterns (*n* individuals) in a hierarchical ascending classification. The composition of the patterns can be seen by following the tree diagram. AM, age at migration; FLM, fork length at migration.
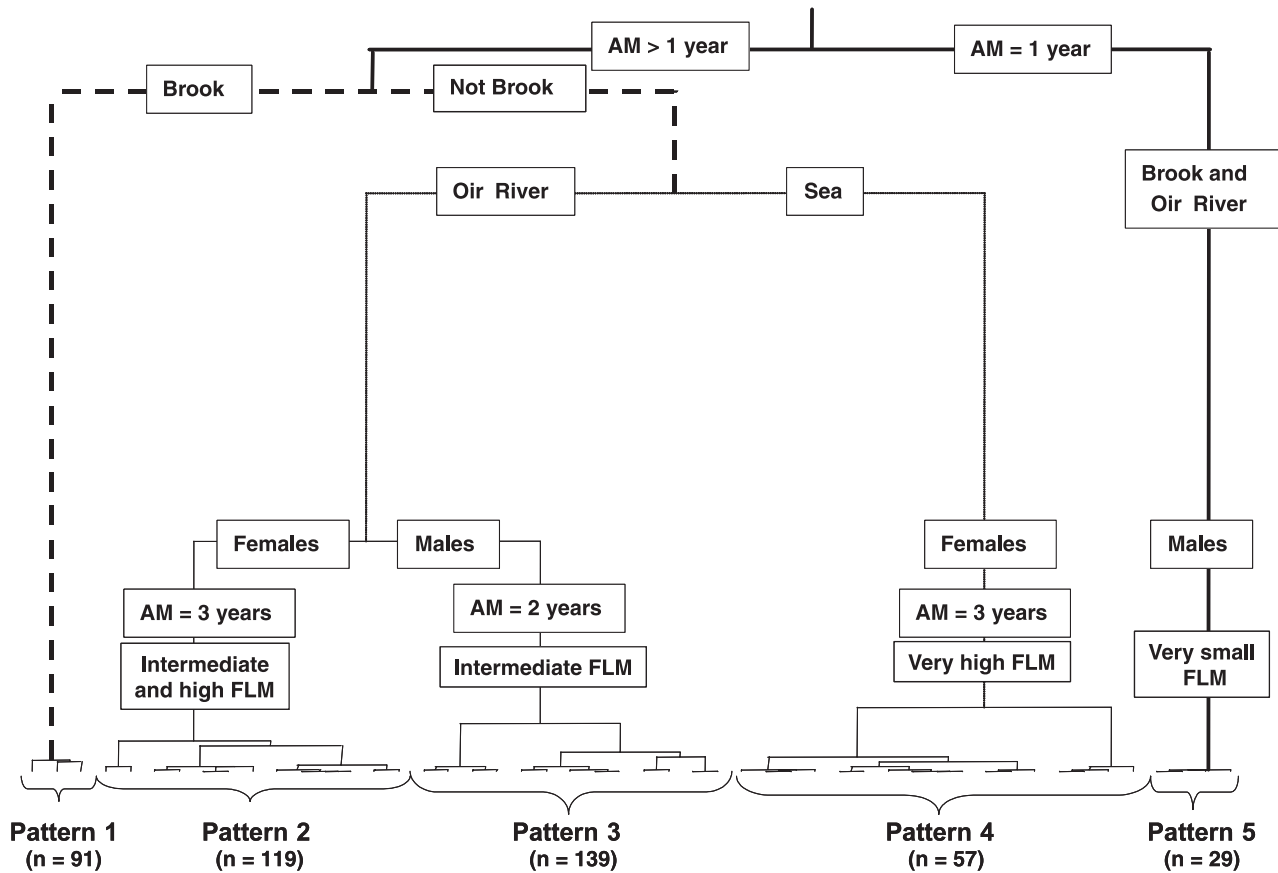
habitat (Jonsson and Jonsson 1993), it would be of interest to investigate how human impacts on environment might affect migratory proccesses. This new emphasis is especially valid with regard to these results. Reconsidering the significance of migration in reference to the migration continuum concept and environmental effects is key to resolving the complexity of the brown trout migratory process and its variability among individuals and populations.

A spatial and temporal continuum of life history tactics

In the population that we studied, we clarify the description of life history tactics by analysing empiric growth and including freshwater migration and detect that tactics are expressed along a continuous gradient. Precocious males, reproducing at age 1, spent their entire life in the nursery brook, some of them with a brief passage in the river (pattern 5). They exhibited strong juvenile growth rate, and maturation rate is positively correlated with first-year growth (Baglinière and Maisse 2002). They participate in reproduction as satellites because they are unable to defend a reproductive territory but may fertilize some of the eggs of the females that are spawning primarily with larger males (Gross 1985; Bohlin et al. 1990; Jonsson and Jonsson 1993). Thus, the size advantage attained in the brook, relative to slower-growing individuals, may be converted into a fitness advantage. Others males grew in the Oir River and reproduced at age 2 (pattern 3). We also observed slower-growing

individuals, which remained in the brook for their entire life (pattern 1). We also found individuals that migrate and grow in the Oir River. They exhibited an intermediate juvenile growth rate and reproduced at age 3 (pattern 2). Some females were found migrating outside the Oir River (Sélune River and Sea) and reproducing when they were age 3, as large bodied-size individuals, and were fast-growing juveniles (pattern 4). Migration advantages, such as an increase of food availability (Gross et al. 1988), might enhance their fitness because female fitness is strongly dependent on their size. Selection seems to favour rapid growth and large body size in females (Jonsson and Jonsson 1993). Nevertheless, some alternative tactics were present within the population, such as males growing in the Sélune River and spawning at age 3. Because of their low frequency, these tactics were not isolated by HAC.

Brown trout males achieve their reproductive success in fresh water after few years of growth (Baglinière et al. 2001), while some of them choose the precocious sexual maturation strategy (detailed in Bohlin et al. 1990; Dellefors and Faremo 1988). Females, whose fitness is strongly dependent on their size (Jonsson and Jonsson 1993), reproduce at older ages than males (Baglinière and Maisse 2002). Since they have higher energetic needs to mature (Euzenat et al. 1999), selection tends to favour faster-growing females (Jonsson and Jonsson 1993), which will need to migrate to more productive environments. Such results confirm previous obser-

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Fig. 5. Continuum of life history tactics in the Oir River brown trout (*Salmo trutta*) population: (*a*) males and (*b*) females. In the middle are the different environments in which fish live, migrate, grow, and spawn. A gradient of juvenile growth (first and second years; numbers on inside of graphic) increasing from the centre to the edge is shown below: the thin solid line, thick solid line, and thick broken line represent low, intermediate, and high juvenile growth rate, respectively. An arrow represents 1 year. Numbers along the top indicate age at maturity. A thin dotted line completing the life cycle is present when most of the fish survived after spawning (multispawners).
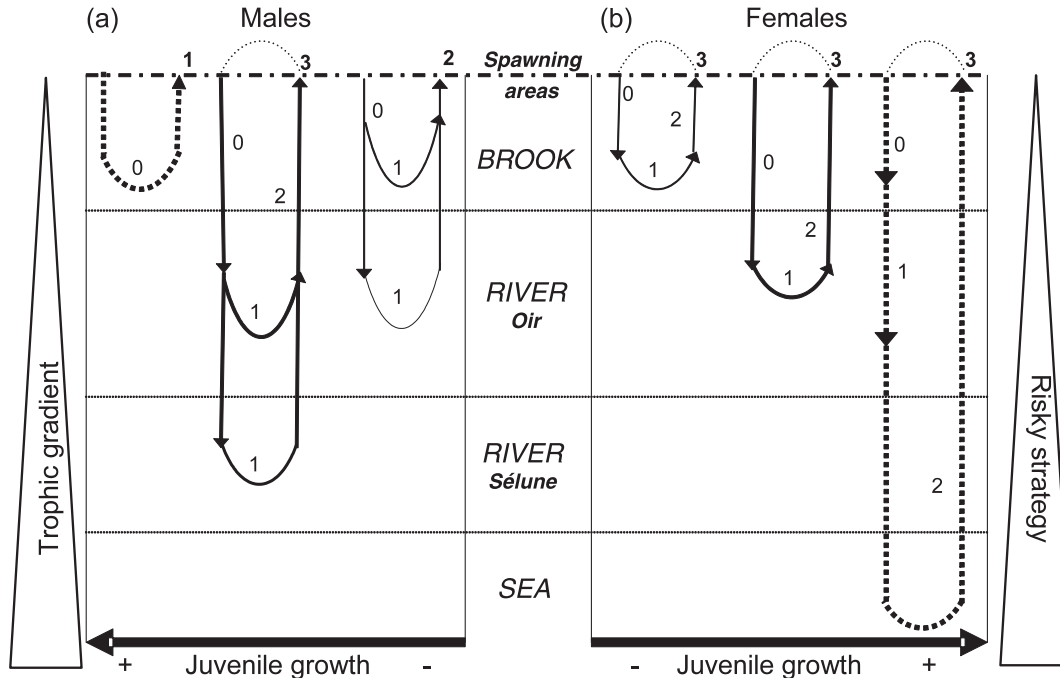
vations that males often predominate among freshwater fish and females among anadromous fish (Jonsson and Jonsson 1993). Nevertheless, whatever the life history tactic is, both sexes are represented. The existence of these alternative tactics provides a selection advantage in a fluctuating environment and when only one ecological niche does not allow for maximizing population fitness (Northcote 1992; Jonsson and Jonsson 1993). This phenotypic plasticity will be favoured as long as individuals can produce polymorphic offspring that have more viable progeny than those without this opportunity (Northcote 1992; Jonsson and Jonsson 1993).

In conclusion, the classical conception of life history tactics in brown trout, opposing only extremes of anadromous versus freshwater resident individuals, can be clarified by analysing empiric data related to growth and reproduction in conjunction with fine-scale migration. Because (*i*) brown trout is a highly polymorphic and ecologically variable species (Jonsson 1989; Elliott 1994; Baglinière 1999), (*ii*) life history traits are phenotypically plastic in response to environment and genetic parameters (Jonsson et al. 2001), and (*iii*) aquatic ecosystems present a continuous gradient of physical conditions (river continuum concept; Vannote et al. 1980), brown trout can exhibit a continuum in time and space of life history tactics to optimize individual fitness and population persistence.

Acknowledgements

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