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LABORATOIRE D'ACCUEIL • UMR INRA-AO Écologie et Santé
des Écosystèmes (ESE)

**Impact des changements
environnementaux sur l'histoire
de vie, la démographie et la
dynamique de population
chez les salmonidés**

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sous le sceau de l'université Bretagne Loire

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and population
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ORE DiaPFC

Observatoire de recherche
en environnement
sur les poissons diadromes
dans les fleuves côtiers

“On a cold March morning, a Nebraska farmer pauses to admire a flock of sandhill cranes passing high overhead, their bugling call notes heralding the return of spring. On a hot, lazy September afternoon, a girl in Delaware chases after a monarch butterfly that is slowly but surely flapping its way to mountaintop in central Mexico, where it will join tens of millions of its kin for the winter. In December a Maasai tribesman climbs a rocky hillside and looks out across the savanna, where hundreds of thousands of wildebeest and zebras are heading from Kenya to Tanzania, tracking the ephemeral rain and the lush grass it promises to deliver, while on the other side of the world, along the shores of Laguna San Ignacio in Baja California, a fisherman awaits the return of the gray whales, which will use the bay’s warm, shallow waters as a combination winter resort and nursery... every aspect of migration inspires awe”

Wilcove 2008, No way home.

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INTRODUCTION

General introduction



1. General context

Environmental variations radically affect both population and evolutionary dynamics (Lundberg et al. 2000, Bjornstad 2001, Ruokolainen et al. 2009, Tuljapurkar 2013). Since the beginning of the 20th century, global environmental changes linked to anthropic activities have increased and one of the fundamental causes is the human population growth. Global changes include over-exploitation, pollutions, noise and luminous perturbations, biological invasions, habitat destructions (e.g. Figure 1), anthropogenic electromagnetism, and climate changes (major threats faced by fish populations are reviewed in the article, Appendix 1, with the abstract in Box 1). They disrupt ecosystems (ice on rivers and lakes breaks up earlier, trees are flowering sooner, sea is more acidic, warmer and has less oxygen...), and cause the decline of numerous natural populations (Butchart et al. 2010, Dirzo et al. 2014, ONU “perspectives mondiales de la diversité biologique” 2010, 2014).

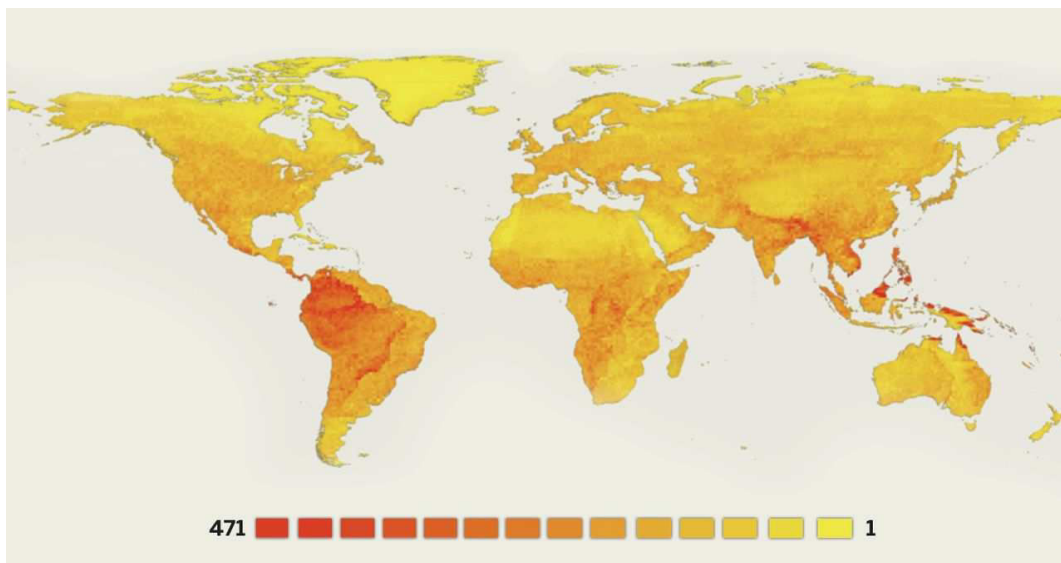


Figure 1. Global population declines in mammals and birds. Illustration from Dirzo et al. 2014. The number of species defined by the International Union for Conservation of Nature (IUCN) as currently experiencing decline, represented in numbers of individuals per 10,000 km² for mammals and birds, shows profound impacts of defaunation across the globe.

Box 1. Abstract: Fishes in a changing world: learning from the past to promote sustainability of fish populations. Annexed article Gordon et al. in review.

Populations of fishes provide valuable services for billions of people, but face diverse and interacting threats that jeopardize their sustainability. Human population growth and intensifying resource use for food, energy and goods are compromising fish populations through a variety of mechanisms, including over-fishing and declines in water quality. The important challenges raised by these issues have been recognized and have led to considerable advances over the past decades in managing and mitigating threats to fishes worldwide. In this review, we identify the major threats faced by fish populations alongside recent advances that are helping to address these issues. Many societies are striving to ensure a sustainable future for the world's fishes and fisheries and those who rely on them. Although considerable challenges remain, by drawing attention to successful mitigation of threats to fish and fisheries, we hope to provide the encouragement and direction that will allow these challenges to be overcome in the future.

Managing the conflicts between wildlife and humans is an intricate process, as it has to consider not only the ecological value of species but also their cultural, social and economic values. In addition, the spatial extent of the conflict makes wildlife management more complex. Indeed, the more the conflict area increases, the more difficult is to apply management actions due to the multiplicity of actors and factors involved (economic, social, ecological, biological). Sodhi et al. in 2011 defined and reviewed three levels of management. (i) The micro or local management, such as the creation of national protected areas, essential for the conservation of habitats and endangered species. (ii) The meso or regional management, including transboundary conservation agreements between neighboring countries and the international regulation of illegal wildlife trade. It can boost micro management outcomes (e.g. mountain gorillas *Gorilla beringei beringei*, Plumptre et al. 2007; Arabian oryx *Oryx leucoryx*, Harding et al. 2007; Indochinese tigers *Panthera tigris*, Lynam 2010). (iii) The macro or global management involving multinational companies or numerous countries. This largest level of management must mainly limit unsustainable business practices.

For instance, following the awareness of the consumers on the deforestation promoted by purchasing beef and leather from ranchers in the Amazon, international companies like Nike and Walmart pressured slaughterhouses to ensure that their products do not cause rainforest deforestation. Since then, ear tags and genetic testing are used in Brazil to track cattle from ranches to slaughterhouses (Sodhi et al. 2011).

Anthropic activities can quickly affect natural populations (in 2004, IUCN estimated that extinction rates were 50 to 500 times higher than previous rates calculated from the fossil records, Baillie et al. 2004), whereas population responses to management actions require time. Long-lived species as trees or large mammals may take decades to respond sufficiently to the effects of an intervention, above baseline variability. In addition, management decisions cannot be based on ease of implementation or accessibility of particular organism life stages (Crouse et al. 1987). These decisions are the end-points of an expensive process in terms of time, money and access to necessary expertise. Commonly, a management process starts with the detection of a decline or degradation of an aspect of the nature being assessed. Once this change has been identified, management goals can be set such as an area of habitat to protect or restore, a species decline to stop or reverse, or a species exploitation to regulate to ensure the resource sustainability. When goals are defined, the management process involves scientific evaluations (Pullin et al. 2013) that can result from various approaches including experimental (Duc et al. 2003), observational (Clarke et al. 2003) and modeling analyses (Freckleton et al. 2003, Norris and Mcculloch 2003). This process of management decision gives a coherent framework to coordinate compatible goals between actors, but it also admits the pervasive problem of uncertainty (Regan et al. 2002, Harwood and Stokes 2003, Refsgaard et al. 2006). Uncertainties occur at several steps of the management process and have different origins (Figure 2): intrinsic to the biological system (e.g. environmental or demographic variabilities, lack of knowledge on the biological system) and extrinsic, linked to the observation process (e.g. subjective judgments, partial observation of the system, measurement errors during monitoring) (Regan et al. 2002). Scientists try to consider uncertainties in their recommendations to managers but unpredictable uncertainties still can cause the failure of management interventions. Consequently, the relative success or failure of these interventions should be assessed to inform future actions and try to reduce uncertainties (Pullin and Knight 2001, Knight et al. 2006, Gouar et al. 2008).

The management process has to be a cycle of doing and learning (Figure 2) called ‘adaptive management’ (Walters and Holling 1990, Westgate et al. 2013) to increase its efficiency. Adaptive management acknowledges that managed resources will always change as a result of human interventions, environmental variability, stochasticity, and the emergence of new uncertainties.

“What I decided I could not continue doing was making decisions about intervening... when I had no idea whether I was doing more harm than good” – Archie Cochrane

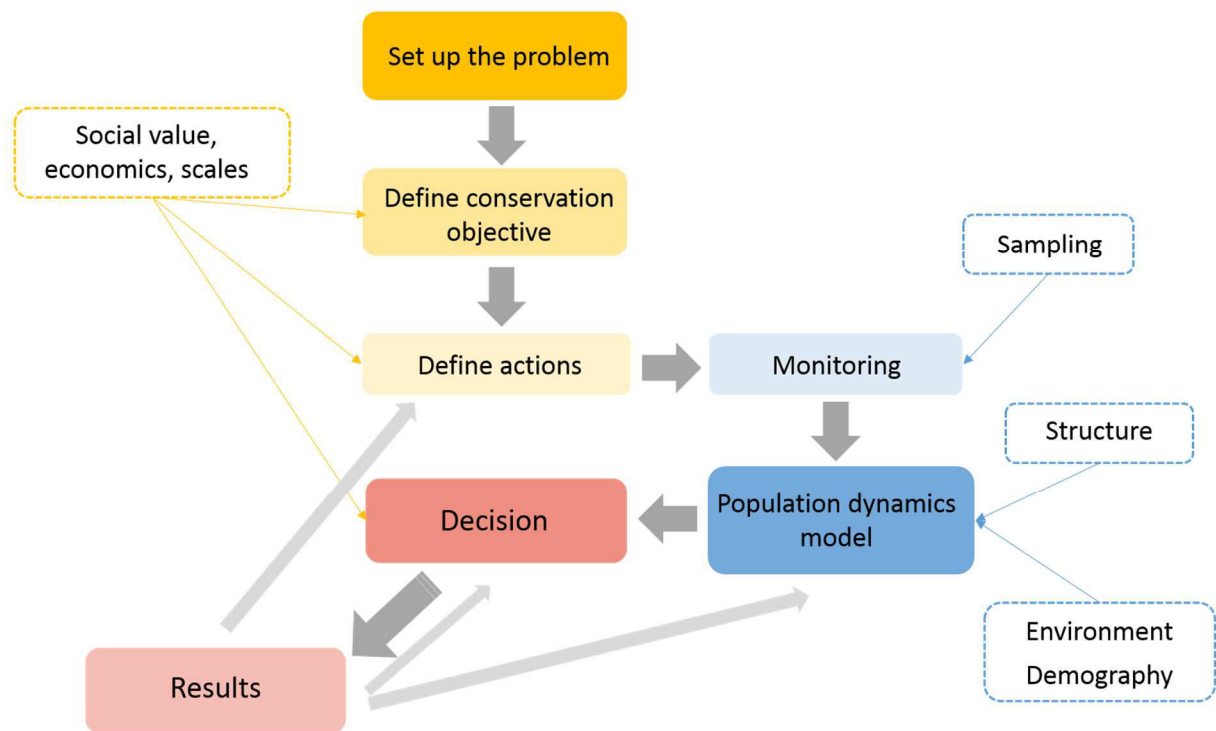


Figure 2. Summary of the management process with uncertainty sources. Dotted cases represent the uncertainty steps.

Linked with management process, scientists try to understand the spatiotemporal dynamics of populations: what does influence the abundance of organisms within a population, and why this abundance changes over time? To achieve these objectives, and identify the demographic mechanisms behind changes in population abundance, we need ecological knowledge provided by population dynamics studies.

These studies investigate the causes of demographic changes (i) in space and in time on short and long-term; (ii) in population structure (e.g. age structure, sex ratio); (iii) in population functioning; and (iv) in population size (Odum and Barrett 1971, Krebs 1972, Williams et al. 2002). Using statistical analyses and simulation modeling (i.e. ‘population dynamics models’), population dynamics studies analyze the past population dynamics, to predict the future response of populations (i.e. growth or viability) to environmental or anthropic changes or management decisions and, as such, provide an ecological basis for decision-making. Population dynamics studies inform environmental management by defining: conservation status (IUCN red lists), general life cycle sensitivity to its different components for ranking effort priorities, optimal strategies for release (reintroduction and reinforcement) (Green et al. 1996), and maximum sustainable yield of harvest for sustaining a viable population. The example described in Box 2 illustrates how population dynamics models can help management decisions.

Box 2. Population dynamics model and management

In the south-eastern of the USA, the population of logger-head turtles *Caretta caretta* (L.) were traditionally managed through nest protection to promote eggs survival. In face of the continuous decline of the population, Crowse, Crowder & Caswell (Crouse et al. 1987) used a stage-based population dynamics model to identify which part of the population should be conserved as a priority. Their results highlighted that managers actually focused Conservation efforts on the least likely part of the turtle’s life to produce long-term results. They argued that management initiatives should instead focus on protecting juvenile stages (with turtle excluder devices on trawler nest) to ensure the viability of the population in a far more effective way than the traditional management. A comparable approach has been applied to many other vertebrate taxa over the last decade (Doak et al. 1994, Heppell et al. 1994, Marschall and Crowder 1996, Plissner and Haig 2000). Thereby, to produce noticeable long-term results, the management process should be preferably based on population dynamics studies.

To understand the demographic mechanisms underlying abundance changes, population dynamics studies estimate the major life cycle transitions: births, deaths, immigration, and emigration, which reflect the primary processes responsible for these changes (Odum and Barrett 1971, Krebs 1972, Williams et al. 2002). However, populations are not homogenous entities. They are composed of individuals with different characteristics (i.e. 'individual heterogeneity', age, sex, quality, etc...) leading to various life histories, which potentially differently influence the population growth rate and abundance (Lindström 1999, Chapman et al. 2011a, Chambert et al. 2013). Consequently, population dynamics studies need information at the individual level. In order to understand life histories, individual-based long-term studies of samples of individually marked or identifiable animals have been set up on numerous species (e.g. Killer whales *Orcinus orca*, Guinet et al. 2015; Soay sheep *Ovis aries*, Ozgul et al. 2009; or Black-browed albatross *Thalassarche melanophrys*, Nevoux et al. 2007). The access to large numbers of individual life histories provides the possibility to study a wide range of questions that are otherwise inaccessible as for instance: the age effects on behavior, reproductive performances and survival, population responses to environmental change (e.g. Pardo et al. 2013, Tettamanti et al. 2015, Fay et al. 2016); or the causes of variations in growth, breeding success and survival within populations (e.g. Buoro et al. 2010, Chambert et al. 2013, Link and Hesed 2015). Even though individual monitoring often represents a sample of a population with scarce data, population dynamics models as matrix models can deal with these imperfections (Hemerik and Klok 2006) and provide precise demographic data and estimations at the population scale.

A major biological trait to consider in management decisions is animal migration (i.e. active movement from one habitat to another, review in Dingle 2014) that shapes the distribution and abundance of a large range of animal species in space and time. It has been one of the nature's most visible and widespread disappearing phenomena, since the recent decades (e.g. Wilcove 2008, Wilcove and Wikelski 2008, Pulido and Berthold 2010). For instance, an emblematic endangered migratory taxon is salmonids. Prior to European settlement in the United States, 160-226 million kilograms of Pacific salmon migrated each year up to the rivers of Washington, Idaho, Oregon and California, whereas today the total biomass of spawning salmonids in the Pacific Northwest is estimated to be only 12-14 million kilograms (Gresh et al. 2000). This decline of migratory animals is mainly due to habitat destruction, the creation

of obstacles and barriers (dams and fences), overexploitation, and climate change (Wilcove and Wikelski 2008). Their life cycle relies on multiple habitats, which potentially increases their risk of exposure to spatially heterogeneous anthropic threats. Migratory animals thus appear highly vulnerable to global change and the distance of migration may accentuate this vulnerability (Wilcove and Wikelski 2008, Vickery et al. 2014). As the number of migrants declines, many of the most important ecological properties and services associated with them also decline.

Migration links with important ecological properties and contribute to the ecosystem functioning through nutrient transport and trophic effects (e.g. in Bauer and Hoyer 2014). For instance, by migrating at sea, and spawning and dying in rivers, some salmonids transfer nutrients from the ocean to rivers, in the form of feces, sperm, eggs and decaying carcasses of adults. These nutrients enhance the growth of phytoplankton and zooplankton in the rivers, which provide food for smaller fish, including young salmon (Wilcove and Wikelski 2008). Gresh et al. (2000) have calculated that the rivers of the Northwest receive only 6-7 % of the marine-derived nitrogen and phosphorus initially brought by migratory Pacific salmon carcasses when the population was abundant. However, so far the consequences of this collapse on the ecology of the region's river or adjacent farmlands are largely unknown. Another example of services from migratory animals is the reduction in phytophagous insect populations by birds in temperate forests (Kirk et al. 1996), or the major role of wildbeest in terms of consuming herbaceous vegetation and redistributing nutrients *via* their urine and dungs (Ben-Shahar and Coe 1992, van der Waal et al. 2011). All these examples raise the question of the impact of ongoing declines in migratory species on the health of on ecosystems, sustainable harvest or pest control.

However, in this context of global environmental changes, migratory species and populations are not all showing the same declining trends. Through a study on recent population trends of 340 European breeding bird populations, Gilroy et al. (2016) showed that migratory species that occupy larger non-breeding ranges than breeding ones were less likely to be declining than those with more restricted non-breeding areas. Their results highlighted that species with a partial migration strategy (i.e. populations including both migrant and resident individuals) were more resilient to environmental changes than solely migrant or solely

resident taxa. This pattern was independent of migration distance, suggesting that migratory diversity may facilitate species responses to environmental changes.

Partial migration is a common type of migration in the animal kingdom and has been reported for many species of fish, birds, amphibians, insects, and mammals (Jonsson and Jonsson 1993, Nilsson 2007, Chapman et al. 2011a, Hebblewhite and Merrill 2011, Mysterud et al. 2011, Chapman et al. 2012). In many bird species, for instance, a fraction of the population remains on site year-round (called 'resident'), whereas the other fraction migrates towards warmer or more tropical latitudes to overwinter (called 'migrant') (Pérez et al. 2013). In some salmonids, a fraction of individuals migrates to the sea to have access to high-quality resources before returning to spawn with a high fecundity induced by a high growth rate, whereas resident individuals spend their entire life in freshwater. However, this migrant advantage is counterbalanced by a high mortality risk due to predation and physiological changes in early sea life (Jonsson and Jonsson 1993, Dodson et al. 2013, Kendall et al. 2014). In addition, in some species migrant individuals can show various life histories and spend either one year or several years at sea. This difference in time spent at sea induces different survival probabilities and fecundities. By being dependent on different environments and showing a different energy allocation among survival, growth, and reproduction, each type of life history can respond differently to environmental changes. This diversity in responses (i.e. response diversity) to environmental changes among individuals from the same population might enhance population viability and explain that partial migration populations are more resilient than solely resident or migratory populations. Moreover, population resilience also depends upon the population capacity to adjust to changing environmental conditions (i.e. phenotypic plasticity). Partially migratory populations are expected to show adaptive evolution in migration distance or in migrant proportion but the decision to migrate can also be environment-dependent (Chapman et al. 2011b, 2012, Ferguson et al. 2017).

However, the influence of variations in demographic parameters in migrant and resident individuals on population dynamics and resilience to environmental changes is currently largely unknown. Despite this lack of knowledge, management actions occur on several partially migratory species with important ecological, social and economic values. Generally, the migrant and resident parts of the population are not under the same management rules

or one of them is not even considered in the management process. For instance, migratory Atlantic salmon *Salmo salar* that spend one year at sea are often less protected than salmon spending several years at sea; in brown trout *Salmo trutta*, most management plans are not considering resident trout. Consequently, in order to understand the resilience of partially migratory populations as Atlantic salmon and brown trout and help management decisions, long-term population dynamic studies have to: (i) determine the effect of environmental factors on the ‘decision’ to migrate or not, when to leave and how long to stay at sea; (ii) analyze the current and past responses and fitness of resident and migratory individuals to environmental changes; and (iii) determine the influence of these two points on the population dynamics.

These objectives are going to be developed under several specific questions defined after placing this work in a more theoretical framework.

2. Conceptual framework

2.1. Life history traits, trajectories, tactics, and strategies

2.1.a. *Life history traits and trajectories*

A population is composed of individuals with different features as age, sex, size, reproductive and social status. Individuals can also differ in traits associated with survival and reproduction (e.g. anti-predator defenses, parasite resistance or exposure, resource use, or competitive ability), which reflect ‘individual quality’ (Wilson and Nussey 2010). All of these differences shape various life histories (Greene et al. 2010) that can respond to changes in the environment through a different morphology, behavior or ecology (González-Suárez and Revilla 2013). This individual variability (also called “individual heterogeneity”) is pervasive and generates variance in survival, fecundity, migration, and dispersal, which characterize the demographic dynamics of a population (i.e. ‘demographic parameters’). These variations in demographic parameters lead to differences in individual fitness (definition in Box 3). Thereby, individuals may not have equal contributions to the population growth rate, which make more complex population dynamics analyses.

Traits describing reproduction, survival, and growth (e.g. age at first reproduction, size at sexual maturity, fecundity or life expectancy) are called 'life history traits' (Figure 3). The successive values of life history traits during life defines the life-history trajectory of an individual (Figure 3). In a population, natural selection selects the trajectories that produce the largest possible number of surviving offspring (i.e. fitness, defined in Box 3). However, a Darwinian Demon (i.e. hypothetical organism that can maximize all aspects of fitness simultaneously; Law 1979) does not exist as life histories are constrained by external factors (resources, competitors, predators, etc.) that limit the energy amount that an individual can allocate to maintenance, survival, growth, and reproduction (i.e. principle of allocation; Levins 1968). Consequently, life history trajectories are constrained by trade-offs in energy allocations among life-history traits. For instance, trade-offs can exist between the current reproduction and the next ones, or between the number of eggs and their size (Parker and Begon 1986, Stearns 1992). These trade-offs generate life history strategies and tactics (Stearns 1992) (Figure 3). 'Strategy' and 'tactic' can be two confusing terms in population dynamics. Gross in 1996 proposed one of the clearest definitions, hence the following descriptions of 'strategy' and 'tactic' come mainly from his work (Gross 1996).

2.1.b. Life history strategies

A life history strategy is a set of co-adapted traits designed by natural selection to maximize fitness (Figure 3). It corresponds to a group of possible evolutionary solutions for a species to ensure the survival of individuals on the short-term, and maximize the contribution of an individual or genotype to futures generations on the long-term. A strategy is a genetically based program that results in the allocation of the somatic and reproductive effort of an organism (such as energy and development) among alternative phenotypes (tactics). An example of strategy is the allocation of energy into migrating *versus* staying in the native habitat. The strategy operates through mechanisms (physiological, neurological, or developmental) that detect appropriate signals and put the strategy decision rule into effect. For instance, migrate when larger than X and stay in the native habitat when smaller (referred to 'a conditional strategy'), or migrate with probability 0.3 and stay with probability 0.7 (referred to 'a mixed strategy').

2.1.c. Life history tactics

A tactic is a set of co-adapted traits designed by natural selection to solve ecological problems and to maximize a given function (Stearns 1976) (Figure 3). It corresponds to a phenotype that results from a strategy. Corresponding to the previous example of a migration strategy, one tactic is residency in the native habitat, while the alternative tactic is migration. The migratory tactic will have associated behavioral, morphological, physiological or life history features that distinguish it from its alternative. Another example is to fight for access to a mate, while the alternative tactic may be to sneak. The 'decision' about which tactic is expressed is driven by the strategy and the chosen tactic must be the one that confers the best fitness related to the individual state. For instance, in a conditional strategy, a life-history tactic can evolve as the 'best of a bad job' where individuals making the best of a bad job can be considered as maximizing their fitness by choosing the optimal tactic considering their internal (e.g. age, sex, energetic status, genetic predisposition) and external state (e.g. environmental conditions, competition, predation risk, density-dependence) (Figure 4) (Lack 1968, Lundberg 1988, Gross and Repka 1998, Chapman et al. 2012, Brodersen et al. 2014). Thus, a life history tactic corresponds to an individual response to biotic and abiotic factors on an ecological time scale, whereas a strategy responds to natural selection on an evolutionary time scale (Southwood 1988).

Box 3. Definition of fitness.

We can consider the fitness as the capacity of an individual to transfer its genes. The fitness is expected to be maximized by natural selection. It is difficult to measure fitness. Thereby, to study the fitness of life history tactics we often compare their advantages and disadvantages by measuring their life history traits. For instance, in some studies, the fitness of a given genotype is defined as the number of fertile offspring produced in the next generation (Einum et al. 2004).

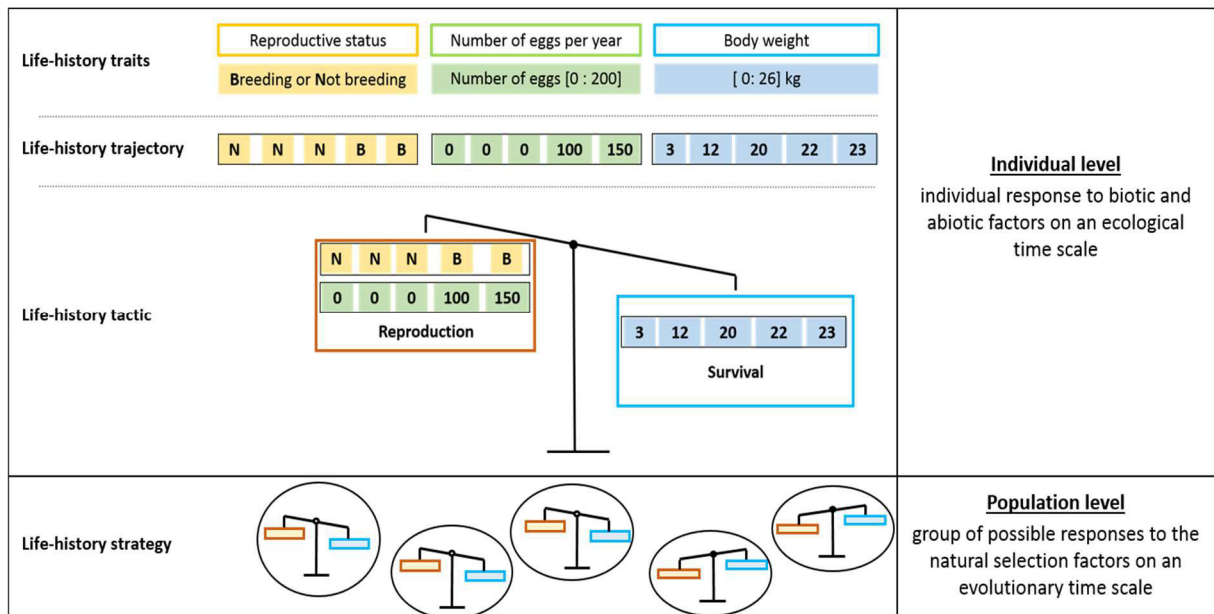


Figure 3. Definitions of the life-history trait, life-history trajectory, life-history tactic and life-history strategy (adapted from Plard 2014). The reproductive status, the number of eggs per year and the body mass are three examples of salmonid life history traits. The successive reproductive status (breeder, **B** or non-breeder, **N**) give the trajectory of reproductive status for instance. The life-history tactic tending to maximize reproduction is described by the individual trajectories of the different traits linked to reproduction, while the alternative tactic maximizing survival is defined by the individual trajectories of the traits linked to it. Finally, at the population level, a strategy corresponds to a group of evolutionary solutions.

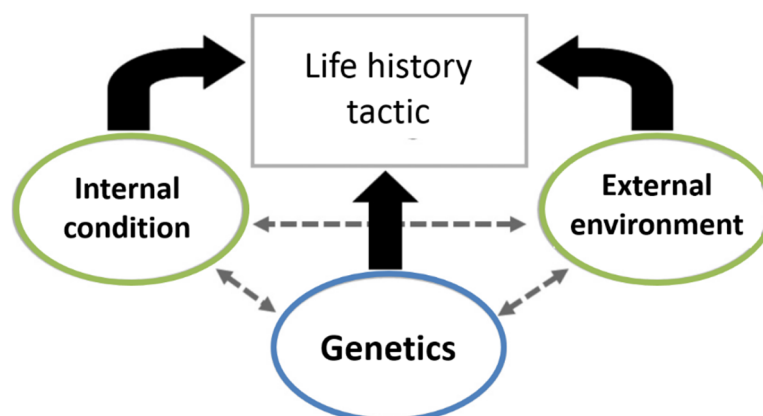


Figure 4. Schematic diagram illustrating how an individual's internal condition, genetic background, and the environmental conditions influence the determination of life history tactic. Black arrows indicate one-way effects, and grey dashed arrows indicate two-way or interactive effects. Illustration adapted from Kendall et al. 2014.

2.2. Partial migration

2.2.a. Migration

In this thesis, we consider migration as an active movement between different sites during the life cycle of an individual involving a return (Dingle 2014). It differs from the dispersion, where individuals move away to settle and breed in another population (Stenseth and Lidicker 1992). Migration requires a genetic determinism of (i) timing and duration of movement in the temporal program of the organism, (ii) physiological adaptations for energy uptake and metabolism, (iii) behavioural adaptations for responding to the variable conditions (weather, wind, currents) during the journey, and (iv) control of orientation and navigation (Berthold 2001). It acts on life history traits and thus, can have major consequences on the individual fitness. Indeed, migration is associated with the visit of environments with better feeding opportunities often, which can confer a higher growth rate, body size, fecundity or survival to migrant individuals compared to resident individuals. Thus, generally, the different cost-benefit trade-off between resident and migrant individuals is apparent through differences in body size and survival. However, migration requires the use of energy supplies (growth, survival, adaptation to a new environment) that are not going to be directly used for reproduction (Ganter and Cooke 1996, Alexander 1998, Kinnison et al. 2003, Pomeroy 2006). Migration benefits can be counterbalanced by higher predation risks, energy consumption linked to migration distance, physiological adaptations, and an older age at first reproduction (Gross 1987, Jonsson and Jonsson 1993, Kinnison et al. 2001, Bohlin et al. 2001, Alerstam et al. 2003). In some cases, migration increases survival but migrant individuals are exposed to more variable mortality risks than resident individuals as they rely on multiple habitats to complete their life cycle, potentially increasing their exposure to spatially heterogeneous threats (Wilcove and Wikelski 2008, Hebblewhite and Merrill 2011, Vickery et al. 2014).

Migration shows a high level of diversity as reflected by the evolution of a large range of residents, short-distance and long-distance migrants among closely related species. Migration has evolved independently among many taxa in the animal kingdom and has constantly developed or become suppressed over the recent time scale. Indeed, the extent and pattern of migration have changed in some species and some resident species became migratory or vice versa (Visser et al. 2009, Pulido and Berthold 2010). Residency can evolve in populations

after an environmental change favoring a reduction in migratory activity by shorter migration distances. The reduction in migratory distance reduces migration costs and permits rapid responses to changes in the timing of food availability for instance. Recent studies reported a significant shortening of migration distances and an increase in residency associated with environmental changes (Sorte and Iii 2007, Visser et al. 2009, Pulido and Berthold 2010). The transition from a migratory to a sedentary population should result in partially migratory populations with gradually decreasing migration distances and increasing proportions of resident individuals (Pulido et al. 1996, Pulido 2007, Pulido and Berthold 2010).

2.2.b. Partial migration

Partial migration characterizes a population with both migrant and resident (i.e. sedentary in the natal habitat) tactics (Chapman et al. 2011a, b). This diversity in migratory patterns can occur within species and populations. Partial migration is not limited to a dichotomy between two tactics and can occur as a continuum of life history tactics from residency to long distance migration (Cucherousset et al. 2005, Chapman et al. 2011b). Any population with 1 to 99% of migrating individuals can be considered as a partially migratory population. Considering this definition of partial migration, it is likely that many migratory populations are actually partially migratory. For instance, Atlantic bluefin tuna (*Thunnus thynnus*) is often used to illustrate long distance fish migration, but some individuals remain resident around the spawning grounds throughout their entire life (Baker and others 1978).

Currently, numerous studies support the idea that partial migration represents a conditional strategy characterized by different behavioral tactics (Lundberg 1988, Gross 1996, Hendry et al. 2004, Chapman et al. 2012) and corresponding plastic life history responses to a variable environment (Stearns 1992). Migrants can correspond to individuals in good physiological condition to face the significant energetic cost of migration, and residents can be individuals with low energy reserves (Chapman et al. 2011b, 2012). Nevertheless, the opposite pattern can also be observed with larger individuals remaining resident (Ketterson and Nolan 1976, Perez-Tris and Telleria 2002). Migrant individuals may be composed of slow-growers that migrate to a new habitat with better feeding opportunities (Chapman et al. 2011b, 2012, Ferguson et al. 2017).

In both cases, the individual condition in early life seems to have major consequences on migratory tactic determination through individual growth rate that can promote the rapid adaptive evolution of migration distance or the proportion of migrants. For instance, the house finch population (*Carpodacus mexicanus*), introduced in New York in the 1940 showed a migration rate of 36 % in 1960, whereas in their native area in California, this rate was 20% illustrating that the introduced population rapidly adapted to its new environment by changing energy allocation between reproduction, growth, and survival (Able and Belthoff 1998). Nevertheless, the coexistence of different migratory tactics within populations could be promoted by equivalent individual fitness, or frequency-dependent selection (Lundberg 1988, Jonsson and Jonsson 1993, Gross 1996, Chapman et al. 2011b).

Thereby, partial migration can be viewed as “a form of evolutionary turntable between sedentariness and migratoriness”, as proposed by Berthold (2001). It allows the transfer between one and the other tactic by natural selection. If the quality of the unshared environment changes over the years to become consistently better or worse and so shifts the advantage of being a migrant or a resident, then partial migration will allow the population to adapt one way or another and be less prone to decline and more resilient to environmental change than a fully resident or fully migratory population (Gilroy et al. 2016).

2.3. Population diversity and resilience

2.3.a. The concept of resilience

Multiple definitions of the concept of resilience exist (review in Müller et al. 2016) but in this thesis we are going to use the one defined by Holling 1973, which is specifically suited to ecology. Holling defined the resilience as the capacity to persist in face of change and named this definition the “ecosystem resilience” or the “ecological resilience” (Holling 1973, 1996). For instance, the resilience of a population is the capacity of a population to conserve its functioning and to buffer the effect of environmental changes on the population dynamics (Folke 2006). The capacity of an ecological system to conserve its functioning depends on the variable that controls the system, the intensity and the frequency of the perturbation, the time scale, and the population distribution.

The ecological resilience also includes the ability of an ecosystem subject to changes to reorganize or renew itself, and the adaptive capacity of a system (Carpenter et al. 2001). The adaptive capacity reflects the ability of a system to learn how to behave in response to disturbances, crucial to evolution (Gunderson 2000). A relative measure of this resilience can be the extinction probability of a population (Brand and Jax 2007). In conservation science, ecological resilience can be promoted by maintaining a system between limits rather than at one stable point. Nevertheless, what promotes resilience in nature?

2.3.b. Response diversity and portfolio effect

Heterogeneity among individuals is the necessary starting point for adaptive phenotypic evolution. Indeed, natural selection can only occur if individuals vary in both phenotype and fitness, while a response to selection depends on this variation having a genetic basis. Individual heterogeneity appears to play a crucial role in population resilience and in sustaining ecosystem stability in a changing environment (Bjørnstad and Hansen 1994, Peterson et al. 1998, Vindenes et al. 2008) (example in Box 4). These effects are related to genetic and phenotype polymorphisms inducing a diversity in set of functional traits, commonly called the 'portfolios effect'. The diversity in genotype and phenotype induces, within a population, a variation in individual sensitivity and different responses of individuals to an environmental disturbance (Elmqvist et al. 2003). Thus, a part of the population can be affected by an environmental change, whereas another part is not. This variability of responses keeps population functions intact and prevents population extinction. It is called the 'response diversity'.

There is growing evidence that population diversity within exploited species can contribute to their long-term sustainability and should be incorporated more explicitly into management and conservation schemes (Elmqvist et al. 2003, Hilborn et al. 2003, Hutchinson 2008). For instance, Schindler et al. (2010) quantified that phenotypic diversity in the sockeye salmon population in Bristol Bay reduced by 2.2 the variability of annual salmon returns compared to a system consisting of a single homogenous population. In addition, they argued that the variability induced by a single homogeneous population would cause ten times more frequent fisheries closures (Schindler et al. 2010). Similar schemes exist at the community or ecosystem

levels. The loss of one species has a smaller effect in a diverse system than in a species-poor one. Moreover, a high species diversity implies a higher probability of having species that efficiently fulfill functions in a changing environment.

2.3.c. The environmental canalization

Linked to the diversity of life history traits, tactics, strategies and responses, a population shows demographic parameters (survival, fecundity, growth, migration, dispersal) that differ in terms of mean value and temporal variability. Numerous studies showed that the demographic parameters that are the most closely related to fitness have evolved under natural selection to be the least variable ones against environmental variability to maximize the individual fitness and population growth rate (Stearns and Kawecki 1994, Pfister 1998, Gibson and Wagner 2000, Sæther and Bakke 2000, Gaillard and Yoccoz 2003). This phenomenon is named the 'environmental canalization' (or 'environmental buffering') of demographic parameters (Gaillard and Yoccoz 2003).

The first notion of traits' canalization was established in developmental biology studies and in works on the genotype-phenotype relationship (Schmalhausen 1949, Stearns 2002). These studies defined the canalization as a stabilizing selection process that shapes the developmental mechanisms to buffer the expression of the traits in order to maintain them close from the optimal state regardless of the genetic or environmental perturbations (Schmalhausen 1949). Then this concept has been subdivided depending on the cause of phenotypic variations: (i) the genetic canalization, to describe the insensitivity of characters to mutations, and (ii) the environmental canalization to describe the insensitivity to environmental changes (Stearns and Kawecki 1994, Wagner et al. 1997). In 2000, Gibson & Wagner redefined the canalization concept as the reduction in trait variability. From this concept, two hypotheses can be formulated on the demographic parameters variability: (i) for a given population, the variability of the major fitness components should be lower than the variability of the other components; (ii) a negative relationship should be observed between the influence of demographic parameters on the population growth rate and their variability.

Box 4. Illustration of population diversity and resilience (Paris et al. 2015 and Paris et al unpublished). In southwestern England, human mining activities across the medieval period and industrial revolution have caused toxic metal contamination in rivers, inducing poor water quality. The original diversity in those populations may allow the survival of individuals prone to adapt to the change caused by high metal concentration. Subsequently, an increase in the rate of genetic drift has been observed accompanied by an increase in abundance. Genetic analyses have shown that this long-term anthropogenic disturbance has led to metal tolerance through the development of genetic adaptation. Currently, genetic footprints illustrate a distinction in modern trout populations: Populations in metal impacted rivers are genetically distinct from trout populations in relatively clean rivers, despite being geographically proximate. Consequently, brown trout have shown a remarkable ability of resilience, certainly due to the response diversity to anthropogenic disturbances.

2.3.d. How to increase resilience?

According to the previous explanations, this question may have the following answer: by increasing response diversity at the population, community, and ecosystem levels. This response seems to be the groundwork to maintain ecosystem-buffering capacity, in order to maintain the ecosystem services we rely on. However, this theoretical response to resilience increase has generated few empirical applications to date (Laliberte et al. 2010). Only a limited number of field studies have observed that response diversity helps to sustain system functions following disturbances (Schindler 1990, Nyström 2006, Winfree and Kremen 2009) despite the appeals to manage for resilience (Scheffer et al. 2001, Folke et al. 2004). Actually, the hardest part to apply this solution is how quantify the response diversity? To answer this question, in 2014, Kahiluoto et al. proposed a generic procedure consisting of two steps. The first step must empirically assess the responses to factors of change. Then, the second step must determine the response diversity through the construction of a response diversity index and the assessment of the value added by response diversity (Kahiluoto et al. 2014).

Nevertheless, response diversity may not be the only solution to improve population resilience and viability. Diverse systems have been known to suddenly collapse: from the global scale prehistoric mass extinctions (Whiteside and Ward 2011) to the smaller scale

recent cases of Caribbean coral reefs (Bellwood et al. 2004, Downing et al. 2012). The environmental canalization theory highlights that some demographic parameters should more influence the population growth rate than others. This supposes that some tactics in a population may influence more population viability than others. Thus, acting on these major demographic parameters or/ tactics, management actions could increase the resilience of partial migration populations to environmental disturbance. In that case, the intricate part is to quantify the response diversity and the influence of the demographic parameters and life history tactics on the population dynamics to elaborate efficient management actions.

2.4. Summary of key elements

Several theoretical concepts linked to the individual heterogeneity allow the definition of two hypothetic demographic ways to ensure the resilience of a population and to understand why partial migration populations may be more resilient to environmental change than solely migratory or resident populations (Figure 5). However, these concepts also highlight questions that require responses to understand how to promote resilience. Some of these questions (question 1 to 4, Figure 5) constitute the objectives of this thesis that are going to be developed on salmonid partially migratory species after a presentation of those species.

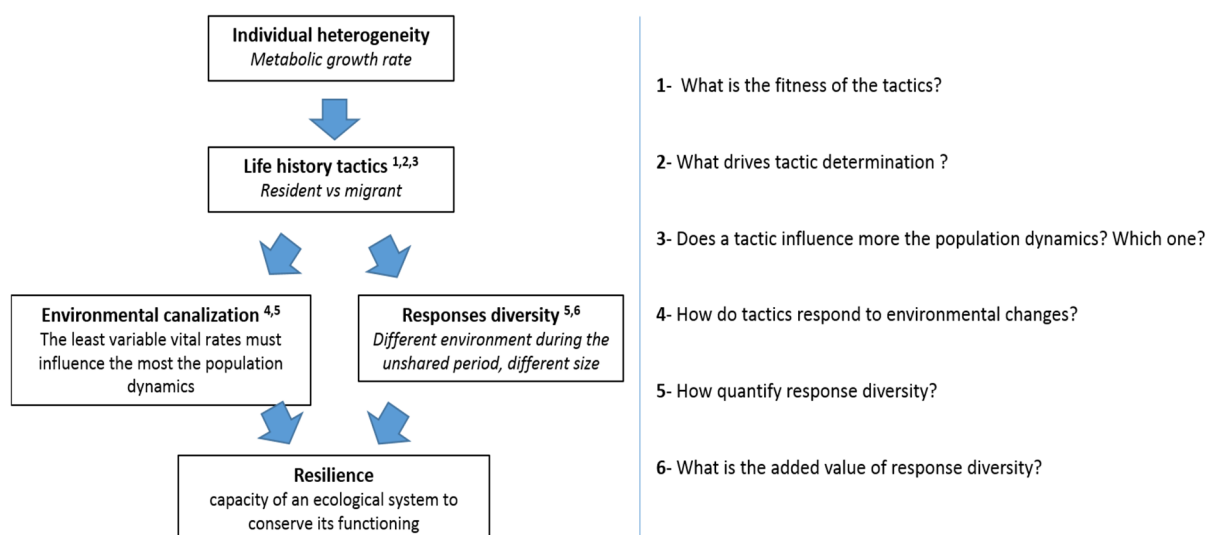


Figure 5. Summary of conceptual framework and questions linked to each concept to understand the resilience of populations. Specific information about partial migration are added in italic.

3. The case of Atlantic salmon and brown trout

The salmonid subfamily Salmoninae includes five genera (Nelson 1994, Crisp 2008). It contains several non-breeding partially migratory species with both marine migrant (called 'anadromous') and freshwater resident tactics (e.g. *Oncorhynchus mykiss*, Walbaum 1972; *Salvelinus alpinus*, Linnaeus 1758; *Salmo salar*, Linnaeus 1758; *Salmo trutta*, Linnaeus 1758). These tactics show deep morphological differences, which cause erroneous identifications by the public and fishermen and led to the creation of different common names for each tactic. The Box 5 describes the example of brown trout. Two of the partially migratory salmonid species belong to the *Salmo* genus: *Salmo trutta*, brown trout and *Salmo salar*, Atlantic salmon (Figure 6) (Linnaeus 1758). The next sections describe the characteristics of the ecology and biology of these species and highlight their main similarities and differences.



Figure 6. Atlantic salmon *Salmo salar* (L. 1758) and brown trout *Salmo trutta* (L. 1758), anadromous form of mature adult male (left panel); freshwater resident male (right panel).

Box 5. The term “brown trout”

One of the most embedded beliefs in salmonids biology is about *Salmo trutta* forms. Taxonomists conventionally use the term ‘brown trout’ to refer to *Salmo trutta* L. (1758) (Figure 6), a species having many life-history tactics, including an anadromous form (Laikre et al. 1999). However, this term has been adopted in the common parlance to mean the resident form hence a large part of the public considers sea trout (corresponding to the anadromous tactic) and brown trout as two different species. To clarify this confusion, Ferguson in Harris and Milner 2008 suggested the use of the term ‘freshwater resident’ for the non-migratory form and ‘sea trout’ for the anadromous form even if actually there is a continuum of tactics from strict residency to pure anadromy. **In this thesis we use “brown trout” or “trout” to cover all morphs where the distinction is unimportant, “resident trout” to refer to non-anadromous migratory trout (i.e. all freshwater trout), and “sea trout” or “migrant trout” to cover anadromous trout. In the chapter investigating migration in river, specific names will be defined (Chapter 1). Brown trout can also migrate between rivers and lakes (Baglinière and Maisse 2000) but this kind of populations are not considered in this thesis.**

3.1. Distribution and habitat

Brown trout and Atlantic salmon have wide natural distributions that overlap in western and northern Europe. Atlantic salmon is found on both north-American and European coasts of Atlantic Ocean whereas trout is native to Europe and has been introduced in North America. Even if partially anadromous brown trout and Atlantic salmon coexist in several rivers, brown trout are commonly found in limestone rivers, plain rivers with sedimentary substrate while Atlantic salmon are more located in steep granitic rivers with metamorphic substrate. Both of these species are highly philopatric, but a part of the population can disperse allowing salmonids to colonize new habitat (e.g. Box 6) (Makhrov et al. 2005, Ayllon et al. 2006, Perrier et al. 2009).

3.1.a. Atlantic salmon

Atlantic salmon (Figure 6) is native in rivers from Canada, United States, and Europe, where it exists in both anadromous and resident freshwater forms (Klemetsen et al. 2003). In Europe, Atlantic salmon can be found from Portugal to the North of Norway *via* Iceland and United Kingdom (Figure 7). In France, the distribution of Atlantic salmon has decreased since the middle of the 18th century due to dam building, fishing, habitat degradation and the degradation of water quality (Figure 8). Currently, Atlantic salmon is only present in about thirty rivers in France, mainly located in Aquitaine, Brittany and Normandy (Thibault 1994) (Figure 8, c) representing 5 distinct genetic units (Perrier 2010, Perrier et al. 2011) (Figure 9).

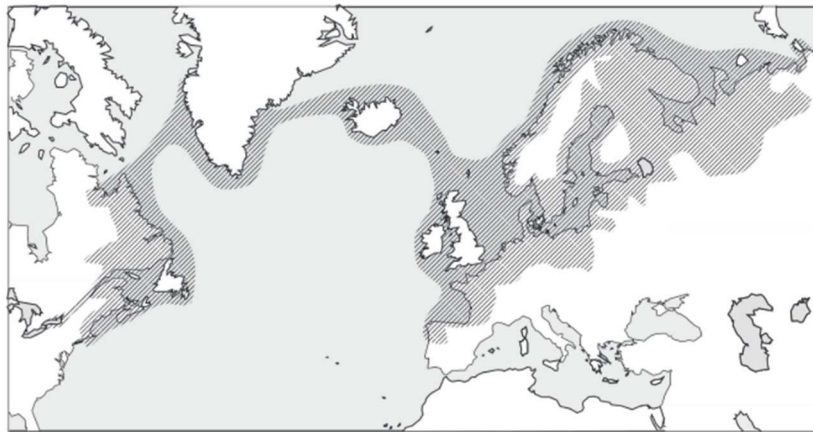


Figure 7. Native range of Atlantic salmon. *Distribution in the ocean is approximate (Jonsson and Jonsson 2009).*



Figure 8. The change in the distribution area of Atlantic salmon in France, from the middle of the 18th century (A); the end of 19^e century (B); to the end of 20^e century (C) (Thibault 1994).

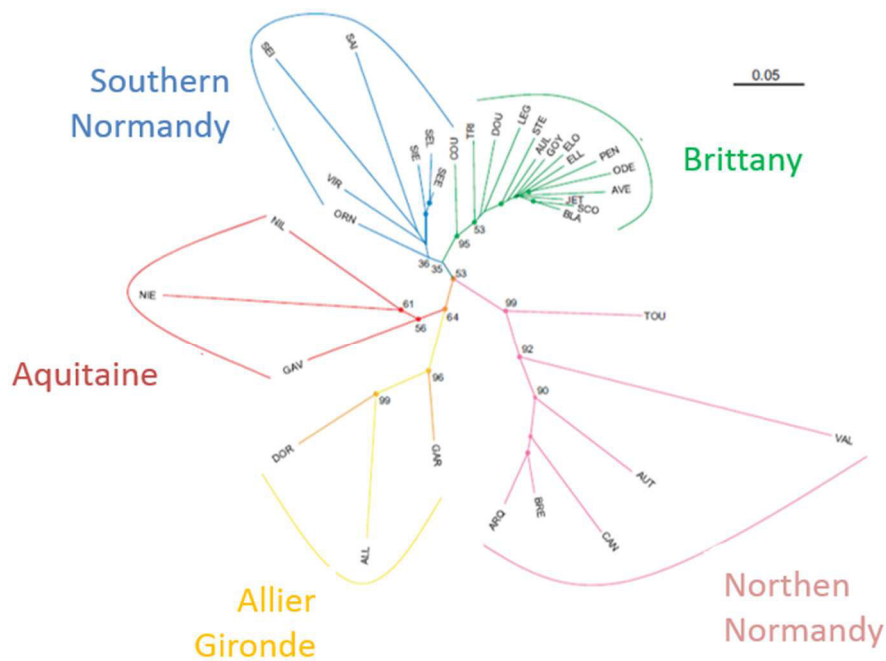


Figure 9. Neighbour-joining tree based on genetic distances among 34 populations, in France. (From Perrier et al. 2011).

3.1.b. Brown trout

Brown trout is indigenous to Europe, North Africa and western Asia (Figure 10) (MacCrimmon et al. 1970). Its distribution limits are defined by the European coastline in the west, the northern coastline of Mediterranean Sea in the south (including Corsica, Sardinia, Sicily and the Atlas mountain of North Africa), northern Scandinavia in the north, and the Ural Mountains in the east (Klemetsen et al. 2003). The anadromous form is found in rivers along the Atlantic and Channel coast from the north of Russia to Portugal but is absent from the Mediterranean Sea. Since 1852, brown trout has been introduced into at least 24 countries outside Europe: in eastern Russia in 1852, New Zealand 1867–1885, USA 1883, Canada 1887, Australia 1888, South Africa 1890, Japan 1892, and South America between 1904 and 1938. Thereby, during less than 90 years (1852–1938), the range of brown trout has shifted from Europe to a worldwide distribution (Elliott 1994). Phenotypic plasticity and a wide diversity in life history tactics confer to this species an excellent ability to spread and colonize new habitat (e.g. Box 6). The proportion in anadromous form appears to increase with latitude and sea trout dominate egg production in most northern European river systems (Jonsson and Jonsson 2009) (Figure 11 illustrates this pattern at a local scale in Normandy, France).



Figure 10. Native range of brown trout. Broken lines give the distribution of anadromous populations (Jonsson and Jonsson 2009).

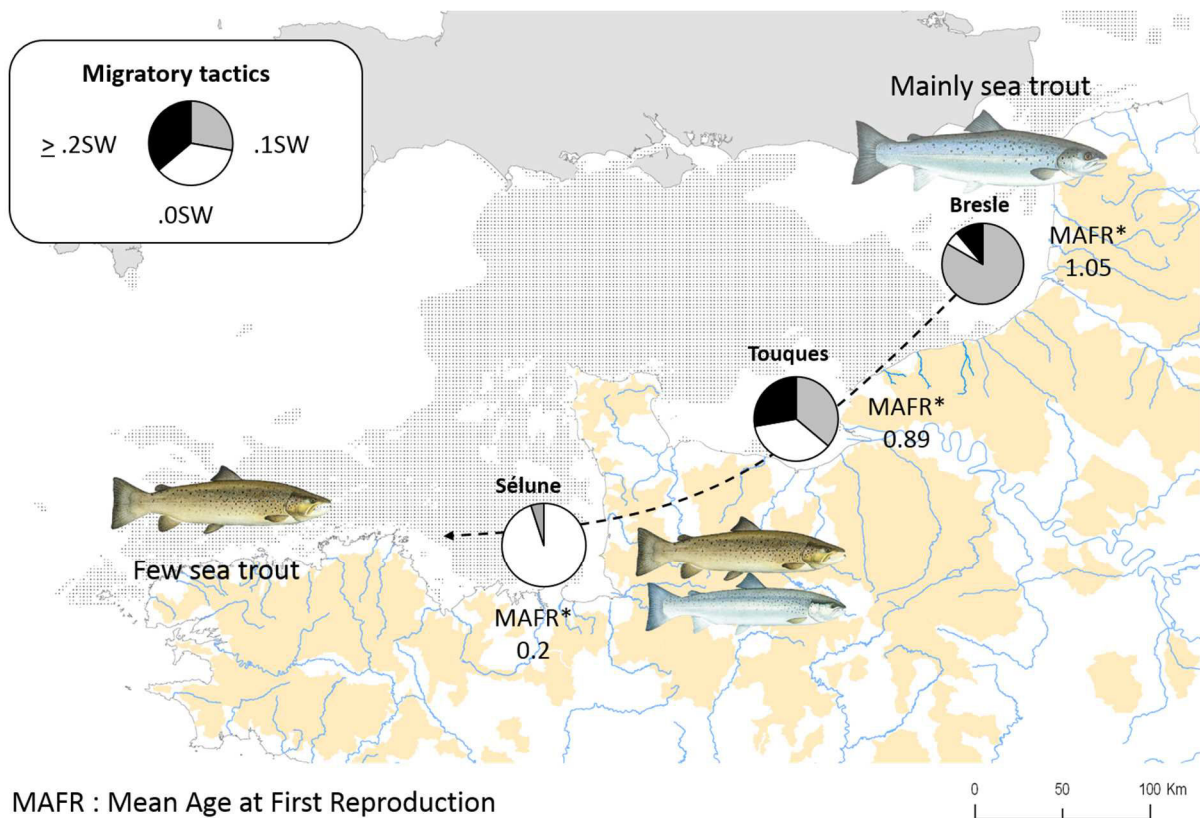


Figure 11. Populations structure in Normandy in France. Illustration by E. Quéméré (Quéméré et al. 2016).

Box 6. The Kerguelen case

Between 1951 and 1991, *Salmo trutta* has been introduced in the Kerguelen archipelago and colonized quickly the river systems accessible from the sea. Brown trout have colonized 32 watersheds in about 10 generations. This high rate of colonization seems to be partly explained by the existence of alternative tactics with a behavioral plasticity in this species (Lecomte et al. 2013). The anadromous form allowed an efficient colonization due to its high fecundity and capacity to migrate (Davaine and Beall 1997). Moreover, after the colonization, the behavioral plasticity enabled changes in migratory behavior, triggered by the new environments, which allowed the most efficient settlement of a new population. Thereby, the phenotypic plasticity and the diversity in life history tactics confer to brown trout an excellent ability to spread and colonize new habitat.

3.1.c. Atlantic salmon and brown trout

The distributions of brown trout and Atlantic salmon are strongly influenced by their habitat requirements that are partially overlapping. They can visit three habitats during their life: (i) the sea, (ii) the estuary, (iii) and the freshwater habitat (i.e. river) where spawning occurs. Generally, they share the same freshwater habitat (Milner et al. 2003), especially in small nursery streams. The key components of these three habitats are the connectivity between them and the hydrological and thermal conditions. The most important habitat features to the distribution and abundance of salmonids in rivers are depth, current, substrate and cover (Heggenes 1990, Crisp 1993, Eklov et al. 1999, Crisp 2008).

In freshwater, the preferred habitat depends on the biological stage and the activity type (reproduction, resting or feeding (Roussel 1998, Haury et al. 1999, Armstrong et al. 2003). For instance, the optimal conditions for reproduction are mostly present in the headwater areas (Huet 1954) or in small coastal rivers without tide influence (Massa et al. 1999, Ingendahl 2001, Roussel 2007, Morita et al. 2014). Moreover, some differences exist in habitat used by Atlantic salmon and brown trout. For instance, during reproduction, old and large trout are located in deeper and slower flowing water than salmon (Heggenes et al. 1999, Jonsson and Jonsson 2011). In addition, there is evidence in the literature that trout can use a very wide range of stream flows, extending almost to the upper limits tolerated by salmon parr.

Trout parr take advantage over salmon in deeper and slower-flowing areas of stream, and salmon parr may dominate in fast-flowing shallow areas, probably because they can hold station with less expenditure of energy than trout (Heggenes 1990, Heggenes et al. 1999, Armstrong et al. 2003). An increase in food availability is likely to make faster flowing areas of stream more available to trout simply because they can gain more energy to compensate costs of holding the position (Armstrong et al. 2003).

3.2. Life cycle

Atlantic salmon and brown trout both show conditional strategies including non-breeding partial migration. The characteristics of the life cycle and the specificity in life history tactics of each species are illustrated in Figure 12 and Figure 13.

Adult Atlantic salmon and brown trout reproduce in freshwater (from December to early January, in France) and in Southern Europe most Atlantic salmon die after a unique reproduction (semelparous strategy), whereas brown trout are mainly iteroparous. Trout tend to spawn earlier than salmon and make more use of small headwaters (Crisp 1993). Moreover, trout are more aggressive and dominant to salmon parr of similar size (Kalleberg 1958, Heggenes et al. 1995, Harwood et al. 2002, Armstrong et al. 2003, Stradmeyer et al. 2008). They are external fertilizers that reproduce by releasing gametes into the water during paired matings (Esteve Cavaller 2005). They produce small offspring in great quantity, presumably to take advantage of highly abundant but patchily distributed planktonic prey (Winemiller and Rose 1993), which in turn generates variability in feeding efficiency, growth and survival during the larval period (Houde and Hoyt 1987). As a result, variability in early life conditions through its influence on demographic parameters and life history can carry over to the demographics and ecology of subsequent stages (Bertram et al. 1993, O'Connor and Cooke 2015).

In France, fries emerge from gravel in March and grow in river during their first summer. In October, the size of young-of-the-year (i.e. 6 months old, called 'parr', 'Yoy', or '0+ old') ranges from 25 to 150 mm (mean size = 78 mm) for trout and from 25 to 130 mm (mean size = 74 mm) for Atlantic salmon. During their first (Yoy) and second winter (1+ old), some individuals migrate to sea (Figure 12, b, c and Figure 13, d) whereas the others stay in their natal river (Figure 12, a and Figure 13, a).

In brown trout, migratory and resident tactics can be identified as the two extremes of a continuum of migratory tactics (Figure 13) (Jonsson 1985, Elliott 1994, Cucherousset et al. 2005). Between these two extreme tactics some trout can migrate downstream at short-distance (Figure 13, b) or migrate to sea during a couple of months (Figure 13, c) (Cucherousset et al. 2005). Brown trout exhibit one of the highest diversity of life-history tactics among salmonids (Jonsson 1989, Elliott 1994, Baglinière 1999, Cucherousset et al. 2005). In brown trout, freshwater resident can be either male or female. In Atlantic salmon, only a small fraction of males (< 5% of reproductive males in December), called precocious mature parr, can reach sexual maturity without migrating at sea (Bagliniere and Maisse 1985). When young salmon or trout migrate for the first time at sea there are called 'smolts'. This name represents the physiological, morphological and behavioral modifications that take place prior to seaward migration to prepare individuals to pelagic life and salinity (i.e. the smoltification, McCormick et al. 1998). In relation to these physiological modifications, the individual color becomes silver. In brown trout, the large diversity of migration tactics is linked to a large gradient of silver colors, which induces some difficulties to visually distinguish individuals that migrate to sea from those that migrate downstream in rivers.

In French populations, migrant salmon can stay at sea for one single year (i.e. Single-Sea-Winter, '1SW', also called 'grilse'; Figure 12, b), or for two or three years (i.e. Multi-Sea-Winter, 'MSW'; Figure 12, c). Migrant trout stay at sea from a couple of months ('finnock' tactic) to up to 2 years (but adults can return to sea after reproduction). After their growth at sea, adult salmonids go back to their natal river (i.e. 'homing') mainly in spring for MSW and in summer for 1SW. They cease feeding upon starting their freshwater spawning migration (Kadri et al. 1995, 1997, Hinch et al. 2005) and their sexual maturation. Consequently, the upstreaming migration is entirely fueled by endogenous energy reserves (Crossin et al. 2009). The age at first reproduction for all tactics in Atlantic salmon and brown trout varies from 1 to 3 years in France, depending on the sex and environmental conditions. After their first reproduction, the migrant survivors migrate downstream to sea, and residents stay in freshwater. Atlantic salmon that migrate downstream after reproduction are called 'kelt' (Aas et al. 2011). The life cycle of Atlantic salmon and brown trout show some differences that allow them to coexist in the same river as their freshwater habitat requirement and distribution are overlapping (Heggenes et al. 1999).

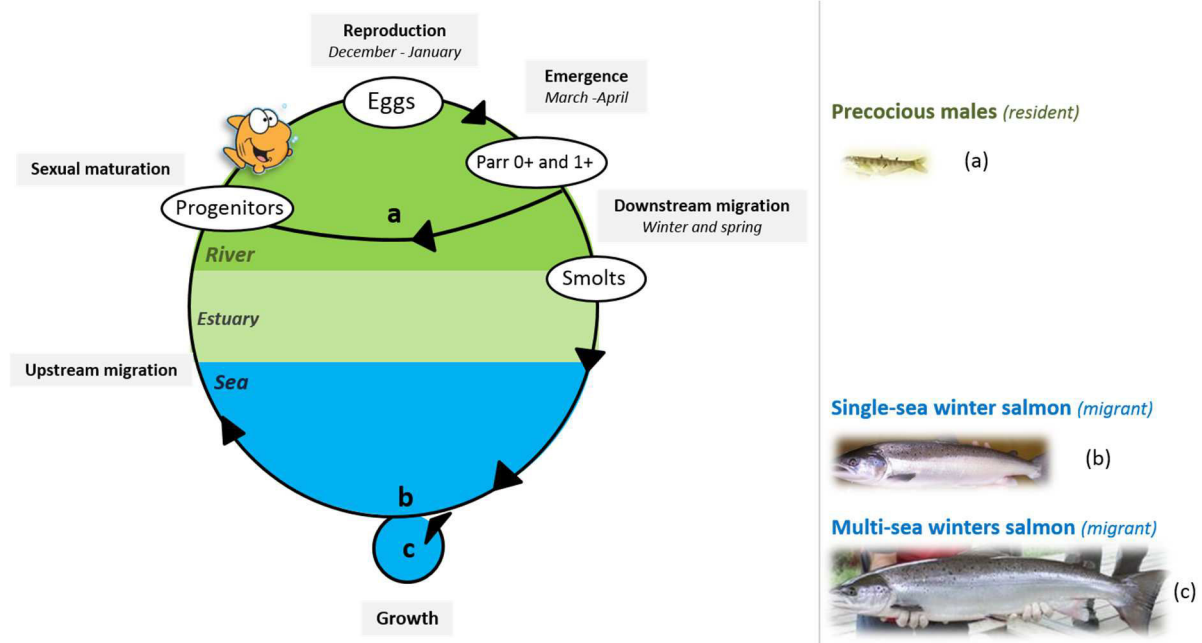


Figure 12. Life cycle of Atlantic salmon, *Salmo salar* and the different life history tactics and phenotypes: precocious males are the resident tactic and single-sea winter and multi-sea winter are the sea migrant tactics (i.e. anadromous).

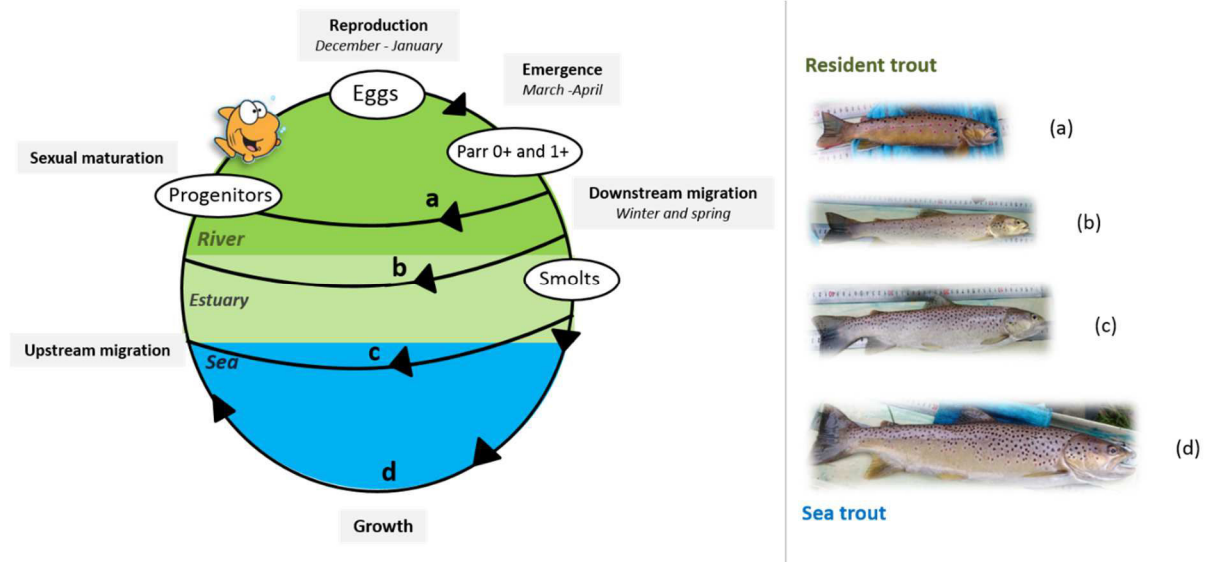


Figure 13. Life cycle of brown trout, *Salmo trutta* and the different life history tactics and phenotypes in the Oir River, France 'a' (resident) and 'd' (sea-migrant trout spending one year or more at sea) are the two extremes of the migratory continuum, and 'b' (freshwater migrant trout) and 'c' (sea-migrant trout spending couple of months at sea) two examples of intermediates tactics.

3.3. Causes, costs, and benefits of migration

A large body of literature on salmonids suggested that migration was determined by a threshold trait linked to multiple genes and environmental influences, and expressed when a combination of factors exceeds a threshold level (Jonsson 1985, Okland et al. 1993, Bohlin et al. 1996, Forseth et al. 1999). Recent research projects studied the extent to which anadromy *versus* residency in brown trout and Atlantic salmon are influenced by genetics or environmental conditions (Chapman et al. 2012, Lepais et al. 2017, Ferguson et al. 2017). In other salmonid species, heritability estimates for anadromy in steelhead (hatchery) and brook charr (wild) of 0.5 to 0.6 indicated that about half of the variation in life-history could be attributed to additive genetic variation (Ferguson et al. 2017).

Several studies showed that migration in salmonids was linked to the metabolic and growth rates (Acolas et al. 2012). Individuals with a high metabolic rate grow faster and have a higher probability to migrate than slow growers have. The available food in the natal habitat is likely to limit fast growers sooner than slow growers. Thereby, fast growers need to migrate to better feeding habitats earlier to ensure continued growth whereas individuals with a low metabolic rate would tend to remain in their natal environment (Cucherousset et al. 2005, Acolas et al. 2012). The sources of variation in metabolic rates are not fully understood, but maternal and developmental effects are believed to play a part (Cucherousset et al. 2005). Nevertheless, all environmental factors affecting the growth rate as food availability or water temperature could indirectly influence the determination of the life history tactic (Elliott 1976, Olsson et al. 2006, Morita et al. 2014). Consequently, the tactic determination appears as a plastic response to environmental changes influenced by growth opportunities (Olsson et al. 2006). In addition, (Thorpe 1990) suggested that the fish's primary objective is to reproduce as early as possible and only secondarily to grow. As the conditions that promote rapid growth also promote early maturity (Alm 1959, Thorpe 1986), good growing conditions in freshwater in early life stage should induce fewer migrant fish. At the opposite extreme, in habitats with poor growing conditions, partially migratory salmonids are more likely to migrate. However, Intermediate conditions enable different proportions of both resident and migratory strategies to be expressed (Thorpe 1990).

Ferguson (2006) suggested that life-history tactics might shift with relatively small environmental changes. The influence of a change in migration probability on population dynamics is unknown whereas this information is crucial as the costs and benefits of migration and residency are deeply different. Anadromous Atlantic salmon and brown trout benefit of a highly productive marine habitat to achieve a higher growth rate than resident fish (Kendall et al. 2014). Returning anadromous trout are significantly larger (range: 210-790 mm, mean size = 392 mm, data from Oir Index river cf. data sets section) than resident trout (range: 110-465 mm, mean size = 255 mm, data from Oir Index river cf. data sets section). This size benefit from migration is larger for female salmonids than for males as female fertility increases exponentially with body size (Jonsson 1985, Kendall et al. 2014). Thus, females are more likely to migrate in more productive environments (Northcote 1992, Cucherousset et al. 2005, Ferguson 2006).

In salmonids where females can be both migrant and resident, migrant females are likely to be the dominant source of total egg deposition in most rivers with a migratory component (Milner et al. 2006, Harris and Milner 2008). For instance, Jonsson and Jonsson (2006) showed that the mean size of sexually mature sea trout in southeast Norway increased significantly with the migratory distance between the feeding area at sea and the spawning area in freshwater. In addition, large female salmonids are more dominant for access to suitable nest sites (Esteve 2005), able to secure better quality nesting sites (Hendry et al. 2001) and they can also dig deeper redds (Crisp and Carling 1989, Fleming et al. 1997, Fleming 1998, Blanchfield and Ridgway 2005). Such deeper nests are better protected against destructive gravel shifts, river desiccation, freezing and nest superimposition by other females (Fleming 1998). Several studies also reported that large females produce larger eggs (Quinn et al. 1995, Fleming 1996, Hendry et al. 2001). Large eggs yield large fry and juveniles that exhibit higher growth and survival rates due to their superior competitive abilities and reduced predation risk compared to smaller juveniles (Hutchings 1991, Einum and Fleming 1999, 2000, Hendry et al. 2001).

In contrast, for males, as sperm is relatively cheap to produce compared to eggs, even small males can produce enough sperm to fertilize all the eggs of the largest females. Salmonid males with a large size have some advantages in attracting females and defending spawning

territories (Jones and Ball 1954). However, smaller freshwater-resident males can adopt a 'sneaking' tactic to fertilize eggs, thereby reducing the advantage of being a large male. Jonsson and Jonsson (2006) showed that gonadal mass in anadromous males decreased with the distance traveled to spawning grounds. Thereby, this decrease in gonadal mass could be a factor promoting male residency when migratory costs are large (Bohlin et al. 2001). No similar decrease was found in female gonadal allocation, suggesting that females are able to better conserve their gonadal allocation than males.

The advantages of migrating are traded against a higher mortality risk as upon sea-entry, migrants are exposed to costly physiological changes (Harris and Milner 2008) and a high risk of predation (Dieperink et al. 2002). In addition, as anadromous salmonids cease feeding before their freshwater spawning migration, they show a higher pre-spawning mortality compared to resident fish. The efficient allocation and expenditure of limited energy stores is thus crucial (Hinch et al. 2005, Young et al. 2006, Crozier et al. 2008, Mathes et al. 2009), especially for populations that complete long migrations (Bernatchez and Dodson 1987).

3.4. States and management

Brown trout and Atlantic salmon have both important patrimonial values in Europe as native species. However, Brown trout has always been considered as a secondary priority in fishery management plans compared to salmon. A clear example of this difference is that an International Council for the Exploration of the Sea (ICES) Working Group on North Atlantic Salmon (WGNAS) advises the North Atlantic Salmon Conservation Organization (NASCO) to manage salmon stocks better since 1952 whereas the equivalent ICES working group on sea trout has only been created in 2016. Atlantic salmon has been historically more exploited and had a higher economic value than brown trout, which may explain this difference in management and scientific considerations. However, both species are currently fragile and subject to similar anthropic pressures as climate change, agriculture, urbanization, exploitation, habitat degradation or barriers to migration (e.g. Schindler 2001).

3.4.a. Atlantic salmon

Since 1950, Atlantic salmon populations have sharply declined, especially in the southern populations as in France (Figure 8). This decline has been characterized by three deep modifications observed in European populations:

- (i) a decrease in abundance (Chaput 2012, ICES 2016);
- (ii) a change in population structure (e.g. Figure 14), with a decline in the proportion of multi-sea winter salmon (Bagliniere et al. 2004, Otero et al. 2012, ICES 2016, Jonsson et al. 2016);
- (iii) modifications in life history traits as length, body mass, and phenology (Aprahamian et al. 2008, Bacon et al. 2009, Valiente et al. 2011, Todd et al. 2012, Jonsson et al. 2016).

Currently, in Europe, the International Union considers Atlantic salmon as a ‘vulnerable’ species for the Conservation of Nature (IUCN). In France, commercial fishing is restricted to a few estuaries and recreational angling is allowed in rivers with strict management rules. To control the long-term effects of recreational angling, a quantitative management of salmon populations has been applied since 1996. This management action is based on a ‘Total number of Catches Authorized per River (‘TAC’). It is fixed annually for each population in order to let enough progenitors escape the fishery to ensure population viability. Different TACs are defined for MSW and 1SW salmon given their different abundances and limit the fishing pressure on MSW. Anglers have to declare their catches and provide some information (date, location, sex, body length and scales) to the National Center for the Interpretation of Migratory Salmonid Catches (‘CNICS’). When the TACs is reached in a River, the fishing period is closed. The TACs are estimated from the number of eggs needed to maintain population size, based on Prévost and Porcher calculations (Prévost and Porcher 1996).

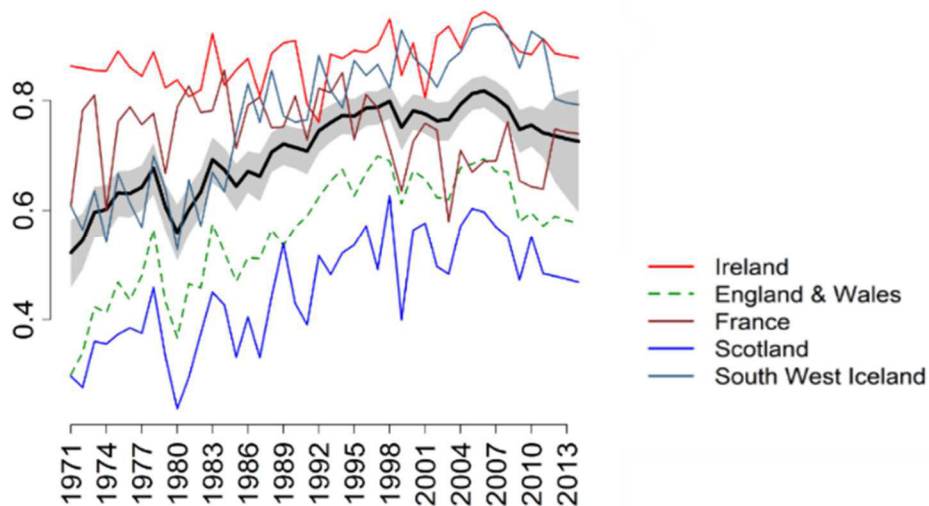


Figure 14. Probability to mature after one year spend at sea in European Atlantic salmon populations. (CIEM/ICES working group North Atlantic salmon)

3.4.b. Brown trout

Brown trout is considered as ‘least concern’ by the IUCN (2016). However, in some regions as in Wales, some changes have been observed in sea trout: an increase in growth, a decrease in age at first maturation and size at maturation in correlation with the sea surface temperature (Milner et al. 2017). These changes can have potential effects on population dynamics and can influence stock composition as well as the fishery value. Only few sea trout stocks have been studied and for an insufficient time period to allow the development of population models and the quality of catches and fishing effort statistics is very variable. Moreover, the main management actions in Europe on brown trout have considered only sea trout. This situation is linked to the hypothesis that resident trout make only a small contribution to egg deposition in many rivers, which suggests that it is reasonable to develop population models considering only sea trout. Nevertheless, the ICES working group on sea trout recently recognized that it might be necessary to consider both resident and sea trout to manage populations better. However, including resident trout in sea trout models may be difficult due to the lack of data on this form in many populations.

In France, *Salmo trutta* has been rarely exploited by commercial fisheries at sea or in freshwater. Sea trout did not show a declining trend but some resident population did and

some have disappeared (Thibault 1983). Recreational angling occurs in rivers and focuses on the largest trout (Changeux 2001) but there is no TAC for this species. In France, brown trout stocks are not assessed at the national level. Angling trout catch records are only collected on a voluntary basis and concern mainly sea trout. The catch statistics thus provide an incomplete picture of the fishing activity for *S. trutta*.

3.5. Summary of key elements

The key elements on differences and similarities in biology of brown trout and Atlantic salmon, are summarized in Table 1.

Table 1. Key elements of the ecology and biology of Atlantic salmon and brown trout useful for the understanding of the different chapters of this thesis.

Species characteristics	Atlantic salmon <i>Salmo salar</i>	Brown trout <i>Salmo trutta</i>
3.1. Distribution and habitat		
Distribution	Overlapping in France	
Marine habitat	Greenland, Feroe Island, and Norway Sea	Coastal marine habitat: Atlantic coast and the North Sea
River habitat (spawning habitat)	Small headwater	
3.2. Life cycle		
Life-history strategy	Conditional strategy	
Type of partial-migration	Non-breeding partial migration	
Life-history tactics	Migrant: one sea winter (1SW) and multi sea winter (MSW),	A continuum from resident to migrant
Resident	Only precocious males	Both sexes
Sea migrant	both sexes	
Time spent at sea in French populations	From 1 to 3 years	A couple of months to 3 years
Reproduction	Mainly semelparous	Iteroparous
Age at first reproduction	From 1 to 3 years	
3.3. Costs and benefits of sea migration		
Benefits	Better feeding opportunity -> higher fecundity	
Costs	High mortality, variability in the access to spawning grounds	
Sea migrant size on spawning grounds in December (mm) <i>data Oir river cf. data sets</i>	[500 - 870], mean = 640	[210 - 790], mean = 392
Resident size on spawning ground in December (mm) <i>data Oir river cf. data sets</i>	[50 - 200], mean = 116	[110 - 465], mean = 255
Yoy size in October (mm) <i>data Oir river cf. data sets</i>	[25 - 130], mean = 74	[25 - 150], mean = 78
3.4 Status and management in France		
European IUCN status (2016)	Vulnerable	Least concern
ICES working group creation	1952	2016 (on sea trout)
Main fishing pressure	MSW	Sea trout
Population structure	Decrease in MSW abundance and more precocious males	NA
Management in France	TACs for MSW and 1SW (resident male not considered)	Time period and size limit

4. Objectives and manuscript organization

In this doctoral project, I investigated the influence of the diversity of life history tactics on population dynamics and resilience to environmental changes in two partially migratory salmonids: Atlantic salmon and brown trout. My specific objectives were (1) to investigate and compare the fitness and responses of the life history tactics to environmental change, (2) to determine the relative influence of each tactic on population growth rate, and (3) to investigate how to increase resilience in partially migratory populations. In this dissertation, I describe the data and the methods used, then I present my main results into four chapters. Each chapter includes an article where the numbering of tables and figures are specific of the article, as well as the references.

In **Chapter 1**, I analyzed the effect of environmental variations on the determination of life history tactics in the juvenile stage. As environmental changes, I considered intra- and interspecific density variations, which potentially resulted from several biotic and abiotic changes in the freshwater environment. For this analysis, I used a multi-event capture-mark-recapture model (CMR) based on long-term individual-based data on an index river in France, where brown trout and Atlantic salmon are closely monitored.

In **Chapter 2**, I investigated the long-term spatiotemporal variations in life history traits of the adult tactics using a general additive model based on French catch declarations data.

In **chapter 3**, I assessed the reproductive success of the migratory and resident tactics in brown trout and compared their contribution to the juvenile production. In addition, I tested a series of hypotheses to understand which life history trait influences the most the reproductive success.

In **chapter 4**, I scaled up the results of the previous chapters to the population level by building a stage-structured matrix population model on brown trout. Using perturbation analyses on this model, I investigated the influence of life history tactics on population dynamics and described the demographic causes of temporal variations in population growth rate. Then, I developed this matrix model to initiate an integral projection model that considers the individual diversity within each tactic with demographic parameters as functions of body size. The aim of this final model was to investigate the role of body size in the population dynamics

of a partially migratory species and test the impact of environmental changes through variations in body size.

I close this manuscript with a discussion synthesizing the main results to highlight how tactic diversity promotes the resilience of partially migratory populations to global change. Then I make some suggestions about the future of partially migratory populations considering the current migration disappearance. At last, I propose management advices and future perspectives.

DATA SETS
&
METHODS

Data sets and Methods



1. Data sets description

1.1. Catch declaration

As explained in the description of the French management plan for Atlantic salmon and brown trout, declare French fisherman (professional and recreational) have to declare their catch of Atlantic salmon (mandatory) and brown trout (voluntary) to the 'Office National de l'Eau et des Milieux Aquatiques' (ONEMA) since 1987 (Figure 15, Table 2 and Table 3). The collected data includes body size, mass, sex, and scale samples. The analysis of growth patterns on scales informs on the age, the migratory tactic (time spent in river and at sea) and the number of reproduction of each individual (Baglinière et al. 1985). These catch declarations create a unique data collection framework of participatory science, that cover the entire French metropolitan territory, and which is easy to implement over years (i.e. low cost). However, captured fish are a biased sample of the population as they only inform about individuals that survived until the adult stage. In addition, as anglers focus their catch on the largest fish, the sampling effort is biased toward individuals that spent more than a year at sea. Incorrect sex identification or measurements may also occur.

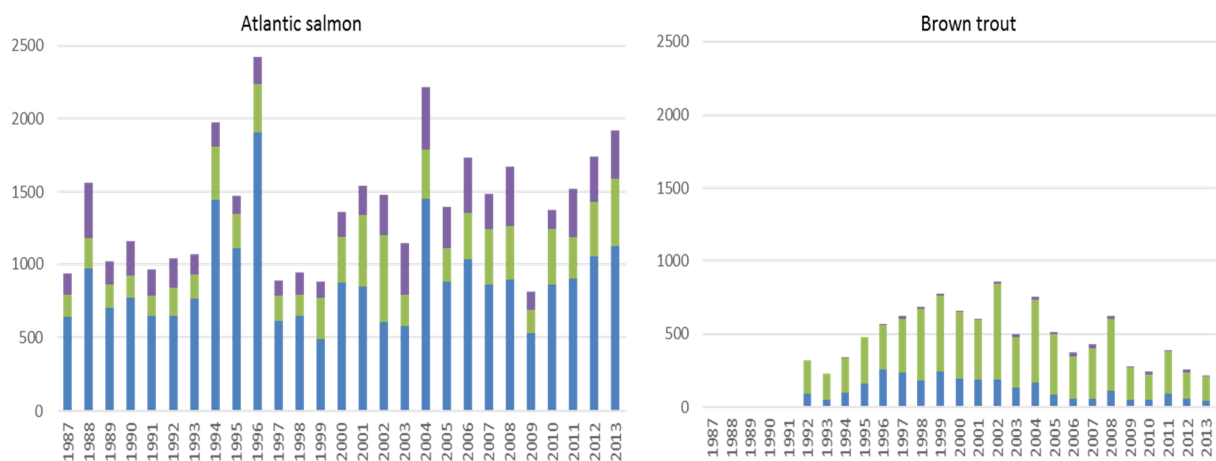


Figure 15. Number of catch declarations on Atlantic salmon and brown trout in Brittany (blue), in Normandy (green), and in Aquitaine (purple).

1.2. Index river, Oir river

We used data collected as part of a long-term individual-based monitoring program in a French river, Oir river (Figure 16). This monitoring program is part of the 'Observatoire de Recherche en Environnement Diadrome Petits Fleuves Côtiers' (ORE Dia-PFC), and technically run by the aquatic Ecology and Ecotoxicology Experimental unit (U3E).

Oir river is a tributary of the Sélune river, which flows into the Mont Saint Michel bay in Normandy (48°30'N, 1°45'W) and break up by three dams (Figure 16). Oir river is 19.5km long with a catchment characterised by farm lands (82%). The annual water temperature varies from 8°C in January to 16°C in summer. Five diadromous species inhabit the Oir river: Atlantic salmon, brown trout, European eel, *Anguilla Anguilla*, sea lamprey, *Petromyzon marinus*, and river lamprey, *Lampetra fluviatilis*. Moreover, other non-migratory species often caught in this river include: stone loach *Barbatula barbatula*, European bullhead *Cottus gobio*, and brook lamprey *Lampetra planeri* (Baglinière et al. 2005). Oir river catchment includes eight tributary rivers including La Roche brook (Figure 16). La Roche brook has been identified as a major nursery ground for Atlantic salmon and brown trout. Indeed, it shows the highest fall juvenile abundance of the Oir system.

The Atlantic salmon and brown trout populations are monitored since 1983 in Oir river with electrofishing capture survey and a fish trap at the Cerisel mill, down Oir river (Figure 16 and picture in Figure 17.b; Table 2, Table 3). The fish trap captures smolts and kelts during their downstream seaward migration and mature anadromous adults in their upstream migration (fish are then release). The fish trap and electrofishing surveys record biometric measurements, reproductive status, sex (on mature individuals), age and tactic (assessed by posterior scale analysis). Since 1986, in La Roche brook, salmonids are monitored three times a year by electrofishing (May, October, December, Table 2, Table 3 and Figure 17.a.d.e.f). In the October survey, juveniles (6 months old) are individually identified with an unique transponder (i.e. PIT-Tag) (not done in Oir main river, and done only recently in other ORE Dia-PFC index rivers) (Table 2 and Figure 17.d). In the December survey the marked individual are recaptured to estimate the number of mature adult (Table 2 and Figure 17.a.e.f) whereas in the May survey the recapture of marked individual enables the identification of the juvenile

that did not migrate at sea during the winter (Table 2). In addition, autonomous Antenna systems located down La Roche brook, since 1996 and in Oir river (close to the fish trap) since 1997 detect and record automatically the identity of marked individuals moving through this detection device all year-round (Figure 17.c).

The joint monitoring by fish trap, electrofishing, and antenna systems form a long-term individual-based data set, where Atlantic salmon and brown trout are monitored from early life to reproduction (Table 2 and Table 3). The individual-based monitoring (with PIT-Tag) contained in this data set is robust as data collection followed a standardized protocol with trained observers, since 1997. Nevertheless, these salmonid populations may not be representative of all French populations knowing genetic and environmental differences (Perrier 2010, Quéméré et al. 2016). In contrast with the catch declarations, this monitoring program is expensive in time, in workforce and in money and are thus hard to maintain in the long term.

Besides the standard electrofishing monitoring survey in La Roche brook, a specific protocol was applied during two consecutive reproductive periods (December 2014- October 2015 and December 2015- October 2016) in order to collect genetic samples from adults. We collected fin clips from electrofished mature Atlantic salmon and brown trout just before the reproduction. Using genetic analysis, we assigned mature adults to juveniles caught in the October following the reproduction season to estimate their reproductive success (Table 3).

Table 2. Description of the available data on Atlantic salmon and brown trout. The ‘anadromous identification’ corresponds to the direct observation of the anadromous forms based on physiological features. The analysis of scales allows a posteriori identification of the age and the migration tactic of individuals. The ‘type’ is the life history stage (e.g. ‘juvenile’, ‘smolt’, and ‘adult’). ‘LR’, La Roche brook.

Data set	Monitoring method	Sampling period	Species	Monitoring aim	Data used to estimate	Localisation	Marking	Mark reading	Length	Mass	Scales	Anadromous identification	Sex	Type	Related thesis chapter	Related thesis article	
Catch declaration	fishermen declarations	During the fishing period	Mandatory for A. salmon, voluntary for b. trout	Index the number of catch	Fishing regulation	All rivers in France			x	x	x		x		2	II	
Index river	Electrofishing	October	A. salmon & b. trout	Mark young of the year	Young density and abundance index	LR	x	x	x	x	x			x	1, 4	I, IV	
				Capture probability	Three section in LR										1	I, IV	
				Abundance index	Oir											Not used	
		December	A. salmon & b. trout	Recapture during the reproduction season	Recruitment, survival probabilities	LR	x (trout)	x	x	x	x	x	x	x	x	1, 4	I, IV
						Oir	x (trout)	x	x	x	x	x	x	x	1, 4	I, IV	
	May	A. salmon & b. trout	Recapture after the migrating period	Migration and survival probabilities	LR		x	x	x	x		x	x	1, 4	I, IV		
	Fish trap	All year	A. salmon & b. trout	Recapture downstream migrant or anadromous upstream migrant	Migration probabilities	downstream Oir	x (trout)	x	x	x	x	x	x	x	1, 4	I, IV	
	Antennas systems	All year	marked A. salmon & b. trout	Recapture marked individual	Migration probabilities	LR/ Oir intersection		x								1, 4	I, IV
						Downstream Oir		x								1, 4	I, IV
	Genetic samples	December and October	A. salmon & b. trout	Genetic assignment	Reproductive success	LR	x	x	x	x	x	x (adult)	x (adult)	x	3, 4	III, IV	
Environmental monitoring	At least monthly			Water temperature, pluviometry, flow, physico-chemical quality	Environmental changes	Oir & LR									Not used		
	1988, 1998, 2009, 2012			Habitat description	Environmental changes	Oir & LR									Not used		

Table 3. Time frame of the available data. *The shaded area corresponds to the data used in this study.*

Data sets	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Chapter	Article		
Catch declarations																																				2	II	
Index river																																						
Electrofishing																																					1,4	I,IV
Fish trap																																					1,4	I,IV
Antennas system in LR																																					1,4	I,IV
Antennas system in Oir																																					1,4	I,IV
Genetic sampling																																					3,4	III,IV

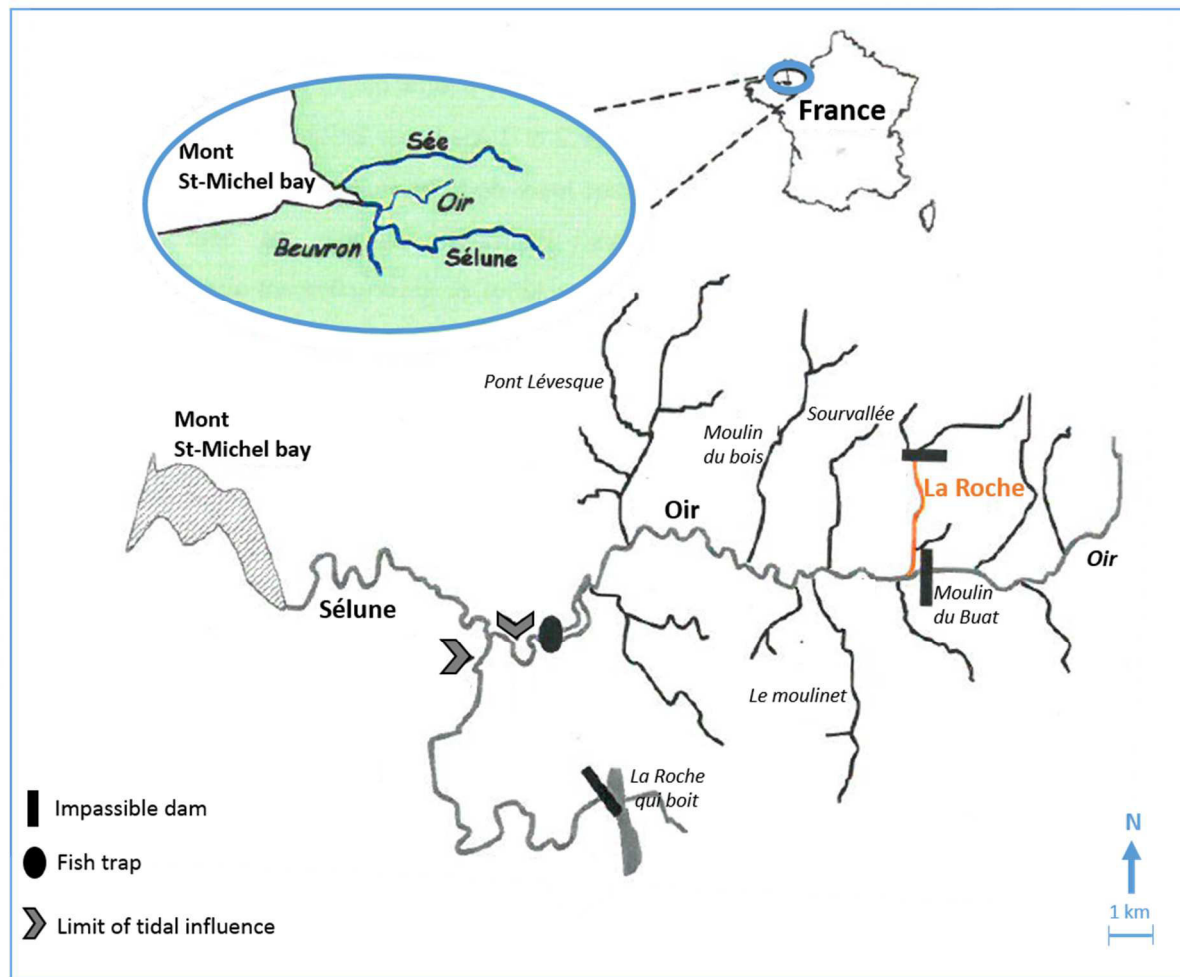


Figure 16. Map of the Oir index river



a. Electrofishing survey in La Roche brook, in December



b. Downstream migration fish trap, Oir river



c. Antennas systems in Oir river



d. Automatic biometry table used during the electrofishing monitoring in October (and in May), in La Roche brook



e. Measurement of A. salmon during the electrofishing monitoring in La Roche brook, in December.



f. Marking, measurement, and genetic sampling of b. trout during the electrofishing monitoring in La Roche brook, in December.

Figure 17. Pictures of the monitoring on La Roche brook and Oir river.

1.3. Summary of the data sets

This thesis is based on two complementary data sets with different advantages and disadvantages (Table 4): (i) A data set based on recreational angling declaration enables the investigation of large spatial trend in life history traits; and (ii) an individual-based monitoring in an index river allows the estimation of demographic mechanisms. Due to these differences and our questions, different methods have been used to analyze them. More details about the data used are described in articles included in the chapters of this thesis.

Table 4. Advantages and disadvantages of the available data set.

Data set	Advantage	Disadvantage	Useful for
Recreational angling	<ul style="list-style-type: none"> • Participatory science: easy to maintain over the years • Cover the entire French distribution area 	<ul style="list-style-type: none"> • Can be biased as fishermen focus on the largest fish and by incorrect measurement or sex identification • No mandatory for brown trout • Information only about adults that have survived until their return in river 	<p>Population level study: Inter populations comparisons</p>
Index river	<ul style="list-style-type: none"> • Similar protocol and trained observers (robust) • Both A. salmon and B. trout • Individual monitoring from early life stage 	<ul style="list-style-type: none"> • Hard to maintain, expensive in time, in workforce, and in money • One system that may not be representative of all French rivers • Include systems with different detection probabilities 	<p>Individual-based study: Capture-Mark-Recapture, matrix population model + Intra and interspecific study</p>

To investigate large spatial trend in traits, classical general additive model has been used (Wood 2011). However, to estimate demographic parameters and model the population dynamics based on the long-term individual-based monitoring from the Oir index river, specific methods have been employed. We describe these methods in the section.

2. Demographic parameter estimates

2.1. Capture-mark-recapture

When studying an animal population in the field, it is rarely possible to follow all the individuals of an initial sample over time, even if they are uniquely marked. Generally, animals will be seen, marked and then recaptured, or recorded from time to time, but the exact time of death remains unknown. Moreover, individuals that are still alive are not necessarily seen and can be classified as dead whereas their recapture might occur later. Thereby, under field conditions, estimating survival probabilities of an individual between two-time steps raises problems, as the detection of individuals is imperfect (individual captured probability, $p < 1$). To estimate the demographic parameters of a population despite the imperfect detection, statistical methods related to the capture-recapture data, called 'Capture-Mark-Recapture' models (CMR) have been developed (Lebreton et al. 1992).

CMR models depict the population life cycle by decomposing the population structure "in states" (Caswell 2001). The states are used to describe the true fate of an individual at each capture occasion. The definition of states is specific to each case of study and ecological question. States can be 'dead' or 'alive' (i.e. single state CMR model, Lebreton et al. 1992). However, when there are obvious differences in the performances of different life history stages and these differences are expected to be important, we use multi-states structured population models (Lebreton et al. 2009). In these CMR models, states can represent development stages, age classes, reproductive status, geographical site, social rank, etc... , which supposes differences in demographic parameters (e.g. young in La Roche brook, mature migrant trout). The state of an individual can change between two-time steps and CMR models estimate the parameters that make the transition between states (e.g. survival, migration) (Lebreton et al. 1992). CMR models rely on four assumptions: (i) no mark lost, missed or

overlooked; (ii) Every marked animal in the population at time (t) has the same probability of recapture (i.e. no trap-dependence); (iii) every marked animal in the population immediately after time (t) has the same probability of surviving to time ($t+1$); and (iv) All samples are instantaneous and each release is made immediately after the sample (Pollock et al. 1990). Goodness-of-fit (i.e. 'GoF') tests have been developed to evaluate the fit of the data to these assumptions to ensure that a CMR model can be used to obtain non-biased parameter estimations (Choquet et al. 2009).

From capture-recapture data (e.g. individual monitoring from Oir index river system), CMR models estimate the detection probabilities and transition probabilities between two states (including the survival) by the maximum of likelihood method: the value of the parameter, which maximizes the probability to obtain the observed captures history in the data is the most likely value of it (Lebreton et al. 1992). However, with this method mortality and permanent emigration are confounded, thus the estimated survival is actually referred to as an apparent survival and not the "true" survival.

Sometimes the observations (i.e. 'events') differ from the biological reality inducing uncertainty in the state identification. A single event can correspond to several states (e.g. Figure 18). For instance, from the brown trout monitoring in Oir index river, an individual detected at the antennas down La Roche brook can be either a freshwater resident or a migrant trout. To consider this uncertainty in the state identification, specific CMR models, called 'multi-events models' separate the observation process from the biological process (i.e. state process) that generated the data (e.g. Figure 18) (Pradel 2005, 2009). With this distinction, multi-events models enable to be closer to the biological reality compared to other CMR model and reduce the potential bias in the estimation of the demographic parameters. Due to the imperfect and device-specific detection probabilities (fish trap vs antennas) and the uncertainty in the identification of the state (e.g. antenna system) inherent to the index river monitoring program, we used multi-events models to estimate demographic parameters specific to the juvenile freshwater stage (i.e. 6 months old, marking age). We estimated the survival of young, resident and migrant, and the migration probabilities of young. However, this method does not allow estimating reproductive parameters, which are required to build a full life cycle model.

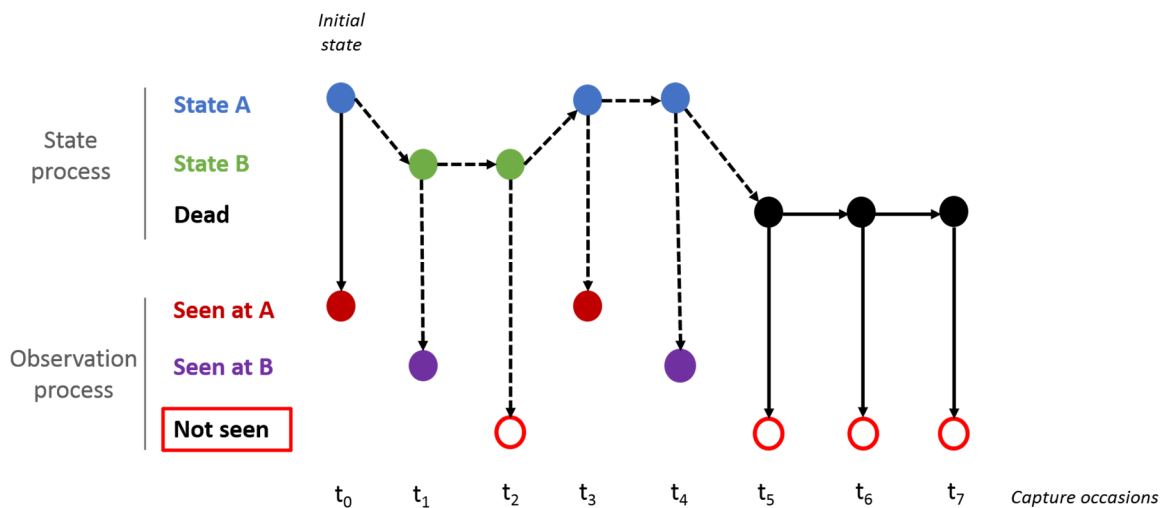


Figure 18. Example of a multi-events model. *The states are linked to the observations by event probabilities knowing the state.*

2.2. Genetic assignment

In fish, the reproductive performance of a female can be evaluated through the number of eggs that it produced (i.e. fecundity). This number of eggs can be estimated before the spawn, by stripping or by killing the female (i.e. number ova), or after the spawn from the nest. However, these methods are harmful. A non-invasive method by ultrasonography (du Colombier et al. 2015) is currently in development on Atlantic salmon and brown trout to count the number of ova (and to estimate their size) carried by females. Nevertheless, the number of ova or eggs in a nest do not always correspond to the number of fertilized eggs. In addition, none of these methods enables the determination of male reproductive performance and the kinship between animal.

To handle all these issues, we decided to estimate the reproductive performances of salmon and trout through the number of offspring produced by an adult during a single reproductive season, which is still alive at six months old (i.e. reproductive success). At this age, juvenile handling is not harmful. However, in most fish species, no parental care exist and kinship between individuals cannot be assessed by visual observations (Serbezov et al. 2010). Thereby, we used molecular markers to assign juvenile to parents through DNA markers

(Jones et al. 2010) from tissue samples collected from mature adults and their potential offspring in La Roche brook (Table 2 and Table 3).

Molecular markers are powerful tools developed since 1966. By measuring the genetic diversity, they are used to trace the fingerprint of each organism and determine the evolutionary history of the species by phylogenetic analysis. In addition, molecular markers are employed to study genetic relationships, population genetic structures, and genetic mapping. Currently, two kinds of DNA markers exist: microsatellites markers (Tautz 1989); and Single Nucleotide Polymorphisms (i.e. 'SNPs') (Weinman et al. 2015). We decided to use microsatellites because they provide the best value for money method for parentage assignment. Microsatellites are very informative molecular markers due to the high mutation rate of microsatellites. They have the advantage of easy and low-cost detection by PCR (we need only tiny amounts of tissue). Moreover, microsatellites have co-dominant feature and thus detect both homozygote and heterozygote genotypes. Importantly, our choice has been driven by the fact that microsatellite markers methods have been already developed on Atlantic salmon (15 microsatellites, Ellis et al. 2011) and brown trout (15 microsatellites, Quéméré et al. 2016).

Even if microsatellites are powerful genotyping tools, they can induce some errors resulting from many variables (reagent quality, Taq polymerase error or contamination) reviewed by Pompanon et al. (2005). The primary consequence of these errors is the misinterpretation of allele banding patterns leading to biased conclusions about parent-offspring relatedness. However, a specific software (GeneMapper) can detect potential genotyping errors leading to the exclusion of the genetic profiles containing errors from the data set before the genetic assignment. After this exclusion, we assigned offspring to parents from their genotypes using commonly used softwares that identify genetic similarity between genetic profiles (CERVUS 3.0 Kalinowski et al. 2007, COLONY Jones and Wang 2010). We determined the reproductive success of each parent as the number of offspring assigned to him. This method enabled us to estimate the minimal number of mates of each assigned parent and to relate offspring and parents characteristics. In addition to survival and migration parameters, the reproductive success allowed us to model a 'closed', full life cycle model without knowing neither the fecundity nor neither the early life stage survival, which are harder to estimate.

3. Population dynamics models

3.1. Definition of a life cycle

The first step in population models is the design of a life cycle representing the biology of the focused population by identifying the different life stages an individual can go through. The life stages are aggregations of age classes, or sex, or size for instance, where each stage can have different survival or reproductive rate. The potential transitions between stages must have equal duration and are defined by demographic parameters as survival, migration, and reproduction. Many ways of splitting a life cycle into stages exist, so the design of a life cycle depends on the ecological question, the hypotheses defined by the study, and the census time related to the data collection. The census time can be either a pre-breeding census when the census is carried out immediately before breeding, or a post-breeding when the census is carried out at some point after the “birth pulse” (Figure 19, Cooch et al. 2003). For instance, to study a partially migratory population where individuals are marked at 6 months old, we can design a life cycle with three stages: ‘young’, ‘resident’, and ‘migrant’, assuming a post-breeding census (e.g. Figure 20).

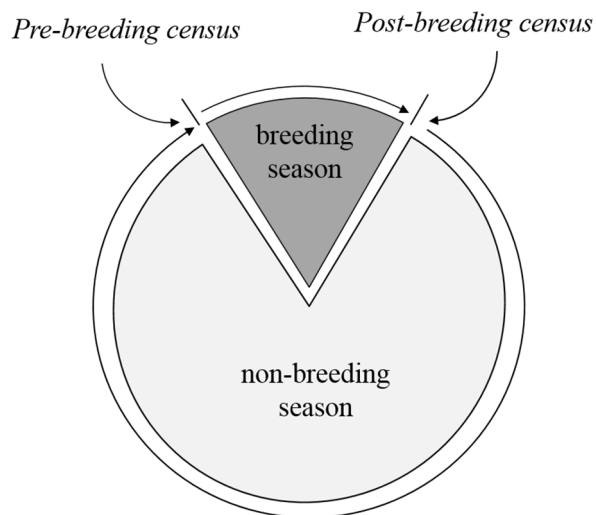


Figure 19. Schematic representation of an annual cycle, partitioned into a breeding and non-breeding season. Adapted from Cooch et al. 2003.

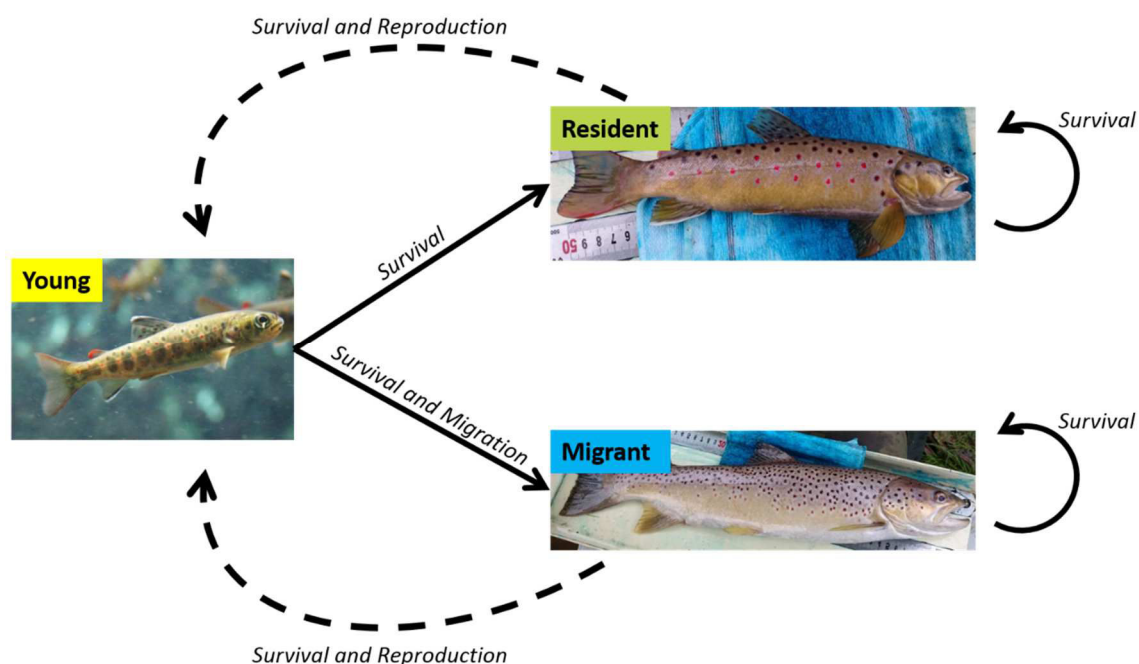


Figure 20. Example of a life cycle of brown trout, with migratory tactics defined as stages to study the influence of partial migration on the population dynamics. The dashed arrows represent the reproduction process.

3.2. Matrix population model

Without considering environmental and demographic stochasticity, the size of a geographically closed population (i.e. without loss or benefit from dispersal) at time $t+1$, can be written as:

$$N(t + 1) = N(t) [b(t) + S(t)], \text{ (Eq. 1)}$$

with $N(t + 1)$, the population size at time $t+1$, is function of population size $N(t)$ at time t , which is going to increase from t to $t+1$ with the reproduction rate per capita (i.e. $b(t)$, the number of offspring produced by parents given survival from t to $t+1$) and the survival rate from t to $t+1$ (i.e. $S(t)$, the number of individuals which survived from t to $t+1$). In complex populations, structured by ages or stages, this equation can be developed to include differences in demographic parameters for the different life history stages in order to be more representative of the life cycle.

The traditional writing of this development is the matrix model writing as Leslie's matrix for age class model (Leslie 1945) or Lefkovitch matrix (Lefkovitch 1965) for size or stage classes. These matrixes are mathematical representations of the life cycle where all transitions between (st)ages must have equal duration. Including the matrix, the size of the population from the equation 1, becomes (e.g. related to life cycle of the Figure 20):

$$N(t + 1) = \begin{bmatrix} 0 & s_r F_r & s_m F_m \\ s_y m & s_r & 0 \\ s_y m & 0 & s_m \end{bmatrix} \times N(t), \text{ (Eq. 2)}$$

This equation 2 represents a post-reproduction projection matrix for a geographically closed population with three stages (young, resident, migrant). It distinguishes the resident survival ('S_r') from the migrant survival ('S_m'). Moreover, it includes that individuals can migrate ('m') and individual in resident and migrant stages can reproduce with different fecundity ('F_r', 'F_m'). The top row of the matrix (orange box) represents the recruitment, the process of adding new individuals to the population by reproduction; the sub-diagonal (blue box), the transition from one stage to the subsequent one; and the main diagonal (green box), the individuals that remain in the same stage in the subsequent year.

The time in matrix models is not seen as a continuous element but as a discrete-time, where the constant time step is called the projection interval. The discrete time scale is commonly used for structured communities and populations with overlapping generations and overlapping growth in their life cycle. With these models called Matrix projection models (MPMs), it is easy to model populations with complex-life histories (Caswell 2001). MPMs assume that individuals occupy stages along a discrete-time with homogeneity in survival and reproduction within each life-history stage (Caswell 2001). From MPMS we determined the population growth rate, the population structure (i.e. the asymptotic proportion of individuals in each state), the reproductive values, and the influence of the demographic parameters on the population growth rate (i.e. perturbations analyses, Caswell 2001, described in Chapter 4, Article IV).

3.3. Integral projection model

For some organisms, where demographic parameters are homogeneous among individual in a life stage it is natural to divide the life cycle into discrete components (e.g. insects with particular instars). However, for many others, where individual characteristics within a life stage may vary related to a continuous life history trait, the artificial discretization imposed by matrix populations models (MPMs) can have substantial effects on demographic predictions because it ignores variability among individuals within each stage (Easterling et al. 2000, Salguero-Gomez and Plotkin 2010). In these cases, using a continuous state variable (e.g. body size) to model life cycle with heterogeneity among individuals in a life stage is more appropriate (e.g. Childs et al. 2003, Jacquemyn et al. 2010, Yule et al. 2013).

This is especially relevant for species with continuous growth as salmonids where demographic parameters are strongly dependent on body size. Models, called 'Integral Projection Models' (i.e. IPMs), based on MPMs have been developed to consider the demographic parameters as functions of a continuous phenotypic trait (Easterling et al. 2000). IPM, thus, can partially account for heterogeneity within a life-history stage (Childs et al. 2003, Ellner and Rees 2006, Jacquemyn et al. 2010, Yule et al. 2013, Merow et al. 2014). To quantify how population growth is affected by changing phenotype–demography relationships, the perturbations analyses developed for MPMs can be applied on IPM (Easterling et al. 2000, Ellner and Rees 2006, Coulson et al. 2011, Coulson 2012).

In this thesis, as salmonids show continuous growth, we transformed a MPM in a length-structured IPM to obtain a more realistic model. From this IPM, we can determine the influence of the body size on the population growth rate and investigate how body size change induced by environmental change may affect the population dynamics.

3.4. Summary of the methods used

An innovative and interdisciplinary approach combining demographic, genetics tools and modeling have been used to address our objectives (Table 5). Demographic parameters estimation was based on the analysis of long-term individual-based monitoring. Multi-events models were used to consider the imperfect detection and the uncertainty inherent to long-term monitoring in the field. In addition, genetic assignment analysis enabled the estimation of the reproductive success and the analysis of the link between parents and offspring characteristics. At last, we built a matrix population model to study the influence of the life history tactics and demographic parameters on the population growth rate. Then, we initiated an integral projection model to investigate the role of individual body size on the population dynamics in brown trout and the resilience of the population to environmental change.

Table 5. Summary of methods used

Aim	Estimation of the reproductive success	Estimations of survival and migration probabilities	Influence of life history tactics on population growth rate	Influence of body size on population growth rate
Method	Genetic assignment using microsatellites markers	Multi-events CMR models	Matrix population model	Integral Projection model
Main reasons of the method choice	<ul style="list-style-type: none"> • identification of kinship between individual can be done by visual observations • the most informative molecular marker • methods already develop on Atlantic salmon and brown trout 	<ul style="list-style-type: none"> • Available long-term individual-based monitoring • Several observation for a single state and uncertainty in state assignment 	<ul style="list-style-type: none"> • First, 'easy' step to model population with complex-life histories 	<ul style="list-style-type: none"> • Enables to include a continuous phenotypic trait • accommodate both discrete and continuous state variables
Complementary description	Chapter 3, Article III	Chapter 1, Article I	Chapter 4, Article IV	Chapter 4

CHAPTER

1.

Responses to environmental changes
in the freshwater juvenile stage



1. Objectives and organization of the chapter

Environmental conditions determine the habitat quality (e.g. food availability and quality, water temperature). These conditions influence in turn the life history traits and behavior of individuals, directly as abundant food resources would improve survival or growth, and indirectly by modifying population density. In particular, the intensity of the competition for resources (food and habitat) between individuals with similar or close ecological niches (i.e. intra and interspecific density-dependence) is expected to vary (Herrando-Pérez et al. 2012, Hasegawa et al. 2014, Hasegawa 2016). At high density of individuals with a close ecological niche, the density-dependent process regulates the abundance and the spatial distribution of the population by acting on survival, growth rate, and movement to less competitive environments (i.e. migration and dispersal), especially in a spatially limited habitat as a river (Hearn 1987, Vøllestad 2002, Milner et al. 2003).

In the freshwater juvenile stage of salmonids, by decreasing the available food per juvenile, density increase is expected to modify the energy allocation in juveniles among reproduction, survival and growth. This modification might result in a decrease in survival or an increase in migration probability. This means that density-dependence might affect individual life history trajectories and population structure. In Atlantic salmon, where all females are anadromous and residency in male is rare, high density can decrease juvenile growth rate and delay sea-migration (Imre et al. 2005). In brown trout, where both males and females are partially migratory and show a continuum of migratory tactics, in addition to a change in age at sea-migration as shown in Atlantic salmon, an increase in competitors density might also promote migration toward downstream river sections and/or at sea. As a result, such a change in the proportion of freshwater resident and sea-migrant adults is likely to modify population dynamics.

The objectives of this chapter is thus to analyze the influence of freshwater environmental changes on the life history traits of juvenile salmonids with a special focus on density. More specifically, we investigate if migration can be a response of partially migratory populations to environmental changes.

Using the temporal fluctuations in density of individuals with a close ecological niche in Oir index river (brown trout and Atlantic salmon), we investigate the following questions on juvenile brown trout (0+ old) in section 2. :

- Are survival and growth rate influenced by the environment?
- Does the environment influence the migratory tactic determination?

Then in the conclusion of this chapter, we draw on findings in trout to discuss tactic determination in Atlantic salmon.

2. Article I

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Intra- and interspecific density shape different life history traits in a salmonid population

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Abstract

Population dynamics can be regulated through intra- and inter-specific density-dependence. In species with close ecological requirements, interspecific competition for resources may add up to intraspecific density, or even exceed its effect; it may impact single or multiple traits. However, the impact of interspecific density on demographic parameters is rarely assessed. We analyzed 18 years of capture-mark-recapture data from brown trout (*Salmo trutta*) coexisting with Atlantic salmon (*Salmo salar*) during the juvenile freshwater phases in the Oir River (France) to estimate the relative effects of intra- and interspecific density on trout early life. In this species with optional migration, we estimated the migration probability of young-of-the-year trout out of their natal site, survival probability during the first winter as well as body size, in relation to density. Trout density correlated negatively to body size and to winter survival in resident but not to migration. Salmon density correlated positively to trout migration, but no impact was detected on body size or survival. Our study highlighted contrasted effects of intra- and interspecific density on trout early life, and the need to account for both factors when studying population dynamics in coexisting species. In particular, by affecting trout migration decision, salmon density may drive trout life history.

Key words

Density-dependence, juvenile survival, life history tactics, migration probability, multi-event model.

Introduction

When population size increases and resource is limited, density dependence can influence individual movement, growth and/or survival (Brook and Bradshaw 2006; Herrando-Pérez et al. 2012). When different species have overlapping ecological niches, an increase in the density of individuals with close ecological requirements can cause competition for resources, aggressive contest and avoidance (Jensen and Kristensen 1990, Chesson 2000, Forrester et al. 2011, Hasegawa et al. 2014, Hasegawa 2016). In general, the intraspecific density effects predominate over interspecific effects due to more similar requirements among conspecific than heterospecific individuals (Chesson 2000, Anderson and Whiteman 2015). However, a stronger competitive species can monopolize limited resources, causing the less dominant species to become displaced or excluded from the habitat (Griffis and Jaeger 1998, McDowall 2003). Studies showed that interspecific competition can affect habitat selection (Hesthagen and Heggenes 2003), growth (e.g. Puffer et al. 2017) and population abundance and distribution (Robertson 1996, Behringer and Hart 2017).

By reducing the available resources per capita, the competition under high intra- and/or interspecific densities can cause a reduction in growth and body size resulting in lower survival and fecundity (Jonsson and Jonsson 2011, Herrando-Pérez et al. 2012, Hasegawa et al. 2014, Anderson and Whiteman 2015). High competition level has also been identified as a key driver of dispersal (Bullock et al. 2002, Matthysen 2005). However, the relative effects of intra- and interspecific densities on individual movement or dispersal, growth and survival have been rarely investigated simultaneously. These combined effects are likely to have important consequences on population structure and dynamics and should be easier to detect in species displaying a wide gradient in these life history traits.

Partially migratory species (i.e. where both resident and migratory tactics coexist), could be a good candidate because of the high diversity in individual growth, dispersal and survival rate within a single population. Brown trout (*Salmo trutta*) is a partially migratory salmonid characterized by an extremely plastic life history. In a given population, individuals can either spend their entire life in their natal stream (resident life history), migrate within their natal river, or migrate to the sea and then return in freshwater for spawning (anadromous life history (Cucherousset et al. 2005). Although the mechanism underlying migration decision

remains unclear, it is commonly accepted that both genetic and environmental drivers are at play (Bohlin et al. 1993, Okland et al. 1993, Forseth et al. 1999, Morita et al. 2014). If high density correlated with poor environmental condition during early life, reduced growth and survival are expected but migration may also be an option. Contrasted environmental condition between stream, river and the marine environment generates marked difference in growth potential, mortality and fecundity between salmonids (Jonsson 1985, Kendall et al. 2014). Such consequences of migration decision in early life may have important demographic and evolutionary implications (Fretwell and Lucas 1969).

In the river Oir in France, a partially migratory population of brown trout shares its freshwater habitat with Atlantic salmon (*Salmo salar*). Both salmonids have similar ecology and phenology during the reproduction and juvenile phases (Heggenes et al. 1999). During their juvenile stage, trout are commonly in deeper and slower-flowing areas of stream than salmon, which may dominate in fast-flowing shallow areas (Kennedy and Strange 1982). Moreover, adult trout use deeper and slower flowing water than salmon during the reproduction period (Heggenes et al. 1999, Jonsson and Jonsson 2011). We took advantage of an 18-year individual-based monitoring (1997-2015) to investigate the effects of intra- and interspecific density-dependence on juvenile growth, migration, and survival. We accounted for uncertainty in field records (imperfect detection and state uncertainty, census (Pradel 2005) with a multi-event capture-recapture approach. We tested for an effect of juvenile density on body size, survival and migration probabilities on short distance (i.e. within river) and long distance (i.e. at sea) in young-of-the-year (0+ old, 'young') trout. Specifically, we modelled i) single effect of trout or salmon density as a reference, ii) additive effects of inter and intraspecific density dependence assuming that a young trout equal a young salmon in the river, and iii) non-additive effects assuming that the presence of a conspecific differs from that of a heterospecific, the effect of trout density could be larger or smaller. Given the very similar ecological niches of *S. trutta* and *S. salar* during the juvenile phase we predict that inter- and intraspecific densities should have additive effects on juvenile traits.

Materials and Methods

Study site and species

The study was carried out in La Roche brook, a small second order tributary river of Oir river (Normandy, France, 48°38'N, 3°37'W) (Fig. 1) where salmonids have been monitored since 1997. This stream is 4.5 km long but an impassable dam restrains its access to migrating salmonids to the 2.2 km downstream section even in years with flooding. This 2 meters wide section of the brook is a habitat where Atlantic salmon and brown trout coexist on the same spawning ground (Cucherousset et al. 2005).

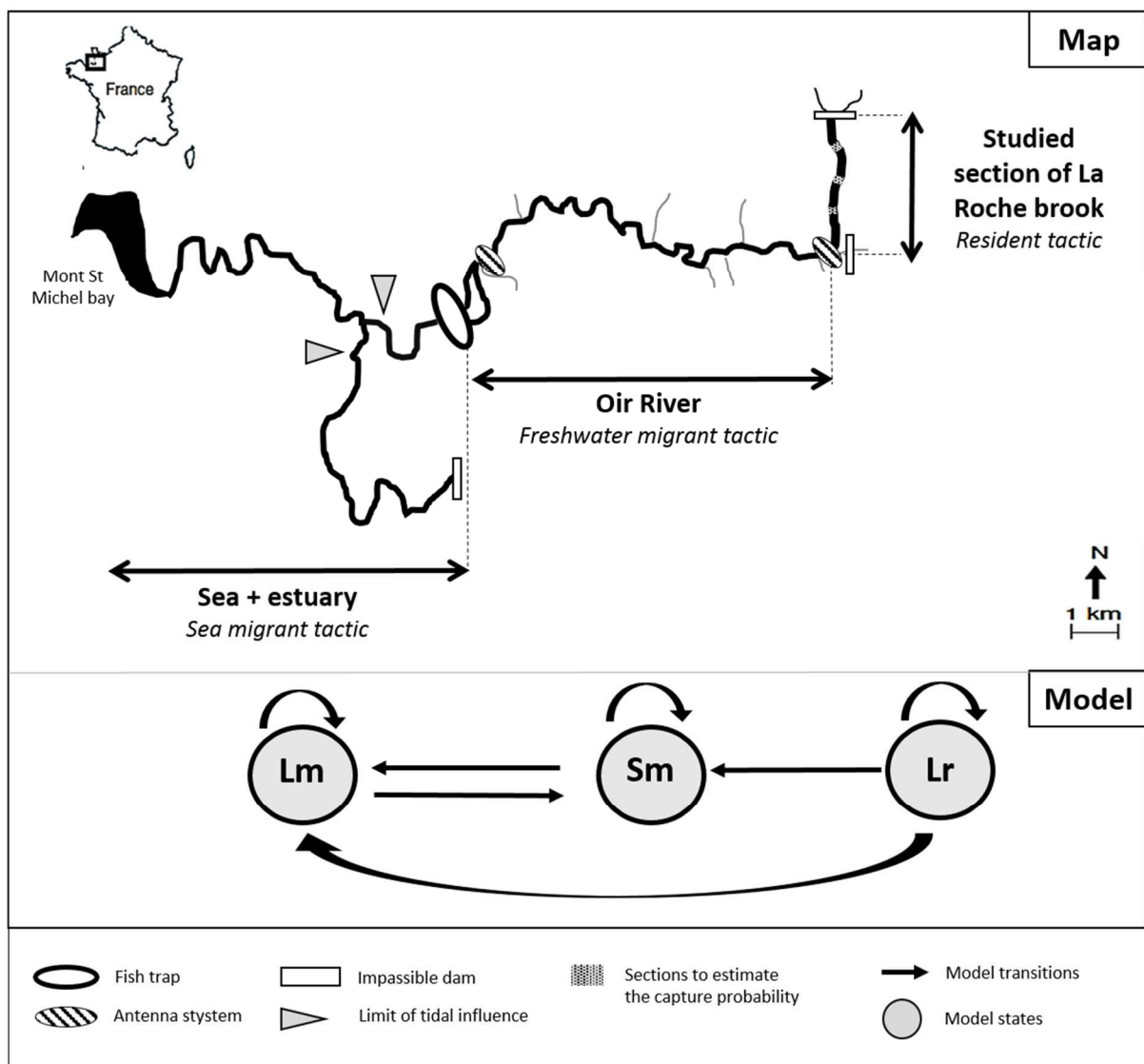


Figure 1. Map of the study site, and schematic representation of the brown trout model. “Lr”, La Roche brook; “Sm”, Oir river; “Lm”, sea.

Adult trout reproduce in La Roche brook from December to early January. Fries emerge from gravel in March. During their first winter, young-of-the-year (i.e. 'young') trout have contrasted migration patterns (Fig. 1): they can either i) be sedentary in their native river (i.e. 'resident'), ii) perform freshwater migration in the Oir River than can be considered as a short-distance migration (i.e. freshwater migrant), or iii) be anadromous (i.e. 'sea-migrant') that can be seen as a long-distance migration (Cucherousset et al. 2005). In French Atlantic salmon populations, young migrate at sea after one or two years in freshwater.

Data collection

From 1997 to 2015, brown trout were individually monitored through three joint standardized-protocols: electrofishing, trapping, and autonomous data recording by antennas systems (Fig. 1, Table 1). Each year, three electrofishing sessions took place (e.g. Fig. 1, Table 1). One session aimed at capturing young trout, marking young trout (mean body size of marked trout = 81.305 mm, SE = 6.109; trout body size observed since 1997 ranged from 25 to 150 mm with mean = 77.86 mm) with unique ID (12 mm passive integrated transponders, Biomark, Prentice et al. 1990) (Table 1) and capturing young salmon (salmon body size observed since 1997 ranged from 25 to 130 mm with mean = 77.29 mm). A second electrofishing session was dedicated to marking adult trout during the reproduction period (Table 1). The third session of electrofishing occurred after the downstream migration of trout to recapture the one-year-old juveniles that stayed in the river, and thus assess residency in La Roche brook (Table 1). Furthermore, a fish trap down the Oir river operated all year round to survey downstream and upstream migration of salmonids (Fig. 1, Table 1). The trapping efficiency estimated by the capture of anadromous trout in Oir river (upstream the trap) was lower than one and varied over years (mean efficiency of: upstream trap = 0.442, SE = 0.299; downstream trap = 62.667, SE = 16.100). In addition, two autonomous antenna systems recorded the passage of migrating tagged trout all year round (Fig. 1, Table 1).

Scales were collected when young trout were marked to estimate individual age with a scale-reading method (Table 1) (Baglinière et al. 1985). On each recapture occasions, new scales were collected to discriminate non-anadromous and anadromous fish from scale growth pattern in addition to morphological features as color and size at age (Table 1) (Baglinière et al. 2001).

Table 1. Description of the data collection on brown trout in the Oir river: monitoring device, sampling period and site. The aim of each monitoring is described together with the type of data collected.

Monitoring	Session	Localisation	Aim	Number of trout marked	Mark identification record	Length record	Scales sampling	Anadromous identification
Electrofishing	October	La Roche brook	Capture and mark young of the year	8497	x	x	x	NA
		Three section in La Roche brook	Estimate electrofishing capture probability	0				
	December	La Roche brook	Recapture trout during reproduction	357	x	x	x	x
		Oir River	Recapture trout during reproduction	92	x	x	x	x
May	La Roche brook	Recapture trout after the migration period	1229	x	x	x	NA	
Fish trap	all year	Downstream Oir River	Recapture trout migrating downstream	932	x	x	x	x
			Recapture trout migrating upstream	191	x	x	x	x
Antennas systems	all year	La Roche brook/ Oir River intersection	Detect migrating trout	0	x			
		Downstream Oir River						

Density estimation

During the October monitoring session in La Roche brook (Table 1), a specific protocol involving successive removals was set up in three sections to assess the capture efficiencies of young trout and young salmon in this brook (Fig. 1) (Bohlin et al. 1989). These three sections were the same over the whole study period and were representative of the whole stretch of the brook in terms of habitat and fish density. Variations in turbidity and water level between year can affect fish detection, but the capture efficiencies showed low variations over time (for young trout mean = 0.788, SE = 0.078; for young salmon mean = 0.797, SE = 0.061). Therefore, we ignored the influence of environmental variability on electrofishing efficiency. The mean capture efficiency of the three sections and the number of young captured in the entire 2.2 km section of La Roche brook were used to determine the annual densities (number of young.m⁻² using the method of Seber and Le Cren (1967).

Demographic parameter estimates

We built a multi-events capture-recapture model to estimate the young trout migration probability from La Roche brook and the survival of resident young-trout (Fig. 1) (Lebreton et al. 2009). The whole database was used to build this model as the adult observations informed on the life history tactic. The model consisted of 3 states and 11 events (Table 2). The three states represented the migration tactics of trout within the river system: resident trout (Lr), freshwater migrant considered as short-distance-migrant (Sm) and sea-migrant considered as long-distance-migrant (Lm) (Fig. 1). In this analysis, the term migration must be considered as

‘apparent’ migration as it contained potential dispersal (i.e. fish that disperse into another river after their seaward migration).

In our study, the state of an individual was not always known with certainty on each occasion due to imperfect detection and partial observation with antennas. Multi-event modeling allowed us to deal with this state uncertainty. This model assesses the identifiable probability corresponding to the likelihood of an individual being in a specific state given the event (i.e. imperfect observations of that individual in the field) in addition to the detection probability (Pradel 2005). Based on field records, we considered 11 events (Table 2 and Appendix S1). Details of the parameterization of the general model can be found in Appendix S1.

Table 2. Description of the events used in the multievent mark-capture-recapture model.

Event number	Event description
1	Captured by electrofishing and recorded as non-anadromous type in La Roche brook
2	Captured by electrofishing and recorded as anadromous type in La Roche brook
3	Captured by electrofishing and recorded as non-anadromous type in Oir river
4	Captured by electrofishing and recorded as anadromous type in Oir river
5	Detected by the antenna downstream La Roche brook with unknown type
6	Detected by the antennas in Oir river with unknown type
7	Captured by the upstream fish trap
8	Captured by the downstream fish trap
9	Captured by the upstream fish trap and detected during the same occasion by the antenna downstream La Roche brook
10	Captured by the upstream fish trap and detected during the same occasion by the antennas in Oir river
11	Not seen

We developed the most parsimonious time-dependent model and achieved an efficient model selection based on Akaike’s information Criterion (Burnham and Anderson 2002). All models were run with program E-Surge v1.7.1 (Choquet et al. 2009a).

Investigating density dependence effects on demographic parameters

To analyze intra- and interspecific density effects, we tested for an influence of temporal variation in density on migration and survival. To test more specifically for density effects in early life we considered an age effect with two age classes in our model to distinguish young-trout (0+ aged) and older trout. We considered the density of young trout as well as the density of young salmon from La Roche brook in October (before the migration period) as two temporal covariates. To test for intra- and/or interspecific density-dependence effects, we compared 3 models: i) an additive effect ii) an interactive effect and iii) a threshold effect of temporal variations in density of young trout and young salmon, on migration and survival.

Indeed, density-dependence effects may only be detectable over a given density threshold representing the carry capacity of the system (Eberhardt 1977).

The young salmon density was highly variable among years and the young trout density greatly varied between two periods (1997-2008, 2009-2014). The very low density of young salmon in 1997, 1998, 2002 and 2004 (Fig. 2) reflected a year with low water levels that prevented salmon from reaching the brook to spawn. Thus, to compare the effects of high and low-density modes we selected a threshold of 30 individuals.m⁻² that represented the mean density observed over the study period (mean density of young trout = 29.8, SD = 10.68; mean density of young salmon = 33.3 individuals.m⁻², SD = 25.41). We tested the hypothesis that below the threshold the carrying capacity of the environment was not reached, whereas over the threshold it was.

We assessed the significance of each covariate with an analysis of deviance (ANODEV) test between the constant model (M.), the model with a covariate (M_{cov}) and the corresponding time-dependent model (M_t) (Skalski et al. 1993), as described in Grosbois et al. (2008). In addition, we estimated the proportion of variance explained by the covariate using the R² (Grosbois et al. 2008).

Investigating the role of body size in the density effects

To test if increasing density caused a reduction in resource per capita we analyzed the relationship between the body size of young trout (Table 1) and both inter- (salmon) and intraspecific densities. We checked whether the intraspecific density-dependent effect on body size was different when interspecific density increased. We tested for both an additive and an interactive effect of these two density variables with linear regression models (Chambers et al. 1992). These statistical analyses were performed using the R software (The R Foundation for Statistical Computing 2010).

Additionally, to test if the density effect on demographic parameters derived from a reduction in growth rate induced by the density we analyzed how individual body size affected the migration of young trout and the survival probabilities in La Roche brook. We incorporated body size of young trout in autumn as an individual covariate in the model. We assigned the

mean body size of the cohort to individuals with missing body size data ($n = 314$, 3.7% of the data). To assess the significance of this individual covariate we used the confidence interval of the estimated slope parameter, as the ANODEV cannot be applied on individual covariates. If the 95% confident interval included zero, the effect of the individual covariate was considered to be non-different from zero.

Finally, we were aware of a conservation program initiated in 2010 on La Roche brook and aiming at restoring riverbanks and water quality, which may have affected the ecological functioning of this ecosystem and its carry capacity for salmonids. In order to check the robustness of our results and rule out potential confounding factors that may not be related to density changes only, we re-ran a model with the selected covariates over the period 1997-2009 only.

Results

Temporal variations in densities and body size

The density of young trout and young salmon increased linearly significantly over the study period (trout $P = 0.010$; salmon $P = 0.015$; Fig. 2.a), with a higher temporal variability in salmon. However, the two variables were not correlated (Pearson correlation test $P = 0.284$; $R^2 = 0.267$; Fig. 2.a), despite a common increasing trend since 2010. The mean annual body size of young trout decreased over the study period ($P = 0.005$; Fig. 2.b). In contrast, the mean annual body size of one-year-old individuals recorded at the fish trap at was constant over time ($P = 0.565$). The body size and the density of young trout were negatively correlated ($P < 0.001$; $R^2 = 0.478$, Fig. 3.a). Neither density of young salmon ($P = 0.435$) nor combined density of young trout and young salmon ($P = 0.089$) were related to the mean annual body size of young trout (Fig. 3.b).

Temporal variations in migration and in survival probabilities

Goodness of fit tests ($\chi^2 = 149.103$, $df = 115$, $P = 0.018$) indicated that the general JMV model fitted the data correctly (model 0, Table 3). Through the model selection procedure, migration probabilities of young from La Roche brook to Oir River and to sea showed significant variations over time (Model 9, Table 3), as well as the survival probability of young trout stayed in the native river (Model 14, Table 3).

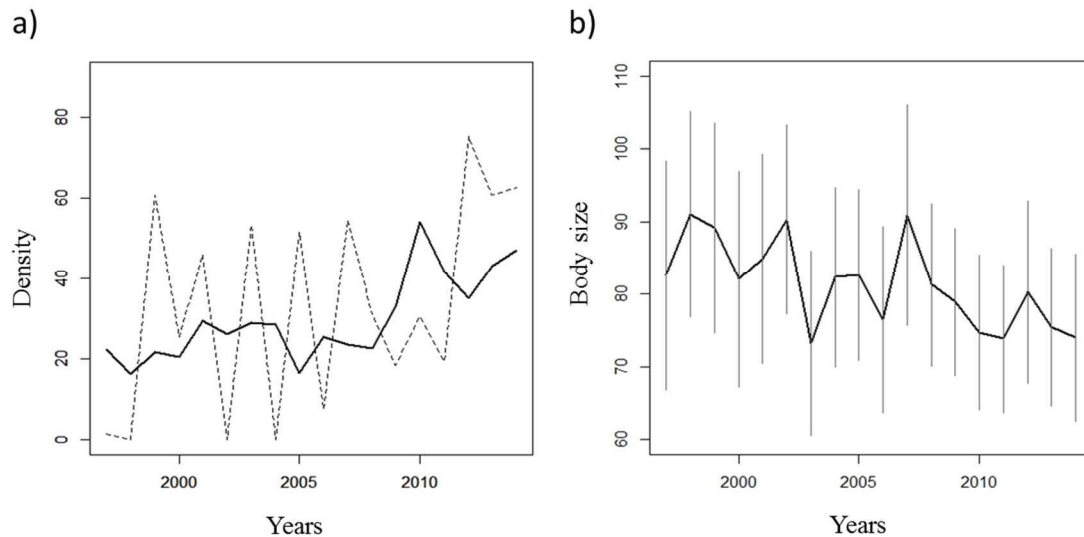


Figure 2. Temporal variations in: a) observed density of young trout (dTR, black line), and young salmon (dSAT, dotted grey line) and b) mean body size of young trout (+/- SD).

Intra- and interspecific density effects

On the temporal variations in the probability of young to migrate from La Roche brook to Oir River we found: no effect of young trout density (Model 15, Table 4), no additive or non-additive effect of the density of young trout and salmon densities (Models 17, 18, Table 4), but a significant positive correlation with young salmon density from the tested threshold (Model 19, Table 4 and Fig. 3.d). Nevertheless, this effect was not significant anymore when considering the restricted period prior to river restoration (1997-2009; $P = 0.053$, Model 20, Table 4). On the temporal variations in probability of young to migrate from La Roche brook to sea we found: no effect of young trout density (Model 21, Table 4), no additive or non-additive effect of the density of young trout and salmon densities (Models 23, 24, Table 4), but a significant positive correlation of young salmon density (Model 22, Table 4), even better with the threshold effect (Model 25 and Fig. 3.f). This effect was also significant over the restricted period (1997-2009; Model 26, Table 4). On the temporal variations in survival probability of young stay in La Roche brook after the migration period, we found a negative correlation with the young trout density (Model 27, Table 4). This effect was more severe at high density, as described by the threshold model (Model 30, Table 4 and Fig. 3.g) and still significant over the restricted period (1997-2009; Model 31, Table 4). We did not detect any additive or non-additive effect of the density of young trout and salmon densities on survival (Models 28, 29, Table 4).

Table 3. Modelling brown trout migration and survival in the Oir River. “Mo”, model identification; “Id.”, Identification probability; “De.”, Detection probability; “Mi”, Migration probability; and “Su”, survival probability. np: number of parameters; “+”, additive effect; “*”, interaction effect; “t”, time effect; “s”, state effect; “→”, transition from state i at time t to state j at t+1; “Y”, young-of-the-year (i.e. Lr state at 0+ old); “Lr”, La Roche brook; “Sm”, Oir river; “Lm”, sea.

Mo	Id.	De.	Mi.	Su.	np	Deviance	QAICc	Delta QAICc
0	s	-	-	-	17	40401.6	40435.7	1067.8
1	s + t	-	-	-	53	40377.5	40483.9	1116
2	s * t	-	-	-	118	40366.3	40604.7	1236.8
3	s	s + t	-	-	53	40059.6	40166.0	798.1
4	s	s * t	-	-	123	39529.2	39777.8	409.9
5	s	s * t	(Y→Sm) * t	-	140	39412.8	39696.2	328.3
6	s	s * t	(Y→(Sm, Lm) * t	-	157	39315.4	39633.7	265.8
7	s	s * t	(Y→(Sm, Lm)+ Lr→Sm) * t	-	173	39285.0	39636.1	268.2
8	s	s * t	(Y→(Sm, Lm)+ Lr→Lm) * t	-	173	39273.2	39624.4	256.5
9	s	s * t	(Y→(Sm, Lm)+ Lr→Lm+ Sm→Lr) * t	-	190	38119.4	39505.7	137.8
10	s	s * t	(Y→(Sm, Lm)+ Lr→Lm+ Sm→(Lr, Lm) * t	-	206	39108.4	39515.2	147.3
11	s	s * t	(Y→(Sm, Lm)+ Lr→Lm+ Sm→Lr) * t	Y * t	207	39016.1	39437.5	69.6
12	s	s * t	(Y→(Sm, Lm)+ Lr→Lm+ Sm→Lr) * t	(Y + Lr) * t	223	38962.0	39416.6	48.7
13	s	s * t	(Y→(Sm, Lm)+ Lr→Lm+ Sm→Lr) * t	(Y + Lr + Sm) * t	239	38952.8	39440.7	72.8
14	s	s * t	(Y→(Sm, Lm)+ Lr→Lm+ Sm→Lr) * t	(Y + Lr + Sm + Lm) * t	239	38879.8	39367.9	0

Table 4. Modeling the effect of density covariates on the migration from La Roche brook as young-of-the-year (young) to Sm, Oir river or to Lm, sea and survival. “Mo”, model identification; “d” = Density; “TR” = young trout; “SAT”= young salmon; “+”=additive effect; “*” = interactive effect; “threshold” = threshold at 30 individual per m²; “2009” = effect of the covariate before 2010 only; “Df” = degree of freedom.

Mo	Covariate model (F _{co})	ID Constant model (F _{cst})	F _{test_{cst/co/t}} Df=2	Corrected P-value	R ²
Migration from La Roche brook to Sm					
15	dTR	14	1.73	0.206	0.098
16	dSAT	14	4.246	0.055	0.209
17	dTR+ dSAT	16	0.021	0.885	0.001
18	dTR* dSAT	16	0.021	0.885	0.001
19	dSAT_threshold_30	14	5.894	0.027	0.269
20	dSAT_threshold_30_2009	14	4.511	0.053	0.258
Migration from La Roche brook to Lm					
21	dTR	14	1.981	0.177	0.11
22	dSAT	14	10.555	0.005	0.397
23	dTR+dSAT	22	0.008	0.927	0.0005
24	dTR*dSAT	22	0.23	0.638	0.014
25	dSAT_threshold_30	14	20.753	<0.001	0.565
26	dSAT_threshold_30_2009	14	23.829	<0.001	0.647
Survival of young stayed in La Roche brook					
27	dTR	14	27.254	<0.001	0.63
28	dTR+dSAT	27	0.058	0.813	0.003
29	dTR*dSAT	27	<0.001	0.996	<0.001
30	dTR_threshold_30	14	27.671	<0.001	0.634
31	dTR_threshold_30_2009	14	107.715	<0.001	0.871

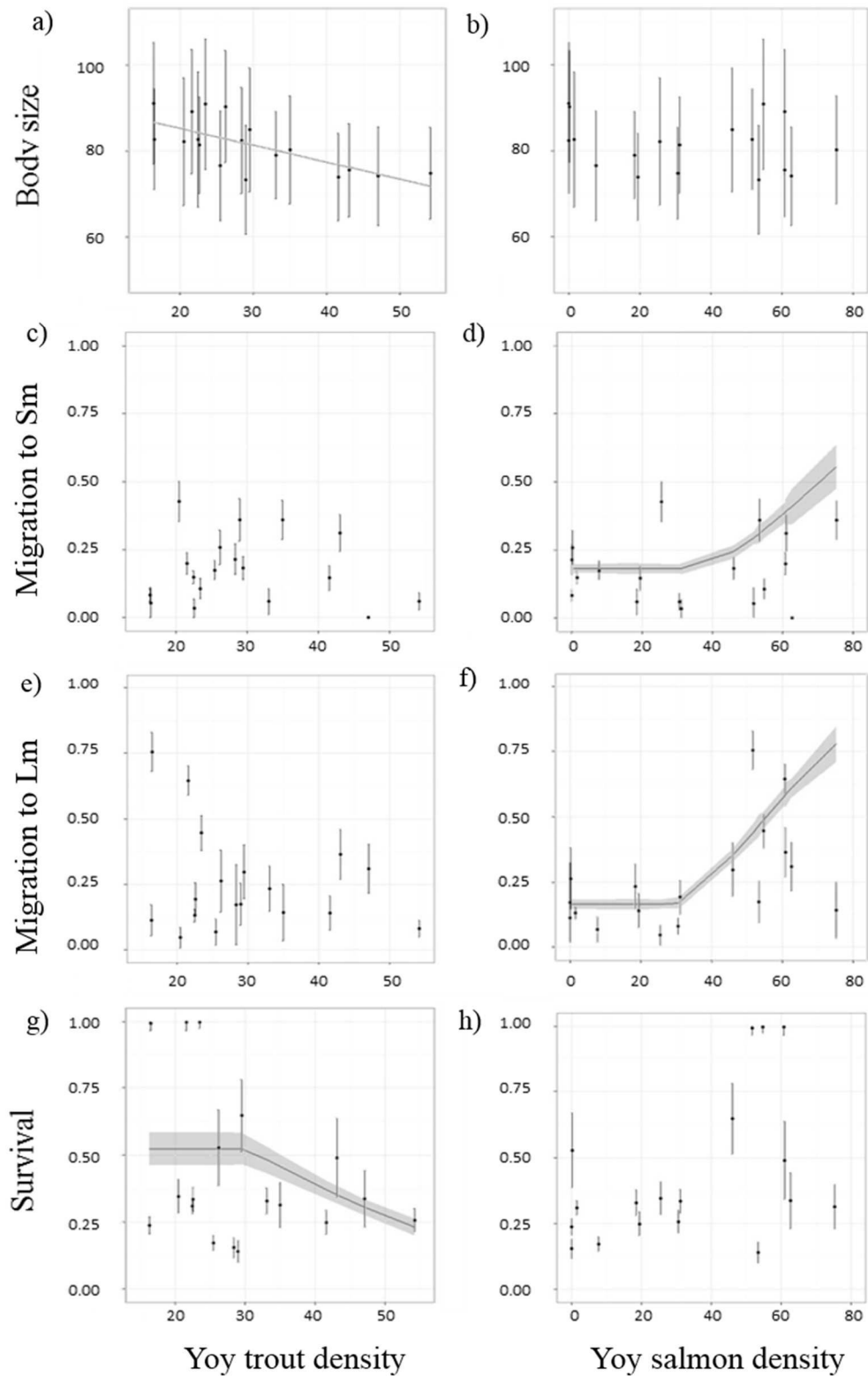


Figure 3. Life history traits of young trout as a function of trout density (left panels) and salmon density (right panels): body size (mm) before migration (a, b); migration probability from La Roche to Oir river (“Sm”; c,d), or to sea (“Lm”,e, f); and survival probability in La Roche brook in resident (g,h). Dots and bars represent time-dependent model estimates (Model 14, Table 3). Lines and grey shadings represent estimates of significant relationships with density.

Body size effect on migration and survival probabilities

Adding individual body size as a covariate in the model highlighted a negative correlation between the individual body size of young trout and migration probabilities (from young in La Roche brook to Oir river: slope = 95%CI = -0.930; -0.151; from young in La Roche brook to estuary-sea: slope = 95%, CI = -1.403; -1.260, Fig. 4.a). The survival probability of young staying in La Roche brook for their first year also increased significantly with individual body size (CI- = 1.236, CI+ = 0.361, Fig. 4.b).

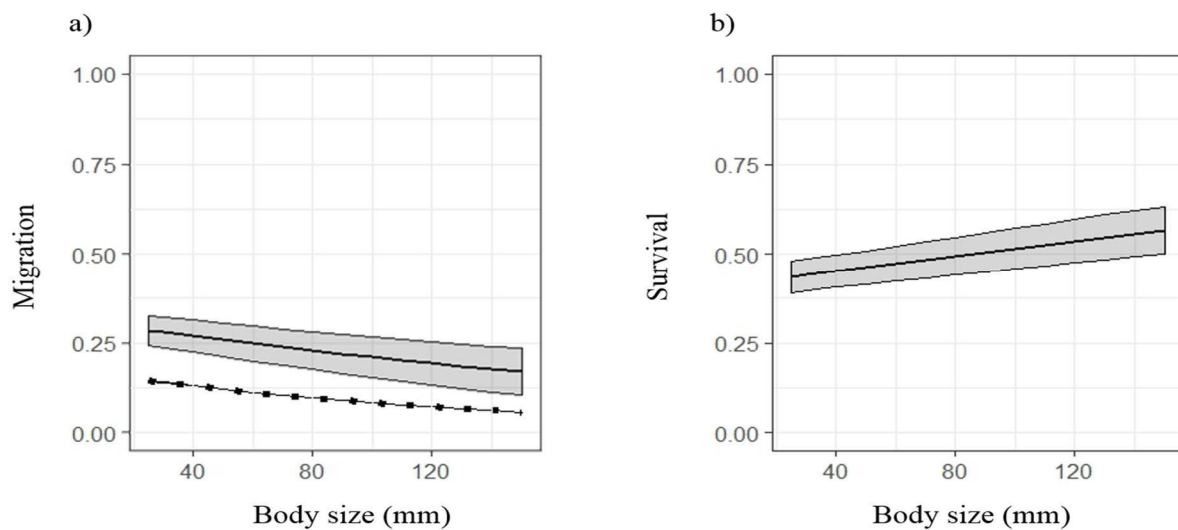


Figure 4. Relationships between individual trout body size and the migration probabilities of young-of-the-year trout (a), and survival probability (b) in La Roche Brook. The dark line in (a) refers to migration from La Roche brook to short distance (Oir river) and the dotted line to migration to long-distance (sea).

Discussion

This multi-trait study highlights contrasted effects of intra- and interspecific density dependence during a critical stage of trout early life, i.e. first winter, when food resource is scarce. Whether both intra- and interspecific density mattered for trout early life, they were reported separately on different demographic parameters. Our results suggest that intra- and interspecific competition may be driven by distinct ecological mechanisms and highlight more complex interaction between two coexisting species than previously shown.

As expected in most vertebrates (Grant and Imre 2005, Brook et al. 2015), the intraspecific density appeared to regulate the abundance of young trout through a decrease in body size and survival. By selecting the threshold model, our results also suggest that critical condition for survival (carrying capacity) may not be reached every year in our study site. Interestingly, we could not detect any effect of salmon density on trout growth and survival, contrary to previous studies (Jonsson and Jonsson 2011, Hasegawa et al. 2014, Anderson and Whiteman 2015). Despite close ecological proximity between the two salmonids, the presence of up to 75 salmon.m⁻² in the river did not seem to interfere with food intake in juvenile trout.

However, the positive effect of salmon density on trout migration probability confirms our prediction of interspecific competition. We did not detect resource sharing between the two species but a direct competitive exclusion of one species as the density of the other species increases above a given threshold. In this brook with high velocity, Atlantic salmon may outcompete brown trout. Thus, young salmon, which are highly territorial, may monopolize limited habitat resources leading to the exclusion of an increasing proportion of trout as salmon density rises (Griffis and Jaeger 1998, McDowall 2003). Also, showing that trout dispersal was biased toward small individuals further support the hypothesis of competitive exclusion against frail individuals.

Small body size may result from high metabolic rate rather than frailty. In young salmonids, future migrant trout grow faster as a juvenile but had smaller body size than future resident, suggesting that the former may face higher energetic needs (Acolas et al. 2012). Those individuals would be more constrained by resources availability under high interspecific density than their conspecifics (Bohlin et al. 1993, Acolas et al. 2012, Chapman et al. 2012). By migrating out of the natal brook to the main river or to the sea, individuals may search for areas with lower competition and higher growth potential (Nelson 1995, Olsson et al. 2006, Nilsson 2007, Mysterud et al. 2011).

In this partial migration species, migration appears as a plastic response to environmental condition. Although sea migration requires costly physiological adaptation to the saline habitat in trout (Gross 1987), it also confers benefits to adults in terms of body size (in this study, anadromous trout length ranges from 210 to 790 mm, mean size = 392 mm; freshwater

resident trout length ranges from 110 to 465 mm, mean size = 255 mm), fecundity and fitness (Jonsson and Jonsson 1993). Previous studies on salmonids showed that migration was related to growth conditions and, thereby indirectly to environmental factors as water temperature or density for instance (Dodson et al. 2013, Morita et al. 2014). Similar results were reported in several other vertebrate studies, as reviewed in Chapman et al. (2011). We highlight that interspecific competition interfered with migration as well and should be considered amongst other potential environmental drivers. This interspecific effect may be exacerbated when interspecific density greatly exceeds the conspecific density or when the total carrying capacity of the environment is reached, thus reinforcing the overlap of species ecological niches (Rose 1986). Ultimately, change in community composition may impact population dynamics as a whole due to contrasted demographic characteristics in resident and migrant tactics.

Conclusion

Our study demonstrated that interspecific density does not affect the same demographic parameters than intraspecific density. This result has important consequences for our understanding of population dynamics in coexisting species. Indeed, our findings advocate for a simultaneous assessment of intra- and interspecific competition to predict accurately population dynamics due to more complex interactions between two coexisting species than previously shown. In particular, the positive effect of interspecific density on migration probabilities during early life stages may partially determine life history tactics in brown trout. Thus, the composition of the community as a whole might interfere with the relative proportion of each tactic in partial migration populations and ultimately influence the population growth rate.

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Supporting material

Appendix 2. Model details and Transition matrices from GEPAT in E SURGE.

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3. Conclusion of chapter 1

We showed that intraspecific density affects the survival and growth rate of juvenile trout. Moreover, we highlighted that the presence of another species with close ecological requirements influences migration probability in freshwater and at sea. Consequently, the environmental conditions influenced the expression of the migratory tactic, with migration being a response to decreasing resource availability. Even if the determination of the sea-migratory tactic seems to be partially determined by genetic effects (Dodson et al. 2013), our results suggest that it is also partly a plastic process. In such a context, the migration may be interpreted as a life-history 'choice' that maximizes fitness under given environmental conditions and considering internal state. Consequently, this possible response to environmental change related to the partial migration may promote the resilience of brown trout populations.

The effect of Atlantic salmon density on brown trout migration was unexpected. Commonly, when these two species are in the same habitat, brown trout is considered as more aggressive (Armstrong et al. 2003, Stradmeyer et al. 2008), more able to monopolize high-quality feeding areas (e.g. Höjesjö et al. 2010) and thus more dominant than Atlantic salmon of similar size (Kalleberg 1958, Heggenes et al. 1995, Harwood et al. 2002, Stradmeyer et al. 2008). This dominance should be related to a high growth rate and a competitive advantage in food intake (Metcalf et al. 1995, Cutts et al. 2001, Höjesjö et al. 2002). In contrast, our results showed no interference in food intake of juvenile salmon on juvenile trout as illustrated by our results on growth and survival, but a competitive exclusion from Atlantic salmon against small brown trout. The high water velocity of the brook, favouring Atlantic salmon, may facilitate this exclusion pattern. Consequently, our results highlight more intricate density regulation processes between these two species than previously observed.

The possibility of brown trout to modulate the migration 'decision' to downstream river or to sea may buffer juvenile mortality and promote long-term coexistence of Atlantic salmon and brown trout in the juvenile freshwater stage in a changing world. This hypothesis also raises the question of the effect of trout density on Atlantic salmon traits, in early life. We did not investigate this question. Nevertheless, we expect intraspecific density-dependence in

Atlantic salmon (Imre et al. 2005, Grant and Imre 2005, Ward et al. 2009). In addition, according to our knowledge of the La Roche study system, we might expect no effect of brown trout density on Atlantic salmon traits in this area. This expectation contrasts with the common observations that under competition for food resource in early life, the presence of brown trout induces a reduction in the growth and survival of Atlantic salmon (Kennedy and Strange 1986, Bal et al. 2011)

Major findings 1.

- Temporal variations in life history traits occur in the juvenile stage in the freshwater environment.
 - Brown trout respond to freshwater juvenile environmental (i.e. shared habitat) changes by modifying the migration probability at sea (i.e. unshared habitat), which may promote the population resilience to environmental changes.
-

CHAPTER

2.

Life history tactic responses to environmental changes



1. Objectives and organization of the chapter

In the previous chapter, we showed that in juvenile brown trout, the survival, the growth, and the migration probability were affected by freshwater environmental conditions, i.e. the shared environment. We also expect that variations in the unshared environment would have an impact on adult traits. In Europe, several studies reported a decrease in body size of adult anadromous salmonids and variations in the date of the upstreaming river-migration (Youngson et al. 2002, Quinn et al. 2006, Aprahamian et al. 2008, Bacon et al. 2009, Saura et al. 2010, Milner et al. 2017). These patterns may be driven by large scale spatial and temporal changes in the Atlantic environment, potentially linked to climate change (e.g. (Jonsson and Jonsson 2004, ICES 2016, Jonsson et al. 2016).

Within populations, individuals are not identical. Anadromous salmonids spend different amounts of energy at different times of the year in growth, maturation, and maintenance, leading to different migratory tactics at sea, in terms of the duration of the marine sojourn. Due to these differences, individuals may respond to environmental variations by showing trait variations specific to each sea-migratory tactic. Previous studies have shown that variability in demographic traits can be selectively disadvantageous. As a consequence, traits that influence the most individual fitness must be buffered against temporal variability (i.e. canalization process, sensu (Waddington 1961, Gaillard and Yoccoz 2003, Doherty Jr et al. 2004, Péron et al. 2016). Moreover, Pardo et al (2013) showed that environmental variability can also differently affect age classes with different demographic characteristics (e.g. survival, fecundity), suggesting that the age class to which the population growth rate is more sensitive should show a lower variability in traits linked to individual fitness. As age classes, life history tactics are defined by different energy allocations. Thereby, we expect the tactics be differently affected by environmental variations.

Consequently, the objective of this chapter is to identify how sea-migratory tactics respond to environmental changes by detecting large spatial patterns in temporal variations of the phenology, body size, mass, and body condition of anadromous salmonids.

To reach this objective, we used the long-term data set of catch declarations (Table 2) on Atlantic salmon and brown trout populations in France. Thereby, this chapter focuses on anadromous adults, returning in river to spawn, after the marine phase. By studying life history traits of captured adult salmonids we investigated the following questions:

- Is the response to environmental variations specific to the anadromous tactic?
- Is there a trait and/or a migratory tactic that shows a lower temporal variability than others?

The section 2 of this chapter focuses on Atlantic salmon. This work is an actualization of a previous study conducted by Guillaume Bal during his Ph.D. (2007-2011) in the ESE lab. I collaborated on this work as a second author in a publication, which is presented in section 2 (Article I). To go further, I conducted a similar work on brown trout, summarized in the conclusion of this chapter.

2. Article II

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Evidence for long-term change in length, mass and migration phenology of anadromous spawners in French Atlantic salmon *Salmo salar*

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Abstract

This study provides new data on Atlantic salmon *Salmo salar* life-history traits across France. Using a long-term recreational angling database (1987–2013) covering 34 rivers in three regions (genetic units), a decline in individual length, mass and a delayed adult return to French rivers was reported. Temporal similarities in trait variations between regions may be attributed to common change in environmental conditions at sea. The relative rate of change in phenotypic traits was more pronounced in early maturing fish [1 sea-winter (1SW) fish] than in late maturing fish (2SW fish). Such contrasted response within populations highlights the need to account for the diversity in life histories when exploring mechanisms of phenotypic change in *S. salar*. Such detailed life-history data on returning *S. salar* have not previously been reported from France. This study on French populations also contributes to reducing the gap in knowledge by providing further empirical evidence of a global pattern in *S. salar* across its distribution range. Results are consistent with the hypothesis that the observed changes in life-history traits are primarily associated with environmental changes in the North Atlantic Ocean. They also emphasize the presence of less important, but still significant contrasts between region and life history.

Key words

body size; environmental buffering; environmental variability; life-history strategy.

Introduction

Global climate warming is responsible for rising sea-surface temperature in the Atlantic Ocean since the 1970s (Levitus *et al.*, 2000; Polyakov *et al.*, 2009). There is also strong evidence that climate change is altering ecosystem functioning and driving a major shift, observable across multiple trophic levels in the North Atlantic Ocean (Durant *et al.*, 2004; Beaugrand *et al.*, 2008). Concomitantly, Atlantic salmon *Salmo salar* L. 1758 populations have suffered a tremendous decline in abundance across their distribution range (Jonsson & Jonsson, 2004; Chaput, 2012; ICES, 2016), together with marked changes in life-history traits and population structure. In particular, a decline in the proportion of late maturing fish has been reported for many European and North American stocks (Baglinière *et al.*, 2004; Otero *et al.*, 2012; ICES, 2016; Jonsson *et al.*, 2016). Those changes have been accompanied by a decline in length and mass of fish and a variation in age at maturity (Aprahamian *et al.*, 2008; Bacon *et al.*, 2009; Jonsson *et al.*, 2016) together with a delay in adult migration timing (Valiente *et al.*, 2011; Todd *et al.*, 2012). For instance, higher proportions of 1 sea-winter (1SW) fish in the late 20th century and more multi-sea-winter (MSW) fish in this century have been reported by Jonsson *et al.* (2016). Such changes are expected to affect population growth rate, raising concerns about the viability of this species of high economic value.

Identifying the causal link between driving factors and phenotypic changes is difficult and may be one of the greatest challenges for fisheries ecology and for *S. salar* in particular (Crozier & Hutchings, 2014). Owing to a complex life cycle shared between fresh water and the marine environment, diadromous fishes are vulnerable to various factors of stress in a hierarchy of spatial scales (Armstrong *et al.*, 1998; Mather *et al.*, 1998; Limburg & Waldman, 2009). Evidence has accumulated for a major effect of changes in the marine environment encountered by *S. salar* (Jonsson & Jonsson, 2004; ICES, 2016; Jonsson *et al.*, 2016). Both direct and indirect effects of rising sea surface temperature have been suggested. Temperature increase would directly impede post-smolt growth (Friedland *et al.*, 2000, 2005). Indirectly, temperature increase would contribute to decreasing the productivity of the North Atlantic pelagic food web, thereby indirectly affecting feeding opportunities for *S. salar* at sea (Friedland *et al.*, 2000; Peyronnet *et al.*, 2007; McCarthy *et al.*, 2008; Jensen *et al.*, 2011). In particular, the abundance or energy content of key pelagic crustaceans and small pelagic fishes, on which *S. salar* largely prey, may have declined (Beaugrand & Reid, 2012;

Friedland *et al.*, 2013; Mills *et al.*, 2013; Miller *et al.*, 2014). Recent stock rebuilding in some pelagic fishes competing for similar resources to *S. salar* may further amplify this process (Mäntyniemi *et al.*, 2012; Jonsson *et al.*, 2016).

Simultaneous temporal trends in growth, length, mass and phenology variations have been observed in Norway (Jensen *et al.*, 2011), Ireland (Quinn *et al.*, 2006) and Scotland (Summers, 1995; Todd *et al.*, 2008; Bacon *et al.*, 2011). Given that these populations breed in very distant rivers, the existence of a large-scale mechanism taking place at sea has been suggested. To further support this hypothesis, large-scale data for southern populations are required. Yet, precise ecological and demographic mechanisms that underline these changes are still unclear (Crozier & Hutchings, 2014). Additional data should also help to better understand the still rather elusive mechanisms regulating *S. salar* responses to ongoing environmental change for more robust management and policy recommendations.

Anadromous *S. salar* attain maturity after 1SW orMSW at sea (Gueguen & Prouzet, 1994; Hutchings & Jones, 1998; Aas *et al.*, 2011). The differences in their respective life-history traits (*e.g.* body size, growth rate, age at maturity, fecundity or migration timing) reflect the strategy of resource allocation to growth, survival and reproduction (Cody, 1966; Williams, 1966; Stearns, 1976; Schaffer, 1983). The assembly of a specific set of traits, *i.e.* a tactic, seems to be partially determined by sex and genes (Gueguen & Prouzet, 1994; Fleming, 1996; Barson *et al.*, 2015). Females, for which breeding success is strongly related to body size (Prouzet *et al.*, 1984; Fleming, 1996), are more abundant among MSW fish, while males tend to mature earlier *i.e.* most of them are 1SW fish (Hutchings & Jones, 1998; Aas *et al.*, 2011). Thus, any change in resource availability or more generally in environmental conditions at sea is likely to induce different responses in 1SW and MSW fish, because of differences in their resource allocation (Stearns, 1976; Gaillard *et al.*, 1989; Reznick *et al.*, 1996). In southern Europe, growing areas at sea used by MSW are farther away than in 1SW *S. salar*, resulting in an even greater contrast between sea-age groups (*i.e.* tactics) in marine mortality. Also, differences in age and sex ratio may generate differences in the balance between somatic growth and gonad development in 1SW and MSW fish. For instance, somatic growth might be affected more by poor environmental conditions during the first year at sea in 1SW, as more energy might be allocated to gonad development, relative to somatic development, in this early maturing

group. As a result, different abilities in buffering external forcing in 1SW and MSW might be expected, as already observed in mammals for instance (Coulson *et al.*, 2001). Monitoring and studying life-history traits by sea-age class is essential to better understand and predict species response to ongoing global changes and provide sound insights for the management of *S. salar* across its distribution range (Armstrong *et al.*, 1998; Mather *et al.*, 1998).

In this study, long-term changes in length, mass and migration phenology of French *S. salar* populations over the past three decades are investigated using a recreational angling database comprising a mandatory catch declaration scheme for 34 rivers. Although the available literature accumulates evidence of temporal changes in life history traits in a high number of *S. salar* populations, only few results concern south European rivers (Valiente *et al.*, 2011) and no results have been published for France. *Salmo salar* length, mass, condition factor and migration timing during 1987–2013 were described and used to test for common patterns in these variables between distant populations. The hypothesis that the response to environmental variation in *S. salar* is tactic-dependent was tested. The relative rates of change in key life-history traits between 1SW and MSW fish over the study period were assessed.

Materials and methods

Recreational fishery data

The analyses were based on the French recreational angling database based on a mandatory catch declaration scheme with input data from 1987 to 2013 from 34 rivers (Fig. 1). In France, *S. salar* recreational rod and line fisheries takes place in more than 40 rivers of the Atlantic Ocean and English Channel coast. These rivers are mainly localized in three regions that represent more than 90% of French *S. salar* abundance: Normandy, Brittany and Aquitaine (Fig. 1; Gueguen & Prouzet, 1994). This stratification results from genetic and demographic population structure and morphometric characteristics of the rivers (Prévost, 1987; Perrier *et al.*, 2011). In addition to the recreational fishery, a small commercial fishery takes place in the Adour River, Aquitaine, on average accounting for 10 · 5% of the annual *S. salar* catches. The fishing season extends from the beginning of March to the end of October for rod fishing and to the end of July for commercial fishing. Since 1987, the *S. salar* fishery has relied on a

national compulsory catch declaration scheme, which offers a national sampling survey of adult *S. salar* and constitutes one of the largest data sets for a salmonid fishery in Europe. Catch data are collected by anglers and centralized by the National Centre for the Interpretation of Salmonid Catches. For each fish caught, the recorded data are date (D , day of the year), river, total length (LT , mm), mass (M , g) and a sample of scales. All scales are analysed following a standardized protocol (Baglinière *et al.*, 1985) to estimate both the time spent in fresh water during the juvenile phase (freshwater age) and the time spent at sea during the adult phase of the life cycle (sea-age). Current French *S. salar* populations are mainly composed of 1SW, two-sea-winter (2SW) and (rarely) three-sea-winter (3SW) fish. Because of the unbalanced fishing effort between sea-age classes (being historically more intense on large 2SW fish than on 1SW ones), the data do not allow the drawing of any inference on the relative abundance of the two tactics and its variation over time.

The ordinal date of capture (D) was considered as an index for the date of river entry. Indeed, as already discussed in Bacon *et al.* (2009), the rod capture data mostly concerns newly arrived fresh-run fish, often caught in lower parts of rivers just after their entry into freshwater. Several studies have shown that the movements and capture rates of *S. salar* decline rapidly after river entry (Thorley *et al.*, 2005), suggesting that *S. salar* may be harder to catch by rod after several days in fresh water.

Because salmonids are considered to have a standard body shape, the Fulton's condition coefficient (K) was used as a proxy for *S. salar* body condition (Bolger & Connolly, 1989; Nash *et al.*, 2006). It was calculated for each fish as $K = M \times L_T^{-3}$.

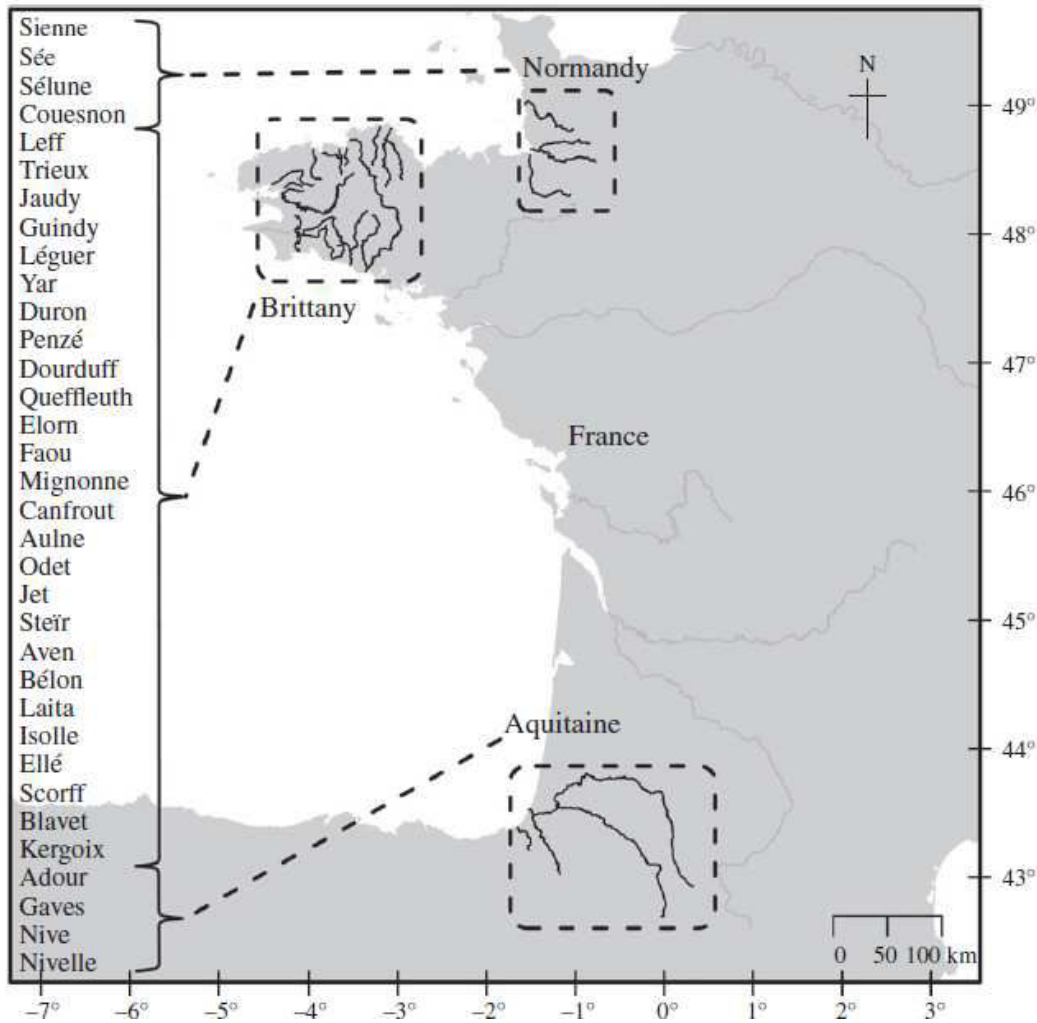


Fig. 1. The three regions considered in the analysis of French *Salmo salar*, Normandy, Brittany and Aquitaine, and their respective rivers.

Quality control and data processing

Three-sea-winter fish and repeat spawners are rare in the study rivers (Baglinière & Porcher, 1994). Data from these were few and omitted from the analyses. Unrealistic combination of length and mass (*i.e.* K outside the range 0.4 – 1.6) coming from erroneous records in the data set, were discarded. The date of capture was also used as a filter criterion in the data set. In France, MSW *S. salar* dominate in the spring run while 1SW dominate in the summer run.

Depending on summer hydrological conditions (Baglinière & Porcher, 1994), some *S. salar* were caught unusually late in the season. These fish may have lost mass during a prolonged residency in the river estuary, when feeding is scarce. In males, the length may also increase towards the spawning period with the development of elongated jaws (Maise & Baglinière,

1986; Baglinière & Porcher, 1994). To avoid these biases, only fish caught before the end of August were used in the analyses.

Populations from the Loire River and from northern France, which represent <5% of the records, were excluded from the data set for three main reasons: fishing for *S. salar* in the Loire River has been forbidden since 1994; *S. salar* catches in northern France are low; stocking practice takes place on all these rivers, which may mask ecological signals (Le Cam *et al.*, 2015). The analysis included 27 709 individuals (11 466 1SW fish and 16 243 2SW fish) collected over the period 1987–2013 in 34 rivers. Sample size per river was small, thus records from single rivers were pooled into three study regions (Normandy, Brittany and Aquitaine) to reduce sampling noise (Fig. 1 and Table I) and because of the homogeneity of the genetic and morphometric characteristics within these regions. Despite an unbalanced number of rivers per region and contrasted river profiles, this regionalization of the catch data may reflect the spatial distribution of *S. salar* abundance in France.

Table I. Sample size: number of one sea-winter (1SW) and two sea-winter (2SW) *Salmo salar* per region considered in the study

Sea-age	Normandy	Brittany	Aquitaine
1SW	3716	12 053	959
2SW	3110	9577	3870

Characterizing trends and the effect of covariates

Temporal trends in D , L_T , M and K (Figs S1 and S2, Supporting Information) were analyzed using generalized additive models (GAM) as implemented in the R-package *mgcv*, 1.8-6 (Wood, 2011) to capture the non-linearity in the trends. Independent models were built for each of the four response variables, here denoted as Z for genericity. The effects of the sea-age class (1SW or 2SW) and regions (Normandy, Brittany, Aquitaine) were introduced as categorical effects and the year was considered as a continuous variable in the non-parametric smooth trend. The most complex model considered was: $Z_{Y,A,R,i} \approx A \times R + s(Y, A \times R) + \varepsilon_i$, where $Z_{Y,A,R,i}$ is the variable D , L_T , M or K for any fish i of sea age A , caught at year Y in region R , $A \times R$ is a sea age by region interaction, $s(Y, A \times R)$ is a sea age by region specific smooth time trend

and ε_i are independent and identically distributed residuals $c. N(0, \sigma^2)$ for any individual fish i . To test for the existence of trends specific to sea age and region, simpler nested models without time trend, or with identical time trend for each region or sea age were considered. Competing models were compared using the Akaike information criterion (AIC; Burnham & Anderson, 2002). The reduction of the model deviance as the models get more variables (*i.e.* increase in complexity) was also used to comment on the relative importance of the covariates in explaining the data variability. No data transformation was needed, as the residuals from the models did not reveal any departure from the assumptions of normality and homogeneity of variance.

Common fluctuations among regions

Time trends in each life-history trait were then examined to test for common temporal fluctuations among regions (for any sea-age strategy). To ensure that two regions would not appear to be correlated simply because both showed comparable long-term trends, any long-term trend (low frequency signal) in the data was first removed by fitting a spline *a priori* forced to be very smoothed by fixing the d.f. to 5 in the GAM procedure. Correlations across years between any two regions were then analyzed on the detrended time series by calculating the Pearson correlation coefficient. Following the methodology developed in Pypers & Peterman (1998), the significance of the correlation was tested using modified *t*-tests with a reduced d.f. to correct for any remaining autocorrelation in the detrended time series.

Comparing rates of change between strategies

The relative rate of change in life-history traits (L_T , M and K) over the study period was investigated to test for potential difference in the intensity of the response between strategies (1SW or 2SW). The average rate of change (in % year⁻¹) of each life-history trait was estimated as the slope of a linear model over time, based on standardized data. The effects of the sea-age and region on the rate of change were introduced as categorical effects and the year was considered as a continuous variable. Nested models without time trend or with time trends identical for each region and sea-age (additive models) were also considered. The best models were selected using the AIC. For each region, the difference in the rates of change (*i.e.* slopes) in the 1SW and 2SW were tested using the Wald test using the *glht* function of the *multcomp* R-package (www.r-project.org) that automatically corrects for multiple comparisons.

Results

Differences in mean life-history traits between regions and sea ages

For each trait (L_T , M , K and D), the data were best explained by a GAM including both an average term and a smoothed temporal trend specific to each combination of region and sea-age (Table II). The average interaction term ($R \times A$) explained most of the observed variability in the data, revealing high differences in the average level of life-history traits across sea-age classes and regions. The strongest difference occurred between the north-west (Normandy and Brittany) and the south-west (Aquitaine) regions. Fish from Aquitaine were noticeably larger and heavier than fish from Normandy and Brittany for both 1SW and 2SW fish. 1SW fish from Normandy were also heavier than in Brittany, but no clear difference was detected in 2SW fish between the two regions. 2SW fish from Aquitaine were caught later than fish from Normandy and Brittany, the average difference in the date of river entry between the three regions being much weaker for 1SW. Comparatively, the smoothed time trends explained a much lower part of the deviance, even when considering an interaction with sea-age and region (Table II).

Table II. Modelling for date of river entry, total length (L_T), fish mass (M) and Fulton's condition factor (K) for *Salmo salar* caught in France as a function of sea age (A), region (R) or year (Y). % of Deviance explained (% Dev.) and ΔAIC are presented for each model, $s(Y, by=A)$ and $s(Y, by=A \times R)$ indicate generalized additive model smoothing.

Covariates	Date of river entry		L_T		M		K	
	% Dev	ΔAIC	% Dev	ΔAIC	% Dev	ΔAIC	% Dev	ΔAIC
A×R	61.26	-91970	71.94	-153634	68.68	-91117	3.34	-113143
A×R + s(Y)	63.7	-1790	72.84	-889	70.17	-1335	5.24	-533
A×R + s(Y,by=A)	64.47	-572	72.95	-95	70.29	-96	6.26	-283
A×R + s(Y,by=A×R)	64.95	-313	73.17	-161	70.55	-177	6.65	-61

Time trends in life-history traits and common fluctuations between regions

Overall, the non-linear smoothed temporal trends for the 1987–2013 period revealed a general delay in the date of river entry (Fig. 2.a)) and a decrease in L_T and M (Fig. 2.b, c, respectively). Time trends, however, were specific for each region and sea-age. In particular, K showed more contrast between sea-ages than the other life-history traits. K exhibited a clear downward trend in 1SW fish (Fig. 2.d), but remained rather stable in 2SW fish (Fig. 2.e). Changes in the date of capture also exhibited differences between regions and sea-age. 1SW fish from Normandy and Brittany showed the most important delays of return migration, with a lag of up to 40 days throughout the study period. Meanwhile, the observed delays for 2SW fish and 1SW fish in Aquitaine were only 20 days. Also, smoothed time trends also suggested synchronous fluctuations across regions with a 7–8 year period, with high similarity between Brittany and Normandy (Fig. 2). Variations in size and mass suggested a common temporal pattern across regions, characterized by repeated declines in both phenotypic traits around years 1990, 1998 and 2007.

The analysis of correlations between detrended time series further supported the hypothesis of a synchronous change in L_T , M , K or D across regions (Table III). Indeed, for each trait, most of the correlations between regions were positive and significant, even after accounting for autocorrelation. The strongest correlations between regions were found for L_T and M . The strongest correlations were also found between Brittany and Normandy, which are geographically close. Correlations between more distant regions (*i.e.* Brittany and Aquitaine, Normandy and Aquitaine) were generally weaker. Also, with the exception of D , between region correlations seemed stronger in 2SW fish than in 1SW fish.

The date of river entry showed opposite trends to L_T and M , a later date of river entry being associated with a decline in the L_T and M of the fish. Interestingly, the opposite time trends were associated with negative correlations at a shorter time scale, with 7–8 years periodicity in the date of river entry being in antiphase with those of length and mass (Fig. 2).

Rate of change 1987–2013

Consistent with the analyses of non-linear trends, average rates of change in traits were almost all negative (Fig. 3) and depended upon both region and sea-age (based on AIC and

explained deviance). Pair-wise comparison tests of the difference between rate of change in traits (per sea-age and per region) revealed a stronger decline in M , L_T and K for 1SW fish than for 2SW fish. The largest rates of change were found for mass, with an average rate of -1.00% per year for 1SW fish and -0.32% per year for 2SW in Brittany. The K of 1SW fish declined by 0.20% (Aquitaine) to 0.51% (Normandy) per year while the rate of change in K was close to zero for 2SW and could even be positive in some regions. The relative rate of change in L_T was not different in 1SW and 2SW ($P > 0.05$), fish having lost on average 0.10% (Brittany) to 0.20% (Aquitaine) of their initial body length each year between 1987 and 2013.

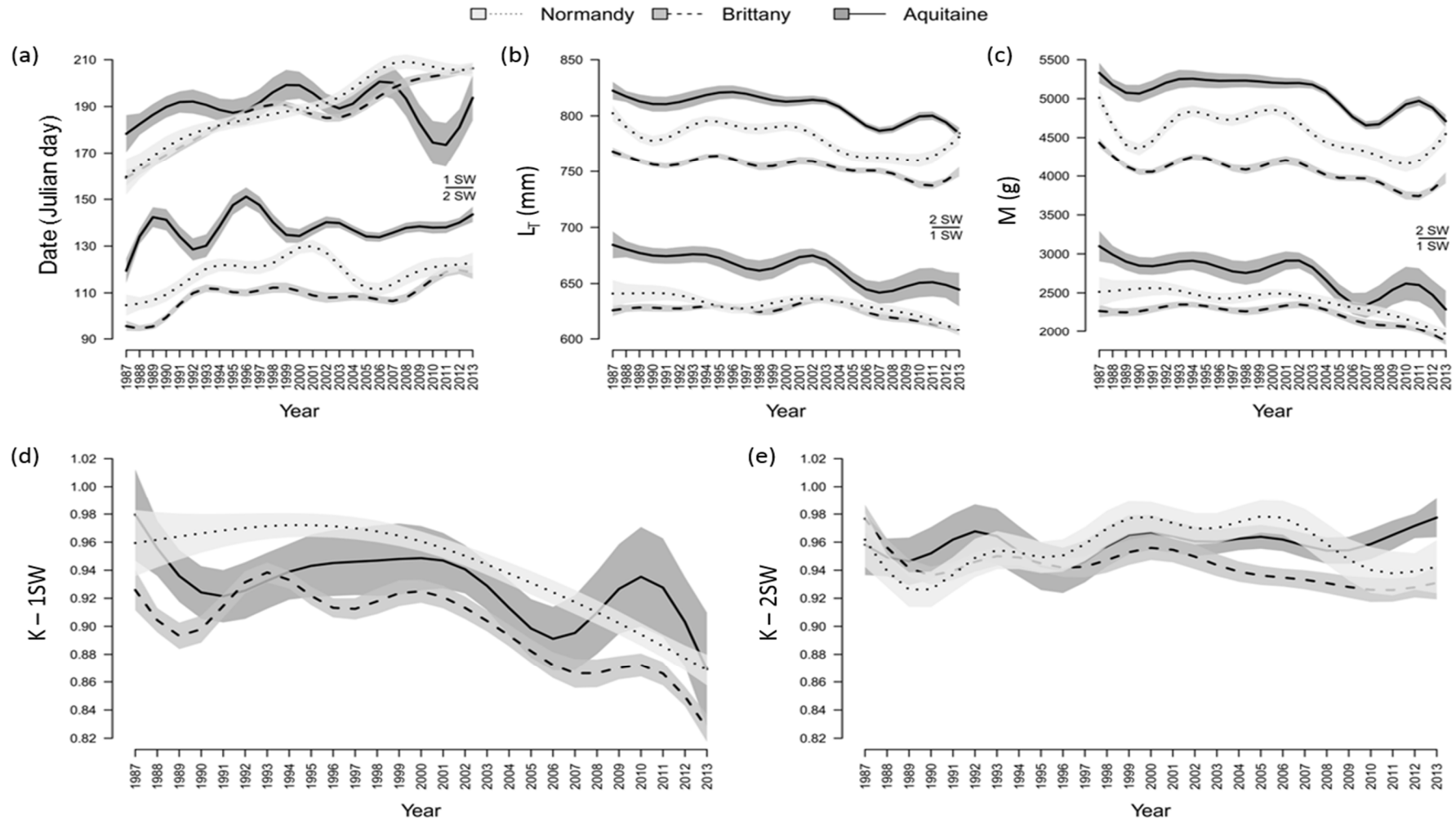


Fig. 2. Change in (a) the date of river entry, (b) total length (L_T), (c) fish mass (M) and (d) and (e) Fulton's condition factor (K) in one sea-winter (1SW) and two sea-winter (2SW) *Salmo salar* from Normandy (.....), Brittany(- - -) and Aquitaine (—) 1997–2013. The shaded bands represent 95% c.i.

Table III. Cross correlations in date of river entry, total length (L_T), fish mass (M) and Fulton's condition factor (K) for *Salmo salar* between regions for each sea-winter (SW) age class. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, all corrected to account for the autocorrelation in the times series.

	Normandy - Brittany	Normandy - Aquitaine	Brittany - Aquitaine
1SW sate	0.46*	0.38*	0.01
1SW L_T	0.35.	0.56**	0.57**
1SW M	0.46*	0.44*	0.68***
1SW K	0.47*	0.34.	0.45*
2SW date	0.32.	0.01	-0.02
2SW L_T	0.75***	0.54**	0.52**
2SW M	0.86***	0.57**	0.42*
2SW K	0.66***	0.46*	0.25



Fig. 3. Linear rate of change [mean (■) ±50% (—) and 95% (—) c.i.] in total length (L_T), fish mass (M) and Fulton's condition factor (K) in one sea-winter (1SW, black) and two sea-winter (2SW, grey) *Salmo salar* from Normandy (N), Brittany (B) and Aquitaine (A). The difference in the rates of change between 1SW and 2SW was assessed with a Wald test: $P < 0.1$; ** $P < 0.01$; *** $P < 0.001$.

Discussion

The present analysis provides new insights into temporal changes in *S. salar* life-history traits across France over the last three decades and contributes to reducing the gap in knowledge by providing further empirical evidence of a long suspected change in life history of *S. salar* throughout its entire distribution area. Using a large data set from rod and line and commercial catches, this study describes a decline in individual length and mass, together with a delay in the migration phenology of adult *S. salar* returning to French rivers. This analysis highlighted similarities in time trends between regions, but the rate of change in life-history traits clearly depends upon the tactic at sea.

Strength and limitations of the data

Commercial fisheries for *S. salar* at sea have almost all been closed since the early 1990s (ICES, 2016) and scientific data are only available for a few rivers and generally cover only short periods of time. In contrast, recreational hook-and-line fisheries are operating in almost all rivers across the species' distribution range. Thus, when available, catch data provide the broadest spatio-temporal sampling of *S. salar* populations across several countries (Bacon *et al.*, 2009; Valiente *et al.*, 2011; Fjørtoft *et al.*, 2014). Here, time trends in *S. salar* life-history traits were analysed using catch data from both recreational and commercial freshwater fisheries. This provides a large scale data set of wild French *S. salar* populations within this context.

The advantages offered by the large spatial and temporal coverage of this fishery data set are balanced by the difficulty in controlling the sampling effort. Freshwater fishery data may indeed suffer from non-random sampling caused by fishery management rules and intrinsic variability in fishing effort (Bacon *et al.*, 2009). Although catch data virtually only come from newly arrived freshrun fish (Thorley *et al.*, 2005; Bacon *et al.*, 2009), the date of capture may still provide a biased estimate of the date of river entry and this bias may differ between regions. For instance, fish from Aquitaine generally undertake a longer upstream migration in freshwater before being caught than fish from Brittany and Normandy (smaller and shorter rivers). Hence, the late migration timing reported for Aquitaine (2SW) may be partly explained by a specific spatial setting compared with the other regions rather than by a later return to coastal waters. This late migration can also reflect a distinct flow regime in early spring, that

is driven by melting snow on the Adour–Gaves rivers (where most catches come from). In contrast, results on the relative variability and the rate of change in this trait within a given region are assumed to be robust.

By removing catches happening in the end of the fishing season, the analysis might miss key ecological signals. In particular, any potential compensatory mechanism that would occur between early and late migrating fish would not be detected. For instance, it can be hypothesized that a decline in body size among studied fish might be balanced by an increasing number of large fish in a potential late run. Although such a process cannot be ruled out, the late captures represented only a small proportion of fish in France, which may thus have a limited influence on results (repeat breeders were not included in the analysis). Migration monitoring using a fish trap on the Scorff River shows that <10% of all maiden 1SW and 2SW fish were trapped in autumn, with no evidence of growth compensation (E. Prévost, pers. comm.).

Lastly, although raw data were available at the scale of single rivers, samples were pooled at the regional scale to dampen the effect of uncontrolled sampling variability and local heterogeneity. Indeed, the low signal to noise ratio due to low sample size or uncontrolled variations of the fishing effort in space and time for single rivers (*e.g.* due to report of the fishing effort from one alleged river to the other within the fishing season) would impede the detection of time trends. Aggregating data on several rivers of the same region helped in disentangling the temporal variation attributable to large scale environmental change, from very local factors.

Evidence for change in phenotypic traits

In France, differences in average phenotypic traits and migration date were detected between regions. These patterns have already been described in previous analyses on older data (Prévost, 1987), thus highlighting the stability of the regional contrast over several decades. As discussed previously, the date of river entry may be overestimated in Aquitaine due to uneven sampling design across regions. Genetic drivers of the migration timing may also be considered (Hansen & Jonsson, 1991). Such phenotypic differences are likely to reflect distinct genetic pools (Perrier *et al.*, 2011).

This study highlighted important temporal changes in phenotypic traits in French *S. salar* populations over the period 1987–2013. In all regions, a significant decline in fish length and mass, as well as a delay in the date of river entry were detected. Results are consistent with patterns already reported in several other rivers in northern Europe. Similar declines in *S. salar* LT (c. 1 cm per decade), mass (200–400 g per decade) or 1SW body condition have been observed in Scotland (Bacon *et al.*, 2009; Todd *et al.*, 2010), Ireland (Quinn *et al.*, 2006), Norway (Jonsson *et al.*, 2016) and North America (Friedland *et al.*, 2005). The observed delay in migration timing (c. 5–10 days per decade) is also congruent with previous findings in Scotland (Youngson *et al.*, 2002; Todd *et al.*, 2012), England (Arahamian *et al.*, 2008) or Spain (Valiente *et al.*, 2011).

Moreover, the correlation analysis highlighted common interannual fluctuations in phenotypic traits across all three French regions. Interestingly, this analysis detected more similarities in the temporal variability of those traits between neighbouring French northern regions (Brittany and Normandy) than between these two northern regions and the more distant Aquitaine. These results support the hypothesis of a segregation of populations by distance (Juanes *et al.*, 2004; Jensen *et al.*, 2011; Perrier *et al.*, 2011), which may be driven by spatial or temporal segregation in post-smolt migration route and feeding zone at sea (Bacon *et al.*, 2009; Jensen *et al.*, 2011) or by a difference in river profiles (Juanes *et al.*, 2004; Valiente *et al.*, 2011). French *S. salar* populations face environmental conditions that differ in many ways from the conditions encountered by north European populations (*e.g.* longer migration routes, higher freshwater temperature and high anthropogenic pressure). The effect of a large scale phenomenon in the marine environment, initially described in northern Europe, however, seemed to prevail in France as well. Therefore, by providing empirical evidence for southern populations, this study nicely complements existing literature to better describe the big picture.

A response to marine environmental change

There appear to be coherent changes in the life-history traits of adult *S. salar* across Europe. This strongly supports the hypothesis of a common environmental mechanism affecting *S. salar* populations throughout the eastern Atlantic Ocean. Temporal similarities across regional patterns, *e.g.* time series varying in phase or antiphase, further suggest a response to common

environmental drivers jointly affecting the marine phase of the life cycle of different populations spawning in distant rivers. Several studies suggested that a major decline in marine growth condition would be responsible for the decrease in *S. salar* length and mass (Friedland *et al.*, 2000; Peyronnet *et al.*, 2007; McCarthy *et al.*, 2008; Jensen *et al.*, 2011), while within river migration timing was delayed. As a mechanism, it has been suggested that bottom-up control on food resources during the early marine phase of post-smolt migration may have affected both growth and survival negatively (Friedland *et al.*, 2009; Jensen *et al.*, 2011; Beaugrand & Reid, 2012). Triggered by ocean warming, a major trophic shift in the North Atlantic Ocean has been documented in the 1990s with reported changes in zooplankton communities up to seabird population dynamics (Durant *et al.*, 2004; Beaugrand *et al.*, 2008). As a result, decrease in prey abundance and energetic quality may have altered *S. salar* growth potential at sea (Otero *et al.*, 2012; Mills *et al.*, 2013). Jonsson *et al.* (2016) advocated that direct effects of temperature were unlikely to explain observed changes and argued that stock rebuilding in herring *Clupea harengus* L. 1758, mackerel *Scomber scombrus* L. 1758 and blue whiting *Micromesistius poutassou* Risso 1827 was probably the most likely candidate because of competition for resources with *S. salar* smolts, as observed in the Baltic Sea (Huse *et al.*, 2012; Utne *et al.*, 2012).

It has been demonstrated that the mortality of fish at sea is size dependent (Lorenzen, 1996; Gislason *et al.*, 2010). In particular, *S. salar* marine mortality is believed to be mostly caused by predation and will then be size and growth dependent (Friedland *et al.*, 1993, 2000), *i.e.* larger and more robust fish have a higher probability of escaping predation. As a consequence, decreasing growth rate at sea may also be responsible for the decline in marine survival observed across northern Europe (Friedland *et al.*, 1993, 2000; Peyronnet *et al.*, 2007; Chaput, 2012). Catch data, however, do not inform about survival in French populations. Nevertheless, *S. salar* monitoring using a fish trap on the Scorff River, Brittany, showed substantial change in marine survival, the average return rate decreasing from 10 · 3% 1997–2003 to 4 · 8% 2009–2013 (ICES, 2016).

The temporal coherence (*i.e.* direct anti-phase) in declining length–mass and delaying run migration observed in these populations appeared compatible overall with such a degradation of feeding conditions at sea. Within a given sea-age class, the spawning run lasts several weeks

and its seasonal timing is expected to be driven by the trade-off between reproduction and survival. The reproductive benefit associated with extra feeding opportunities at sea would be balanced against the risk of mortality during an extra time at sea (Clark, 1994). As a consequence, decreasing growth rate may call for an extra time at sea, probably aiming at maximizing growth potential, as also observed in some Scottish rivers (Todd *et al.*, 2012). If resource conditions, however, turn out to be so degraded, the decline in growth rate would be too large to be compensated by a mere delay in the date of river entry. Such a mechanism may generate opposite patterns of temporal variability in migration timing and length or mass (using detrended data), as observed in French populations. Interestingly, Valiente *et al.* (2011) also reported negative correlations between medium term fluctuations of length–mass and the date of river entry.

Different responses between 1SW and 2SW

Present results stressed that the relative change in mass and condition of returning *S. salar* was weaker and less variable in 2SW than that in 1SW. Similar differences between 1SW and 2SW have been observed in Scottish (Bacon *et al.*, 2009) and Norwegian populations (Jonsson & Jonsson, 2004) as well. Those results stress the need to better account for differences in *S. salar* anadromous tactics to improve our understanding of the demographic and ecological mechanisms underlining population changes.

1SW 2SW *S. salar* have similar migration routes at the beginning of their journey at sea and then separate migration routes where they may encounter different growth conditions. One cannot exclude that change in the feeding condition experienced by 1SW fish has been more stringent than in 2SW fish, thus explaining a weaker decline in 2SW mass. A proportionally lower decrease in the length of 2SW fish may also point to some compensatory mechanism. For instance, 2SW fish may move towards more favourable feeding grounds, which would then support a higher growth rate over the second year at sea (Auer *et al.*, 2010; Hogan & Friedland, 2010). Also, species competing with *S. salar* in the first year and the abundance of which increased over the last few years, may serve as food in the second year at sea. This hypothesis, however, appears poorly supported by recent studies that analysed growth patterns on fish scales for northern populations, showing that growth increment in 2SW fish

during the second year at sea was not significantly higher than growth rate over their first year at sea (Hogan & Friedland, 2010; Jensen *et al.*, 2011; Jonsson *et al.*, 2016).

In *S. salar*, the duration of the marine phase of the life cycle may reflect different strategies of resource allocation between key fitness components (*e.g.* survival, growth and reproduction). Intrinsic differences in allocation rules may generate contrasting responses to a given change in resource availability between 1SW and 2SW fish. Females are largely dominant among 2SW fish (Prouzet *et al.*, 1984; Baglinière & Porcher, 1994; Fleming, 1996; Barson *et al.*, 2015), thus suggesting that differences in allocation rules between 1SW and 2SW could emerge from differences in allocation rules between males and females. Notably, males and females have specific physiological and behavioural constraints over the reproduction period; they are also characterized by distinct tactics at sea. In *S. salar*, female fitness is more strongly driven by body size than in males because their sexual maturation process requires more energy. The tight dependence between sex and sea-age classes might thus explain the difference in individual response to changes in environmental conditions between sea-age classes. As a result, 1SW fish (preferentially males) might have favoured activities related to survival at the expense of mass gain (*i.e.* spending only one year at sea) and 2SW fish (preferentially females) might have favoured a large body size as a way to maximize fecundity in surviving individuals (Prouzet *et al.*, 1984), as suggested by the data.

The rate of change was not uniform for all life-history traits in 1SW and 2SW. These analyses highlight a similar response in 1SW and 2SW fish across regions for L_T . In *S. salar*, growth and body size are considered as key drivers of marine survival and female fecundity (Thorpe *et al.*, 1984; Fleming, 1996; Jonsson *et al.*, 1996), but a large body size is also a key feature of reproduction success in anadromous males, as it confers an advantage in terms of intra-sexual competition for mates (Fleming, 1996). Therefore, L_T appears as an important fitness component (Marschall *et al.*, 1998) in both males and females, *i.e.* in both 1SW and 2SW fish. Not surprisingly, L_T happened to be the most conservative life-history trait in the analysis: low variability and weak decline. Similarly Todd *et al.* (2008) reported a disproportional decline in body mass compared with length in Scottish 1SW fish (22 v. 4% declines, respectively). This pattern seems consistent with the life-history theory, which states that phenotypic traits more strongly connected to fitness are expected to be the more preserved, or canalized, against

environmental stochasticity (Stearns & Kawecki, 1994; Pfister, 1998; Caswell, 2001; Gaillard & Yoccoz, 2003). At the population level, the relative conservatism in L_T , compared with other traits, can be perceived as a positive signal for population viability.

This large scale study on French populations contributes to reducing the gap in knowledge by providing further empirical evidence of a long suspected change in life history of *S. salar* throughout its north-east distribution area. Results also revealed different rates of change between 1SW and 2SW fish, thereby pointing out the importance of considering the complexity of life-history strategies when exploring mechanisms of changes in *S. salar* phenotypic traits. It is hoped that this long-due analysis for France would encourage other authors to make their data sets available to the scientific community, which is a prerequisite to improving understanding of major cross-border ecological mechanisms.

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Supporting material

Appendix 3. Supplementary figures: Box plots of raw data for the date of river entry, total length, fish mass and Fulton's condition factor in one sea-winter and two sea-winter *Salmo salar* caught by the French hook-and-line recreational fishery.

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3. Conclusion of chapter 2

This chapter focussed on the responses of French Atlantic salmon populations to environmental changes over the period 1985 - 2014. We reported temporal variations in life history traits that were concordant with similar studies on other European Atlantic salmon populations (ICES 2016). However, here, we also highlighted that temporal responses were specific to each migratory tactic. The body length of multi-sea-winter fish seems to be buffered against environmental changes suggesting that this trait might be the most related to fitness (i.e. canalization process, Waddington 1953, Gaillard and Yoccoz 2003). Consequently, demographic analyses have to consider tactic-specific variability in traits to understand population response to environmental changes.

Highlighting long-term variations in brown trout traits based on catch declarations was difficult (cf. Figure 15). Even by grouping regions, or by comparing freshwater resident *versus* all sea -migrant tactics, we did not detect any change in brown trout body size, mass, body condition, and phenology. Catch declarations were not appropriate to investigate temporal variations in trout traits, due to low sample size and uneven sampling over space and time. A more suitable method for brown trout could be the comparison of details data on two index rivers showing a large sample size for brown trout. In 2016, data from the brown trout population of the river Bresle became available as part of the ORE Dia-PFC, allowing comparison with our Oir study population (cf. Data sets section). Temporal variations in traits related to the resident or sea-migrant tactics in trout could be analyzed in the future. Since 1977, Milner et al. (2017) observed a decrease in the age and size at first maturation in sea trout correlated with sea-surface temperature in four Welsh rivers. Consequently, we can expect similar trends in our sea trout populations, with tactic-specific responses as shown in Atlantic salmon.

Major findings 2.

- Response to environmental changes is tactic specific.
 - The body length of multi-sea-winter salmon is buffered against temporal variability suggesting that this trait is the highly related to individual fitness.
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CHAPTER

3.

Tactics and reproductive success



1. Objectives and organization of the chapter

The previous chapters showed that life history traits of juvenile and adult anadromous salmonids, as well as the propensity to migrate, might vary under environmental changes. In addition, we suggested in chapter 2 that body length might be a trait highly correlated to individual fitness. To understand the potential impact of the observed decrease in body length in salmonid populations (as detected in chapter 2) we need to assess the relationship of this trait with the fitness components (e.g. reproductive performances) of each life history tactic. In salmonids, the anadromous individuals show better reproductive performances (higher fecundity in females and better access to females in males) than the freshwater resident individuals due to their larger body size at reproduction (Fleming and Reynolds 2004, Jonsson and Jonsson 2006). Nevertheless, at the population level the migration cost may prevent a high contribution of the anadromous tactic to the juvenile production.

Consequently, the objective of this chapter is to quantify the reproductive success and the contributions of the migratory and resident tactics to the annual juvenile production in brown trout and Atlantic salmon. From these quantifications, I will investigate the role of body length in the reproductive performance and discuss the consequences of a decrease in body length on individual fitness.

Using genetic parentage analyses on both Atlantic salmon and brown trout during two reproductive seasons (2014-2015 and 2015-2016), we estimated the reproductive success and addressed the following questions:

- Which life history trait maximizes the reproductive success?
- Which tactic produces the largest number of offspring?

The section 2 (Article III) focuses on brown trout. For Atlantic salmon, a Master student François LeCor (6 months) has investigated under my supervision these questions through an exploratory work. The section 3 summarizes this preliminary work.

2. Article III.

Manuscript in preparation

The reproductive success of resident and anadromous brown trout females

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Abstract

Quantifying intraspecific variation in reproductive performances and identifying the traits that drive this variation over reproductive seasons is crucial to understand and predict population dynamics in a changing world. These objectives are especially relevant in non-breeding partially migratory populations where migrant and resident females coexist but encounter different environment during the non-breeding season. In salmonids, partial migration induces a large range of female size. Large anadromous are considered as the key driver of the population dynamics, while residents are generally overlooked. Moreover, the life history traits that drive the reproductive success of females are debated. We used microsatellite genetic assignment to compare the reproductive success and offspring body length of resident and anadromous female brown trout during two reproductive seasons (2014-2015 and 2015-2016) with contrasted environmental conditions (i.e. water level). We tested whether the anadromous tactic produced more juveniles in the population through a higher reproductive success and larger juveniles than the resident tactic, regardless of environmental conditions. We highlighted that the reproductive success depended on the number of mates as well as the female body length. The relative influence of these two drivers varied over the two reproductive seasons. Moreover, we did not detect any relationship between female body length and offspring body length. Resident females contributed more to the recruitment of juveniles than anadromous females. The higher number of resident females compensates their smaller body length that limit their fecundity. Our results suggest that in trout populations with partial migration, resident individual might ensure the viability and the resilience of population dynamics against environmental change.

Key words

Genetic assignment, *Salmo trutta*, partial migration, life history tactic

Introduction

Individual heterogeneity induces variation in reproductive performances within population. The number of juveniles produced by different components of a population during a reproductive event, i.e. different parental life history, may vary due to distinct trade-offs for energy allocation between survival, reproduction, and growth among tactics. For instance in partially migratory populations, migrant and resident females coexist but encounter different environment during the non-breeding season (i.e. non-shared environment). The different tactic costs and benefits related to the resources in the non-shared environment, and the migration costs induce differences in female survival and fecundity (Chapman et al. 2011). Consequently, quantifying the reproductive performances and identifying the life history tactic that maximize the production of juveniles within a population is crucial to better understand and predict population dynamics.

The female tactic that invests the most in fecundity should confer the highest individual reproductive success in a reproductive event (i.e. number of offspring). However, the reproductive advantage of this tactic may be counter-balanced by a high mortality limiting the number of high fecund female in a reproductive event and the number of juvenile produced from this tactic. Moreover, in the actual context of global change, the conditions of non-shared environment of partially migratory populations can vary to become consistently better or worse hence shifting the relative advantages of being a migrant or resident. As each tactic generates different traits (e.g. survival, fecundity), this shift supposes that the main drivers (traits and/or tactic) of juvenile production of the population may vary over generations. However, the variations in these drivers are rarely quantified in some partially migratory species as salmonids species due to the difficulty of collecting reproductive success data over reproductive seasons with different environmental conditions.

In salmonids, distinct cost-benefit trade-off among tactics induce differences in body size and survival between freshwater resident and sea-migrant (i.e. anadromous). Anadromous individuals take advantage of the highly productive marine habitat to get a higher growth rate than resident fish (Jonsson 1985, Berg and Jonsson 1990, Kendall et al. 2014). This advantage is counter-balanced by a higher mortality due to higher risks of predation (Dieperink et al. 2002) and metabolic changes (Harris and Milner 2008) at sea-entry compared to the resident

tactic. The size benefit is large for female fecundity (i.e. egg production) as it increases exponentially with body size (Jonsson 1985, Jonsson and Jonsson 1997, Kendall et al. 2014). Thereby, female salmonids are more likely to migrate to a more productive environment like sea or lacustrine habitat (Northcote 1992, Jonsson and Jonsson 1993, Cucherousset et al. 2005, Dodson et al 2013). Anadromous females having a higher reproductive success than resident females are considered as the key driver of the population dynamics, while residents are generally overlooked (e.g. NMFS 2005, Harris and Milner 2008).

Nevertheless, environmental variations during the non-shared season can induce fluctuations in the proportion of resident and anadromous females on the spawning ground and in the the number of juvenile produced by each tactic. The number of anadromous females spawning over reproductive events is expected to be more variable than the number of resident females, which face a lower exposure to predation, costs of metabolic changes, and spatially heterogeneous threats (Hebblewhite and Merrill 2011, Vickery et al. 2014). Thereby, the resident tactic appearing as the safest option should be more advantageous for female trout and for the population to be stable over years in a changing world. Nonetheless, the anadromous tactic may boost the juvenile production when favourable conditions occur in the non-shared environment (i.e. increase in survival and access to the spawning ground).

As large body size confers larger fecundity to females (Kendall et al. 2014), this trait has long been identified as the main driver of the female reproductive success (Elliott 1995). Body size might also influence the female reproductive success by being positively correlated to (i) egg and offspring size (both traits being linked to offspring survival) (Bagenal 1969, Einum and Fleming 1999, Hendry et al. 2001, Acolas et al. 2008, Goodwin et al. 2016) and (ii) nest quality through the ability to dig deeper nests that are less prone to destruction, egg desiccation, freezing, and nest superimposition by other females (Crisp and Carling 1989, Fleming 1998). However, studies showed contrasting results (e.g. Jonsson and Jonsson 1999, Kinnison et al. 2001, Hendry and Day 2003, Acolas et al. 2008) and body size also appeared as a weak predictor of female reproductive success (e.g. Garant et al. 2001). Actually, Garant et al. (2001), found a positive relationship (independent of body size) between the number of mates and the reproductive success in salmon females. Mating with multiple partners is likely to reduce the risks of inbreeding (Stockley et al. 1993), sibling competition (Griffiths and

Armstrong 2001), and produce juveniles adapted to a wider array of environmental conditions (Yasui 1998). Additionally, multiple mating can increase offspring heterozygosity and thus potentially fitness (Tregenza and Wedell 2000, Blomqvist et al. 2002).

Identifying the tactic that produce the largest number of juveniles during a reproductive event and the main trait that influence the female reproductive success appear challenging in a changing environment. Using microsatellite parentage analyses, we quantified and compared the reproductive success and offspring body size of resident and anadromous female brown trout (*Salmo trutta*) during two reproductive seasons (2014-2015 and 2015-2016) with contrasted environmental conditions (i.e. low and high water levels). We investigated whether both body length and the number of mates drive the female reproductive success and whether their influences vary over the tactics and over contrasted environmental conditions. In addition, we investigated whether female tactics conferred an advantage to their juveniles.

Methods

Study site and species

The study was conducted in La Roche brook, a second order tributary of Oir river (Normandy, France, 48°38'N, 3°37'W). This stream is 4.5 km long but an impassable dam restrains its access to migrating salmonids to the 2.2 km downstream section. This section is a nursery habitat for natural populations of Brown trout (both anadromous and resident tactics) and Atlantic salmon, *Salmo salar* (Charles et al. 2004, Cucherousset et al. 2005). Anadromous trout return to La Roche brook in November where they spawn at the same time as resident trout from December to January. Fry start to emerge from the gravel in March. Then, in early spring the following year, a part of the young-of-the-year trout migrate to sea (Cucherousset et al. 2005).

Samples collection

We conducted an intensive electrofishing monitoring in La Roche brook during two reproductive seasons: 2014–2015 (season 1) and 2015–2016 (season 2) to collect juvenile and parental tissue samples for genetic analysis. These two reproductive seasons were characterized by highly contrasted environmental conditions. The season 1 had average pluviometry and temperature whereas the season 2 experienced abnormal warm and dry

conditions, resulting in low water levels (see appendix), especially during the spawning period, restraining the accessibility of anadromous trout to the brook.

To sample mature female brown trout, we performed five days of electrofishing from mid-December to early January, in both seasons. We measured each individual (fork length) and we collected individual fin clip and scales samples. We marked caught trout with a temporary marker (methylene blue) to prevent double sampling. We sampled 280 mature brown trout in season 1, and 206 ones in season 2 (details in Table 1). We identified the sex through the presence of sperm or ova. Moreover, we determined the age and the life history tactic (anadromous or resident) by analyzing the scales (Table 1) (Baglinière et al. 1985).

To assess individual reproductive success, we sampled most juveniles in the brook the next October, i.e. October 2015 for season 1 and October 2016 for season 2. We sampled juveniles with electrofishing technique, we measured them (fork length) and we collected a fin clip and some scales (to check their age and select only the young-of-the-year). We sampled 555 juvenile (0+ old) in season 1 and 419 in season 2 (Table 1). All fin samples were stored in 95% ethanol until genetic analyses.

Table 1. Sample size available for parentage analyses.

Brown trout	Season 1	Season 2
Juveniles	555	419
Adult females	126	80
Adult resident females	112	72
Adult anadromous females	14	8
Adult males	150	123
Adult resident males	145	119
Adult anadromous males	5	4
Adult residents, unknown sex	4	3
Adult anadromous, unknown sex	0	0

We performed DNA extraction using a standard chelex protocol and individuals were genotyped with 15 microsatellite loci previously developed for brown trout (details in Quéméré et al. 2016). Parentage analyses were performed using the software CERVUS 3.0.3 (Kalinowski et al. 2007) with an 80% confidence level or higher. We measured reproductive success as the number of juvenile (0+ old that survived until October) assigned per female.

We removed the females with no juvenile assigned from the data set to prevent any bias linked to females captured in La Roche brook but having reproduced in other parts of the Oir river. We determined the number of mates per female as the minimal number of males assigned to their juveniles.

The statistical analysis on the female reproductive success was performed through Generalized Linear Models (GLM) with a Poisson error family and standardized covariates as additive or/and interactive effects. The model was built by adding covariates step by step and keeping only the ones with a significant effects. First, we tested whether the reproductive success varied between the two reproductive seasons. Then we tested the effect of the female tactic. We tested whether difference in body length and/or number of mates explained difference in reproductive success between tactics. In addition, we analyzed variations in the main driver trait of the reproductive success over seasons by testing the effect of interactions between the season and the body length, the season and the number of mates. Furthermore, we investigated whether the female tactic conferred an advantage to their offspring at 0+ old by testing the influence of the female tactic and body length on juvenile body length using a General Linear Mixed model (GLMM) with the identity of the female as a random effect (McCulloch and Neuhaus 2013). These analyses were performed using the R software (version 3.3.3, The R Foundation for Statistical Computing, 2010; Package 'lme4' Bates et al. 2015) and the significance of each covariate added to the model (GLM or GLMM) was tested by comparing the models including the focal covariate with a nested model using likelihood ratio tests.

Results

We assigned 91.5% and 80.2 % of the juvenile sampled to at least one parent in season 1 and season 2, respectively (Table 2). 72.1% of females with a non-null reproductive success were resident in season 1. These resident females produced 58.9% of the juvenile assigned. These proportions strongly increased in season 2: 85.5% of resident females, produced 91.2% of the juveniles assigned (Table 2).

Table 2. Genetic assignment results.

Brown trout	Season 1	Season 2
Total number of juvenile assigned to at least one parent	508	336
Total number of juvenile assigned to females	404	182
Juveniles from resident females	238	166
Juveniles from anadromous females	166	16
Adult females identified as parents	43	55
Resident females	31	47
Anadromous females	12	8
Average number of mates assigned per female	2.7	1.7
to Resident females	2.5	1.7
to anadromous females	3	1.6

Table 3. Body length of females with non-null reproductive success and juveniles assigned to females (mm).

Brown trout	Resident		Migrant	
	<u>Mean</u>	<u>SD</u>	<u>Mean</u>	<u>SD</u>
<u>Body length females</u>				
in season 1	244.467	46.351	356.750	68.080
in season 2	240.851	67.863	336.875	35.623
<u>Body length of offspring</u>				
In season 1	70.471	15.555	73.657	9.615
In season 2	85.235	30.252	95.250	38.739

Anadromous trout were larger than resident trout in both seasons (Table 3, Table 4, M2) and the mean body length of females decreased significantly between the two seasons (Table 4, M1). The number of mates did not differ significantly between anadromous and resident females (Table 2; Wilcoxon test p-value = 0.147 in season 1; p-value = 0.733 in season 2), but it was lower in season 2 (Table 2; Wilcoxon test p-value < 0.001).

Moreover, we detected a difference in reproductive success between seasons and tactics (Table 5, M2). However, by adding the body length as covariate, the effect of the tactic was not significant anymore (Table 5, M4; p-value = 0.474). In addition, we found a significant effect of the number of mates in interaction with the season (Table 5, M8). The reproductive success increased significantly with female body length (Fig.1, Table 6) and the number of mates (Fig. 1, Table 6). We detected no interaction between body length and number of mates and between body length and tactics. The female body length and the number of mates

effects had similar strength in season 1 but the effect of the number of mates was predominant over body length in season 2 (Fig. 1, Table 6).

The mean body length of juveniles was larger in season 2 (Table 3 and 7) but we found no significant relationship between juvenile body length and the female body length or tactic (Table 7, mean = 76.537 mm, SD = 23.873 for juveniles of a resident female; mean = 75.555 mm, SD = 15.692 for juveniles of an anadromous female).

Table 4. Modeling female body length. The p-value refers to the significance of the added covariate (in bold) compared to the previous nested model. '+' additive effect; '*' interaction effect.

Model	Covariates	p-value	Residual deviance
M1	Season	< 0.001	1803.5
M2	Season + Tactic	< 0.001	1205.6
M3	Season + Tactic + Season*Tactic	0.140	1203.4

Table 5. Modeling female reproductive success. The p-value refers to the significance of the added covariate (in bold) compared to the previous nested model. '+' additive effect; '*' interaction effect.

Model	Covariates	p-value	Residual deviance
M1	Season	< 0.001	535.78
M2	Season + Tactic	< 0.001	519.19
M3	Season + Tactic + Body length	< 0.001	448.32
M4	Season + Body length	< 0.001	450.06
M5	Season + Body length + Season*Body length	<0.001	437.79
M6	Season + Body length + Season*Body length + Tactic*length	0.138	429.91
M7	Season + Body length + Season*Body length + Number of mates	0.016	252.78
M8	Season + Body length + Season*Body length + Number of mates + Number of mates*Season	< 0.001	219.33
M9	Season + Body length + Season : Body length + Number of mates + Number of mates*Season + Number of mates*Body length	0.864	219.30

Table 6. Details of the effect of the covariates of the best-selected model (Table 4, M7) explaining variation in reproductive success. '+' additive effect; '*' interaction effect.

Covariate	Estimate	Standard Error	z value	Pr (> z)
<i>Intercept (season 1)</i>	1.799	0.069	26.008	< 0.001
Season 2	-0.583	0.105	-5.556	< 0.001
Body length	0.344	0.039	8.715	< 0.001
Number of mates	0.392	0.037	10.713	< 0.001
Season 2*Body length	-0.223	0.093	-2.402	0.016
Season 2*Number of mates	0.484	0.082	5.910	< 0.001

Table 7. Modeling the influence of the female characteristics on juvenile body length, with the p-value of the added covariate (in bold). '+' additive effect; '*' interaction effect.

Model	Covariates	p-value	Residual deviance
M1	Season	< 0.001***	4911.9
M2	Season + Body length mum	0.1757	4773.6
M3	Season + Body length mum + Season*Body length mum	0.9514	4773.6
M4	Season + Tactic mum	0.2986	4910.8
M5	Season + Tactic mum + Tactic mum*Season	0.7109	4910.6

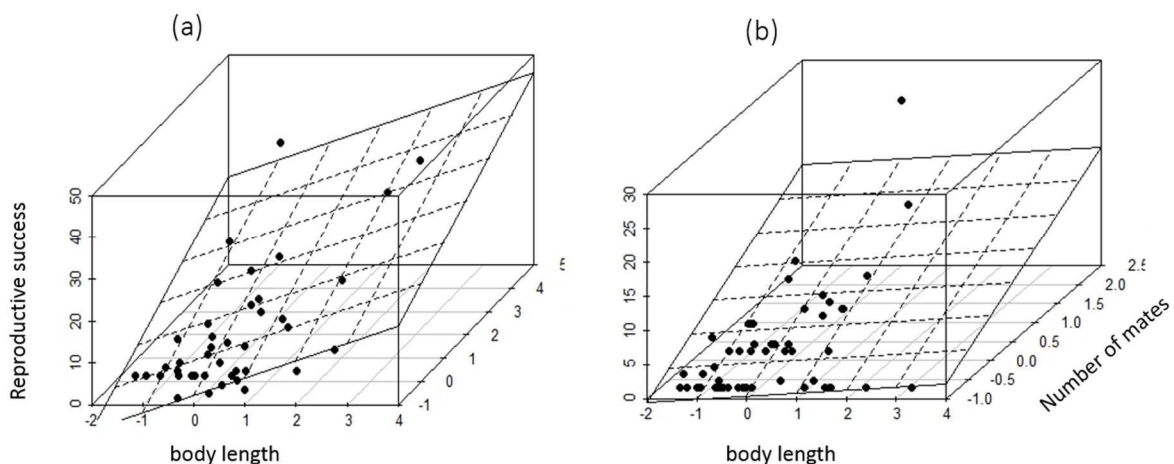


Figure 1. Variations in female reproductive success with the female body length and number of mates (standardized), (a) in the reproductive season 1 (2014-2015) and (b) in the reproductive season 2 (2015-2016).

Discussion

Quantifying the reproductive performances of resident and anadromous females is central to understand and predict the population dynamics of partially migratory population in a changing world. We detected no influence of the life history tactics on the juvenile body length but we showed a difference in female reproductive success between tactics. This difference was explained by a difference in body length between residents and anadromous, but the number of mates strongly influenced the reproductive success as well. The relative effects of these two drivers varied over reproductive seasons. Moreover, we highlighted that resident females contributed more to the juvenile production, suggesting the predominance of this tactic driving the population viability.

We showed that resident females have a lower individual reproductive success but that they contribute more than anadromous to the juvenile production at the population-level. Despite their size advantage, the low number of reproductive anadromous females on the spawning ground limits the number of juveniles produced by this tactic. In addition to a higher mortality in the marine environment, the number of anadromous females present on spawning grounds can be reduced by environmental factors like low water levels that alter freshwater migration. Even though a larger female body size may be favored because of its strong correlation with fecundity (Jonsson et al. 1996), our results raise the question as to why the migratory tactic would persist if migration advantages do not counterbalance the migration costs anymore? In the case of partial migration, the relative benefits of residency might have emerged recently, as a result of environmental change. This suggestion appears particularly plausible in salmonids, where many European populations have shown a reduction in the number of anadromous or in the time spent at sea during the last decades (Gargan et al. 2016).

Moreover, our results suggest that variations in proportion of anadromous and resident females on the spawning ground and thus to the relative cost/benefit ratio of each tactic correlate to changes in the relative influence of the body length and the number of mates on the reproductive success over environmental conditions. This result can potentially explain the variable effects attributed to these factors in previous studies (e.g. Jonsson and Jonsson 1999, Garant et al. 2001, Kinnison et al. 2001, Hendry and Day 2003, Acolas et al. 2008).

We highlighted that female body length explained the difference in reproductive success between anadromous and resident females. Our results suggested that at equal body length, anadromous and resident female have similar reproductive success. Nonetheless, we observed that the number of mates influenced the reproductive success of female trout as well. Both anadromous and resident females have to increase the number of males to mate with to maximize their reproductive success. Even if body length increases the fecundity (Fleming 1998), the genetic diversity within offspring induced by multiple mating appears decisive for the reproductive success (Tregenza and Wedell 2000, Blomqvist et al. 2002). By not being only dependent on body size, the reproductive success of females and the number of juveniles produced may be buffered against environmental changes. Indeed, the body size is highly related on the environment condition (i.e. the resource availability and quality) (e.g. Sheridan and Bickford 2011) whereas the number of mates may be less impacted by environmental variations.

However, our results showed that female tactic and body length did not influenced the juvenile body length, at 0+ stage. Consequently, neither the anadromous nor the resident tactic may confer an advantage to their offspring survival at this stage. This result contrasts with the hypothesis of Goodwin et al. (2016), which suggested that offspring of anadromous adults should be larger than offsprings of residents. This absence of relationship also contrasts with evidences of a trade-off between fecundity and eggs size (Lobón-Cerviá et al. 1997, Jonsson and Jonsson 1999, Olofsson and Mosegaard 1999, Acolas et al. 2008), where smaller females may produce larger eggs. Indeed, it is expected that larger eggs should result in larger juvenile with higher survival (Elliott 1990, Hutchings 1991, Ojanguren et al. 1996, Einum et al. 2002). A selection by the environment during the early life may buffer the potential variability in juvenile body length, which may mask a potential relationship between mother and offspring (0+ old) body length in October.

This two years study highlighted the necessity to consider the resident females as potentially the most important part of the population to ensure its long-term viability. In the future, estimating the reproductive success of anadromous and resident females over a larger range of conditions may allow a finer understanding of these variations in a changing world and an evaluation of their population dynamics and evolutionary implications.

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Authors' contribution

GE, LM and MN designed the study, LM contributed to the fieldwork, the genetic analyses, performed the analyses and drafted the manuscript. JT organized and carried out the fieldwork. ALB, TJ, and FLC contributed to the fieldwork and the genetic analyses. GE and MN contributed to the fieldwork and to the manuscript preparation. All authors gave final approval for publication and

Supporting material

Appendix 4. Water level during the reproductive season 1 (2014-2015) and 2 (2015-2016)

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3. Atlantic salmon

The exploratory work on Atlantic salmon was based on adult and juvenile samples collected during a single reproductive season (2014-2015) (Table 2). We randomly sampled 576 juveniles on the 962 juveniles 0+ old (i.e. 6 months old) captured in the La Roche brook. This sampling method induces an underestimation of the reproductive success defined as the number of juvenile sampled assigned to each adult. In females, we compared the reproductive success of single-sea-winter females (i.e. 'SSW'; 65 % of the mature females captured in December 2014, Table 2) to the Multi-Sea-Winter females (i.e. 'MSW'). In contrast, for males, we compared the resident (70.3% of the mature males captured in December 2014, Table 2) and the migrant SSW males (Table 6) as no MSW males were captured.

We assigned 71.7% of the juvenile sampled to at least one parent (Table 7). From this assignment, we observed that the sea-migratory tactic confers an advantage in male reproductive success as SSW males showed the highest mean individual reproductive success (Figure 21, resident males = 5.846, SD = 3.788; SSW males = 13.034, SD = 6.578). In addition to an advantage at the individual level, sea-migrant males highly contributed to the annual juvenile production. The SSW males (27.6 % of males captured and assigned) produced 50.7 % of the juvenile assigned to males captured (Table 7).

In females, the time spent at sea seems to increase the reproductive success and the MSW females appear crucial for the annual juvenile production. These females showed the highest mean individual reproductive success (Figure 21, SSW females = 10.125, SD = 8.509; MSW females = 32.5, SD = 11.504) and the highest contribution to the juvenile production (Table 7). The MSW females (33.3 % of females assigned) produced 61.6% of the juvenile assigned to females captured in La Roche brook.

Using General Linear Models (GLM, McCullagh 1984) we observed that the differences in body length between tactics explained the difference in reproductive success for both males and females (likelihood-ratio test, $p < 0.01$). However, the body length did not explain the variability in reproductive success within each tactic (likelihood-ratio test, $p > 0.05$), suggesting that other parameters may drive the reproductive success within each tactic. These results

show that thanks to their large body length the MSW females and SSW males contributed the most to the annual juvenile production, even if they are less abundant on the spawning ground. Thereby, our results provide another demonstration that body length confers a large fitness advantage for both males (female access) and females (fecundity, egg size, quality of the spawning site) (Jonsson 1985, Aas et al. 2011, Kendall et al. 2014). Noting the high contribution of the MSW, our findings suggest that these females might represent the most important part of the population to ensure its viability.

The difference in body length between tactics causes differences in reproductive success, but we did not observe that these differences linked to offspring body size. Using a General Linear Mixed model (GLMM, Mcculloch and Neuhaus 2013), no difference were found in body length and mass of offspring in relation to either their sex (likelihood-ratio test, $p > 0.08$; Figure 22.b) or the tactic or body length of their parents (likelihood-ratio test, $p > 0.05$, Figure 22.a). Moreover, each life history tactic seemed to produce a balanced sex-ratio in juvenile (52.4 % of males; GLM, likelihood-ratio test, $p > 0.05$).

Table 6. Characteristics of the samples of Atlantic salmon collected. SSW, *single-sea-winter*; MSW, *multi-sea-winter*.

Sample characteristics	2014-2015
Offspring	576
Adult female	20
Adult SSW female	13
Adult MSW female	7
Adult males	192
Adult Resident male	135
Adult SSW male	32

Table 7. Results from the genetic assignment on Atlantic salmon sampled. SSW, single-sea-winter; MSW, multi-sea-winter.

Genetic assignment results	2014-2015
Offspring assigned	412
Offspring assigned to females	211
to SSW females	81
to MSW females	130
Offspring assigned to males	343
to resident males	169
to sea-migrant males	174
Adult females assigned	12
SSW females	8
MSW females	4
Adult males assigned	76
Resident males	55
Sea-migrant males	21

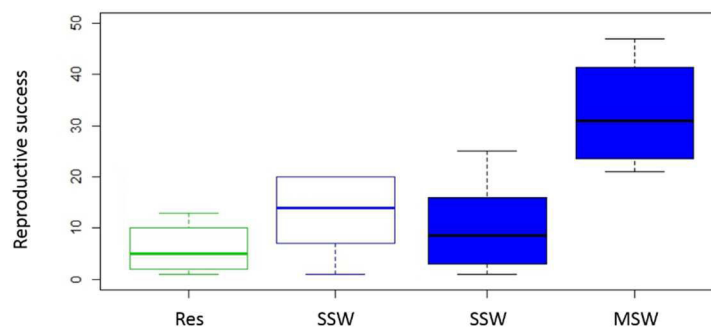


Figure 21. Reproductive success of Atlantic salmon females (full boxes) and males (empty boxes). With resident tactic in green, Res and sea-migrant tactic in blue: SSW, single-sea-winter; MSW, multi-sea-winter.

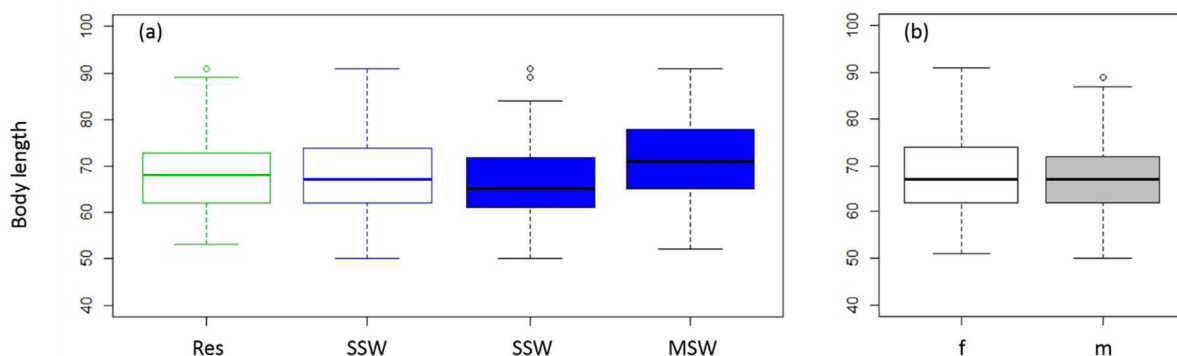


Figure 22. Body size of offspring (mm) vs (a) assigned to each mother (fill boxes) and father (open boxes) tactic. With resident tactic in green, Res and sea-migrant tactic in blue: SSW, single-sea-winter; MSW, multi-sea-winter; (b) their sex, with f, females; m, males

4. Conclusion of chapter 3

In this chapter, using genetic parentage analyses, we obtained robust estimations of the reproductive success for each life history tactic of Atlantic salmon and brown trout. Nevertheless, these estimations were underestimated as we did not sample all captured juveniles and the capture probability was lower than 1. In addition, the sample size of adult Atlantic salmon from La Roche brook (3 mature males and 3 mature females) in this second season was low. So, due to limited funding and time we decided to focus the genotyping of the second reproduction season on brown trout (where both males and females show partial migration) to focus on the influence of the diversity of life history tactics on the population dynamics.

As expected, the reproductive success of both males and females increases in anadromous forms in relation to a larger body length. However, we showed that not only body length matters to maximize the female reproductive success. Our analyses on brown trout identified that the number of mates also increases the reproductive success probably by increasing offspring genetic diversity. A similar relationship has been observed in Atlantic salmon (Garant et al. 2001). Thereby, even if sea-migration increases body size, hence promoting a high egg production, both anadromous and resident females may benefit from multiple mating through a greater viability of their eggs. However, in both Atlantic salmon and brown trout, we showed that the tactics do not confer specific characteristics (i.e. growth or sex ratio) to their offspring.

The life history tactic that produced the largest number of offspring during a reproductive season differs between Atlantic salmon and brown trout. In salmon where females are all anadromous (and are thus all impacted by a high mortality risk at sea), MSW females contributed the most to the juvenile production. In contrast, brown trout females can be either resident or migrant (with different mortality risks), and our results revealed that the resident tactic contributed the most to juvenile production, especially when environmental conditions restricted the access to the spawning ground for anadromous individuals. Even though we did not estimate the reproductive success of Atlantic salmon in the second reproductive season, fieldwork records indicated almost two times lower number of juveniles

produced that year than in the first season (516 salmon 0+ captured in October 2016, against 962 in 2015; whereas the number of juvenile trout decreased by a quarter between 2015 and 2016). Consequently, the limited access to the spawning ground had probably a stronger impact on the reproduction and population dynamics of Atlantic salmon than brown trout.

Major findings 3.

- The migratory tactic confers a higher reproductive success than the resident tactic due to a larger body size. However, for both resident and migratory females, the number of mates increases the reproductive success.
 - The female resident tactic contributed the most to the juvenile production in brown trout, whereas in Atlantic salmon it was the MSW tactic.
 - The juvenile production in our study site appears be less affected by environmental change in brown trout than in Atlantic salmon.
-

CHAPTER

4.

Influence of the life history tactics on the population dynamics



1. Objectives and organization of the chapter

This chapter is the final point of my investigation, with the ultimate goal of understanding the influence of the tactics diversity on partially migratory population dynamics and their resilience to environmental changes. The previous chapters showed that variations in life history traits and fitness components are tactic-specific, and the 'decision' to migrate of individuals within each life history tactic may be a plastic response to environmental changes. Nevertheless, do these responses increase or decrease the population size through time? And how large are going to be these changes in population size?

To answer these questions we have to scale up the individual information to the population level to know how individual-level variations translate into the population dynamics. **Consequently, the objective of this chapter is to identify the influence of the demographic parameters in migratory and resident tactics on the population dynamics.**

To achieve this goal, I collaborated with Arpat Ozgul (POPECOL team) from the University of Zurich through an internship of three months where I learnt and developed population models. Using robust estimations of brown trout female demographic parameters, we built and parameterized population models to investigate the following questions:

- Which life history tactic and demographic parameter matter the most for the population viability?
- Can the tactics diversity improve the resilience of partially migratory population to environmental change?

To address these questions we divided the life history into discrete stages (young, i.e. juvenile O+ old; resident, i.e. freshwater-trout; and migrant, i.e. sea-trout) to build a stage-structured matrix population model ('MPM'). An MPM allows the estimation of the long-term population growth rate (λ) and other population parameters from individual-level information (Caswell 2001). By using a MPM in section 2 (Article IV), we investigated the sensitivity of the population growth rate to demographic parameters within each life history tactic. We also assessed the contribution of demographic parameters to an observed change in population growth rate over the study period (i.e. perturbation analysis).

Perturbations analyses on MPM give a description of the direct effect of changes in demographic parameters on the population dynamics. Nevertheless, we showed that brown trout length influences the juvenile survival, migration probability, and reproductive success (Chapters 1 and 3). Moreover, given the continuous somatic growth, the particular growth of an individual in one year can have carry-over effects many years later (Gimenez 2006). Thereby, a change in size–demography relationships can alter demographic rates, which in turn can influence population dynamics indirectly (Ozgul et al. 2010). To synthesize all these complex information and separate the contribution of body size vs other factors in the modification of the life history traits and population growth, we built a length-structured Integral Projection Model ('IPM') (Easterling et al. 2000, Ellner and Rees 2006) based on our MPM. This final work is presented as a draft IPM in section 3, where we describe the current structure of the model, the preliminary results, and the future development needed.

2. Article IV

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Diversity in life history tactics promotes population viability in a partially migratory fish

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Abstract

In the context of global change, populations with partial migration where both resident and migratory tactics coexist, appear more resilient than solely migratory or resident populations. The intraspecific diversity in migratory tactics could be the key element driving this pattern. Using a long-term individual monitoring system and a stage-structured matrix population model for females, we quantified the influence of resident and migratory tactics on the population growth rate in a brown trout (*Salmo trutta*) population (Oir river, France). In addition, we took advantage of a riverbank restoration in the middle of the study period leading to an increase in population density to quantify the contribution of resident and migratory tactics to change in population growth rate between the two periods. The population growth rate was the most sensitive to variations in resident adult survival. However, increase in migrant adult survival was the main contributor to the observed increase in population growth rate in period 2. Using simulations, we found that a balanced (~50-50%) proportion of residents and migrants would maximize population growth rate under the scenario of positive changes in migrants' vital rates (e.g. increase in survival and reproductive success). Our results support the hypothesis that partially migratory populations are better able to buffer the impact of environmental changes than solely resident or migratory populations.

Key words: Partial migration, vital rates, salmonid.

Introduction

In the context of global climate change and habitat loss, a wide range of migratory vertebrates and invertebrates have shown population declines in recent decades (Wilcove and Wikelski 2008). However, Gilroy et al. (2016) showed that the decline in partially migratory populations, where both resident and migratory tactics coexist (Chapman et al. 2011), was less pronounced than in solely resident or migratory populations. Through a correlative analysis between tactic diversity and population growth rate, these authors suggested that partially migratory populations might be more resilient to environmental change. This suggestion is concordant with recent studies showing that populations with a complex structure (i.e. heterogeneity in behaviour and life-history traits) are more resilient towards environmental change than less complex ones (Carlson et al. 2011, González-Suárez and Revilla 2013). Consequently, the intraspecific diversity of migratory tactics may buffer environmental change and allow partially migratory populations to be more resilient than solely resident or migratory populations but the evidence for this hypothesis is strongly limited (Carlson et al. 2011, Chapman et al. 2011, González-Suárez and Revilla 2013).

The population growth rate, λ , is an approximation of the viability of a natural population (Fisher 1930) and depends on underlying vital rates (e.g. stage-specific survival and fecundity, Tuljapurkar 1992) and environmental and demographic stochasticity affecting these vital rates (e.g., Sæther 1997, Grant and Benton 2000). λ is not equally sensitive to each of the underlying vital rates, this sensitivity pattern being dependent on the life-history strategy of the focal population (Sæther et al. 1996, Sæther and Bakke 2000). Thus, a decrease in these most influential vital rates would cause a larger decline in the population growth rate than a similar decrease in other vital rates. In a stochastic environment, the most influential vital rates are often the least variable as they are evolutionary buffered against environmental fluctuations (Pfister 1998, Gaillard and Yoccoz 2003).

In the case of partially migratory populations, migrant and resident individuals do not share the same environment during a part of their life cycle, when the migrant individuals relocate to an unshared site (Chapman et al. 2011). Differences in local environmental factors could drive differences in vital rates, between the two types/tactics. Thus, each tactic may

contribute in a different and variable way to λ (Chapman et al. 2011). As a result, partially migratory populations would take advantage of positive environmental changes in the unshared environment compared to solely resident populations. They would also be able to better buffer negative environmental changes in the shared and unshared environments, than solely resident and solely migratory populations, respectively.

Salmonids include solely resident, solely migratory, and partially migratory species. Brown trout (*Salmo trutta*) is a typical example of a partially migratory fish. In this iteroparous species adults reproduce in freshwater, and juveniles spend months to years in their natal river. Then, some individuals migrate to the sea (migratory tactic, also called anadromous tactic) whereas others stay all their life in freshwater (resident tactic) (Cucherousset et al. 2005). Migrant fish take advantage of the highly productive marine habitat to achieve a higher body growth than resident fish, which results in larger fecundity in the former (Kendall et al. 2014). This advantage is counter-balanced by a high mortality risk in migrant fish due to physiological changes upon entry to the sea and predation in the marine environment (Dieperink et al. 2001, 2002). In addition, migrant fish are subject to higher exploitation rates by fisheries than resident fish (Gargan et al. 2006, Harris and Milner 2008). These different costs and benefits for growth, fecundity, and survival may confer a similar fitness to resident and migratory tactics and explain the persistence of partial migration in this species (Lande et al. 2003).

Migrant trout are often considered as the most important component of a population to ensure population viability (e.g. NMFS 2005, Harris and Milner 2008). This assumption relies on the larger egg production of migrant females (i.e. fecundity), which depends directly on body size. However, a quantitative description of population growth rate is generally lacking in partially migratory fish populations due to the difficulty of accurately estimating vital rates for each tactic in such populations. Caswell et al. (1984) explored the contribution of reproduction at different stages of the life cycle in Atlantic salmon (*Salmo salar*) to population dynamics but this study focused on males only. In salmonids, the relative contribution of vital rates associated with the resident and migratory female tactics to λ remains unknown.

Here, we quantified the role of intraspecific diversity in female migratory tactics on population growth rate using a unique long-term (1997-2015) individual-based demographic monitoring

of a brown trout population in France. In our study system, riverbank restoration took place in 2009, increasing habitat quality thereafter. This management action positively correlates with a change in the density of young-of-the-year trout (hereafter, young) (Fig. 1). We identified the vital rates that influenced λ the most before and after river restoration and the rate that contributed the most to the observed change in λ between these two periods. We then used simulations to investigate the proportion of migratory and resident types that would maximize λ .

Methods

Study species and site

We studied a brown trout population breeding in a 2.2 km section of La Roche brook, a second order tributary of Oir river (Normandy, France, 48°38'N, 3°37'W (Cucherousset et al. 2005)). La Roche brook is a breeding and a nursery habitat for brown trout (Cucherousset et al. 2005). Both migrant and resident trout reproduce from December to January and show no genetic differentiation (Charles et al. 2005). Fry emerge in March, and a fraction of the young may leave the brook and migrate to sea in early spring (0+ old), while the other fraction remains in freshwater (i.e. resident trout) (Cucherousset et al. 2005). Some of the trout that remained in freshwater can also migrate to sea at 1+ old in spring.

In 2009, local managers implemented a riverbank restoration program in La Roche brook with the aim to improve ecological processes (e.g., filtration, soil stabilization), water quality and then salmonid fish production. The restoration plan consisted of excluding livestock by constructing fences along the entire brook. As a result, we observed an increase in tree abundance and diversity, a decrease in bare soil, but no change in water quality (Muller et al. 2016). The density of young trout increased in the meantime (Fig. 1). To account for this structural change in our study site, we defined two periods: a low-density period before riverbank restoration from 1997 to 2008 (period 1, Fig. 1) and a high-density period after riverbank restoration from 2009 to 2015 (period 2, Fig. 1).

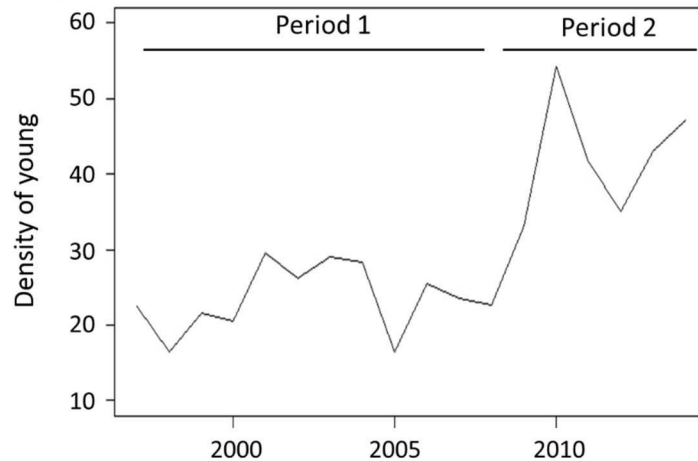


Figure 1. Temporal variation in density of young-trout-of-the-year (individuals per m²) in La Roche brook and periods used in the analyses; period 1: 1997-2008; period 2: 2009-2015.

From 1997 to 2015, three joint standardized protocols were used to individually monitor brown trout ($n=8497$) in La Roche brook and Oir river: electrofishing, trapping and autonomous data recording antenna systems (Cucherousset et al. 2005). Each year, in October most young-trout-of-the-year (ranging in body length from 25 to 150 mm, mean= 77.86 mm) were captured by electrofishing and marked with a unique ID (12 mm long passive integrated transponder, Biomark Prentice et al. 1990) in La Roche brook. Individual age was assessed based on body length and scale-reading method (Baglinière et al. 1985). The recapture of marked individuals may occur: (i) during the reproductive period (December) and after the downstream migration (May) in La Roche brook and in Oir river during dedicated electrofishing surveys; (ii) all year round at a fish trap down Oir river; and (iii) all year round down La Roche brook and along the Oir river through autonomous PIT tag reading antennas (more details about the study site in (Cucherousset et al. 2005). On each recapture occasions, the sex of mature trout was identified based on morphological features. The migratory state of trout, i.e. non-anadromous or anadromous fish, was assessed using both growth patterns on scales and morphological features as color and size at age (Baglinière et al. 2001).

Matrix model structure

We constructed a stage-structured matrix model based on a simplified life cycle of female brown trout structured by age and migratory stage: one young stage y and two stages in

adults: resident r and migrant m (Fig. 2) to model population dynamics. We ran the model separately for period 1 and period 2. The projection matrix was:

$$\begin{bmatrix} Ny \\ Nr \\ Nm \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & Sr(1 - Mr)\left(\frac{Rr}{2}\right) + Sr Mr \left(\frac{Rm}{2}\right) & Sm \left(\frac{Rm}{2}\right) \\ Sy(1 - My)\sqrt{Sr} & Sr(1 - Mr) & 0 \\ Sy My \sqrt{Sm} & Sr Mr & Sm \end{bmatrix} \begin{bmatrix} Ny \\ Nr \\ Nm \end{bmatrix}_t$$

where S_y , S_r , and S_m are the survival probabilities in young, resident and migrant adult stages, respectively; M_y and M_r are the migration probabilities (i.e. probability to become a migrant) at 0+ old (young stage, called hereafter ‘young migration’) and at 1+ old (included in the resident stage and roughly called hereafter ‘resident migration’); R_r and R_m are the female reproductive success in resident and migrant stages. All vital rates are annual rates. We incorporated the square root of annual migrant and resident adult survival to account for the change in survival linked to the migratory tactic during the first year. In addition, we assumed an even sex ratio at the young stage and considered only half of the reproductive success, as we worked only on females. Our model also did not consider inheritance in the tactic determination.

We used this model to estimate the asymptotic population growth rate, λ , for each period. The estimation of λ and the perturbation analyses were performed using the software R (R Core Team 2015) and the *popbio* package (Stubben et al. 2007). Assuming a constant marking effort on young, the proportion of potential immigrant females (i.e. proportion of unmarked trout among the reproductive females captured by electrofishing during the spawning period in La Roche brook) was estimated to be constant between the two periods (1997-2008: 0.49, $n = 102$; and 2009-2015: 0.49, $n = 176$; Student’s test: $P = 0.1$). Consequently, we did not consider immigration in our model and assumed that it did not substantially contribute to the observed increase in λ .

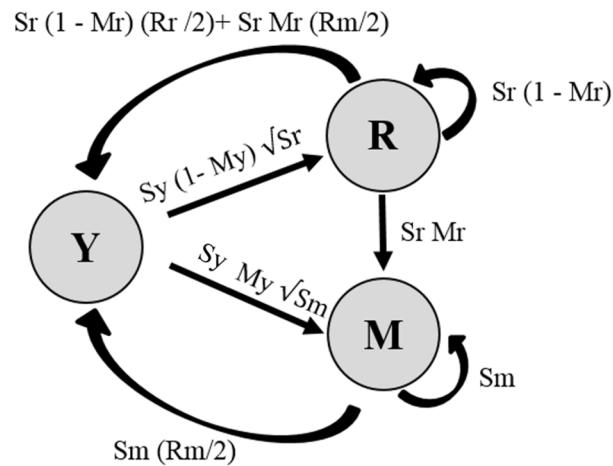


Figure 2. Life cycle of females brown trout. young Y, resident, R and migrant, M stages. The transitions between stages are represented in arrows. The “equations” on top of each arrow correspond to the probabilities of being in each state at $t+1$. S_y represents the young survival; S_r and S_m represent the resident and migrant adult survival; M_y represents the young (0+) migration probability; M_r represents the resident (at age 1+) migration probability; R_r and R_m represent the resident and migrant reproductive success.

Demographic parameter estimates

We built a sex-dependent multi-events capture-recapture model (CR model) (Lebreton et al. 2009) to estimate the survival and migration probabilities of female trout marked in La Roche brook within the Oir River system (CR matrix data available on request). These vital rates were later integrated into the matrix population model (see above). The CR model was structured by sex (males and females), age (two age classes: young and adult) and migratory state (two states in adults: resident r and migrant m) with an annual time step (from October to October) (details in appendix 1). In order to get mean survival and migration parameters for period 1 and period 2, we added a period effect to the CR model. Because of contrasted density levels in periods 1 and 2, differences in mean estimates may result from density-dependence mechanisms. Density-dependence, which has been reported to negatively affect vital rates in young salmonids (Vøllestad et al. 2002, Jenkins et al. 1999, Einum et al 2006), is thus accounted for in our parameter estimates.

In our study, the state of an individual was not always known with certainty on each occasion due to imperfect detection and partial observation with antennas. Multi-event modeling allowed us to deal with this state uncertainty by including in the CR model structure both a detection parameter (p , probability to detect an individual in a given state) and an

identifiability parameter (I) defined as the probability of an individual being in a specific state given its imperfect observation in the field (Pradel 2005). Based on field records, we considered 22 events to account for the diversity of observation protocols (details in Appendix 1).

There is currently no goodness-of-fit test applicable to multi-event models (Kendall 2009). Following Pradel, we used the Jolly Move (JMV) umbrella model with observable states (Pradel 2005) to assess the fit of the CR model to the data with the software U-Care v2.3.2 (Choquet et al. 2009b). In the JMV umbrella model, each parameter is modeled as a function of states (f). Then, we set up each parameter of the CR model to be dependent on the states and periods and we ran the model with the program E-Surge v1.7.1 (Choquet et al. 2009a).

The reproductive success of adult females was defined as the number of 0+ young trout produced per female. We estimated the reproductive success using genetic parentage analyses from parents and offspring fin clips. We sampled adult migrant ($n= 19$) and resident ($n= 261$) trout during four electrofishing surveys in La Roche brook in December 2014 and January 2015. We also collected scales on sampled fish to identify their migratory tactic (resident/migrant). We assessed the sex of adult trout through morphological features and the presence of sperm or eggs ($n= 112$ resident females and 14 migrant females). In October 2015, we collected fin clips in the young-trout-of-the-year (0+ old; $n =555$ young) from La Roche Brook. We used scale samples to check the age of each young and excluded individuals from previous cohorts. All fin samples were stored in 95% ethanol and individuals were genotyped with 15 microsatellite loci following the procedure described in Quéméré et al. (2016). Using the software COLONY (Wang and Santure 2009), we assigned 91.5 % of young ($n = 508$) to at least one parent captured in La Roche brook. The number of young assigned per female (number of females with at least one offspring assigned = 43), with at least an 80 % confidence level (Jones and Wang 2010), was considered as the female reproductive success in 2014. We corrected these estimates by the detection probability of young assessed during the electrofishing monitoring (i.e. catch rate = 0.84). Then, we identified the relationship between the reproductive success and the female body size for each tactic. With these relationships and based on the individual female body size data collected as part of the long-term monitoring program in La Roche brook, we estimated the mean reproductive success of migrant and resident trout for periods 1 and 2.

Prospective analysis

To identify the vital rates that influenced λ the most, we used an elasticity analysis (i.e. proportional sensitivity) that determines how λ would change in response to proportional changes in each vital rate in the two periods (Caswell 2001). We estimated the elasticity of λ to changes in lower-level parameters underlying each matrix element, i.e. vital rates (Caswell 2001). We calculated this lower-level elasticity as:

$$\frac{x}{\lambda} \frac{\partial \lambda}{\partial x} = \frac{x}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}$$

Where a_{ij} is the matrix element in row i and column j , and x is a lower-level vital rate (Caswell, 2001).

Retrospective analysis

We used a fixed-design life-table response experiment (LTRE) to determine the contribution of each vital rate to the observed change in λ between period 1 and period 2 (Caswell 2010). Each contribution was estimated as the product of the change in the vital rate between the two periods and the sensitivity of λ to that vital rate, using period 1 as the reference matrix. If a vital rate was constant, its contribution to the observed change in λ was zero. If a vital rate did change but λ was weakly sensitive to this rate, its contribution to the observed change in λ was small. We decomposed the observed difference in λ ($\Delta\lambda$) between the two periods into contributions from each vital rate (x_i) as:

$$\Delta\lambda = \lambda^{(t2)} - \lambda^{(t1)} \approx \sum_i (x_i^{(t2)} - x_i^{(t1)}) \frac{\partial \lambda}{\partial x_i^{t1}}$$

where $t1$ and $t2$ correspond to matrices for the periods 1 and 2, respectively.

We accounted for parameter uncertainty in our demographic analyses *via* a parametric bootstrap sampling method (Efron and Tibshirani 1994). We randomly sampled with replacement vital rate values from the distribution defined by the parameter estimation. The resulting distributions of vital rates, λ , lower-level elasticities, and LTRE contributions were generated using 10 000 bootstraps.

Simulation analysis

We expected the influence of resident and migrant individuals on λ to vary over time as a function of the relative costs and benefits of each tactic. Changes in the unshared environment are likely to affect the difference of costs and benefits between resident and migrant individuals. Using a simulation analysis, we investigated how a change in the marine environment would affect the diversity of life history tactics, i.e. the proportion of resident in the population. For instance, an increase in the sea-temperature and food availability may improve the growth of migrant trout leading to larger body size, and promote a higher survival and fecundity (Jonsson et al. 2016).

We simulated that kind of 'positive' change in the unshared environment through an increase in migrant survival and reproductive success, everything else being equal. We ran the matrix model for a large range of biologically realistic survival and reproductive success values. We assumed that migrant survival could not exceed resident survival and resident reproductive success could not outperform migrant one (i.e. survival: 0 to 0.418; reproductive success: 0 to 8.224). We used the values from period 1 as a reference for young survival, resident adult survival and reproductive success. For each scenario, we estimated the asymptotic λ and the percentage of resident individuals in the adult population generated by the model from the stable stage distributions.

Results

Demographic parameter estimates

Goodness of fit tests ($\chi^2 = 2.047$, $df = 19$, $P = 1.0$) indicated that the JMV model fitted the data correctly (Deviance = 18592.496; QAICc = 18670.841). The period-dependent model (Deviance = 18451.545; QAICc = 18596.712) and the genetic parentage analysis provided vital rates that differed between the two periods (Table 1). The young and migrant adult survival as well as migrant reproductive success increased between period 1 and period 2. In addition, the young migration probability highly increased between the two periods whereas the resident migration probability decreased. In resident trout, the survival and reproductive success showed no significant change.

Table 1. The female vital rates used in the matrix model population for each period. The reproductive success is the number of young (0+ old) produced by an adult trout.

Vital rate	Period 1		Period 2	
	Estimate	Standard error	Estimate	Standard error
Young survival	0.099	0.018	0.299	0.130
Resident adult survival	0.418	0.053	0.495	0.180
Migrant adult survival	0.122	0.044	0.333	0.082
Young migration	0.0678	0.041	0.979	0.016
Resident migration	0.489	0.073	0.149	0.283
Resident reproductive success	8.224	0.366	8.353	0.434
Migrant reproductive success	16.995	3.282	19.889	2.326

Prospective analysis

The prospective analysis estimated $\lambda = 0.557$ (SE = 0.067) for period 1, which was significantly lower than λ in period 2 ($\lambda = 0.878$, SE = 0.216; student test $P < 0.001$). Not accounting for immigration in our model resulted in these unrealistically low λ , in a population characterized by a stable density of young (i.e. constant recruitment) within each period. The elasticity analysis (Fig. 3) indicated that λ would greatly change in response to a change in resident survival in both periods, whereas the elasticity of λ to the migrant survival was low. However, this elasticity to migrant survival increased in period 2. In addition, the elasticities of λ to reproductive success in resident and migrant were high (but lower than the elasticities to resident survival) and almost similar between tactics. λ would not change in response to a change in survival or in migration probabilities of young in both periods. Moreover, the elasticity of λ to the resident migration probability was low.

Retrospective analysis

The LTRE analysis indicated that the increase in migrant survival was the only vital rate that contributed significantly to the estimated increase in λ (Fig. 4). The increase in resident survival and migrant reproductive success tended to also contribute to the change in λ , but these trends were not significant as well as the negative contribution of the resident migration.

Simulations

Simulations predicted that λ would increase in response to an improvement in the unshared marine environment, due to a combined increase in migrant survival and reproductive success (Fig. 5.a). The environmental scenario that would provide the highest λ would generate a proportion of resident adults close to 55% (Fig. 5.a,b) in our population at equilibrium.

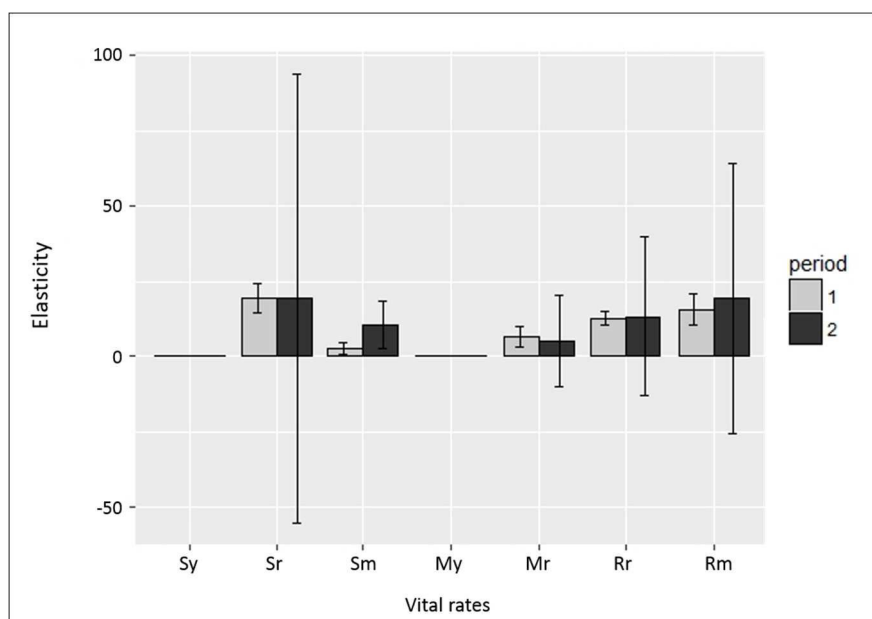


Figure 3. Elasticity of population growth rate to changes in brown trout vital rates in period 1 (white boxes) and period 2 (grey boxes) (lines representing the standard errors). Sy: young survival; Sr: resident survival, Sm: migrant survival; My: young migration probability; Mr: resident migration probability; Rr: resident reproductive success, Rm: migrant reproductive success.

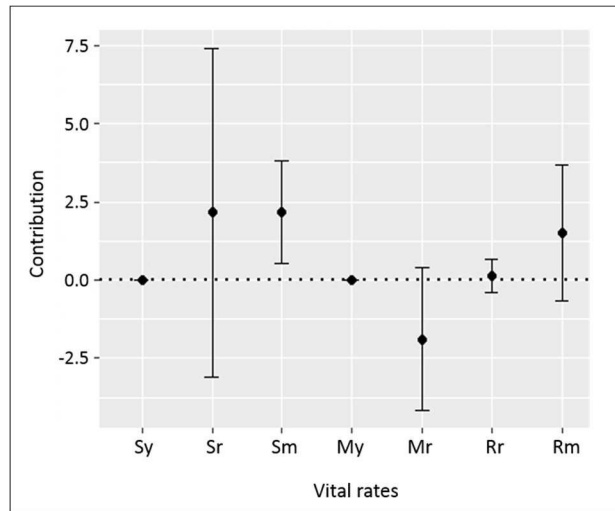


Figure 4. Contributions of these changes to the estimated change in population growth rate (lines representing the standard errors). Sy: young survival; Sr: resident adult survival, Sm: migrant adult survival; My: young migration probability; and Mr: resident migration probability; Rr: resident reproductive success; Rm: migrant reproductive success.

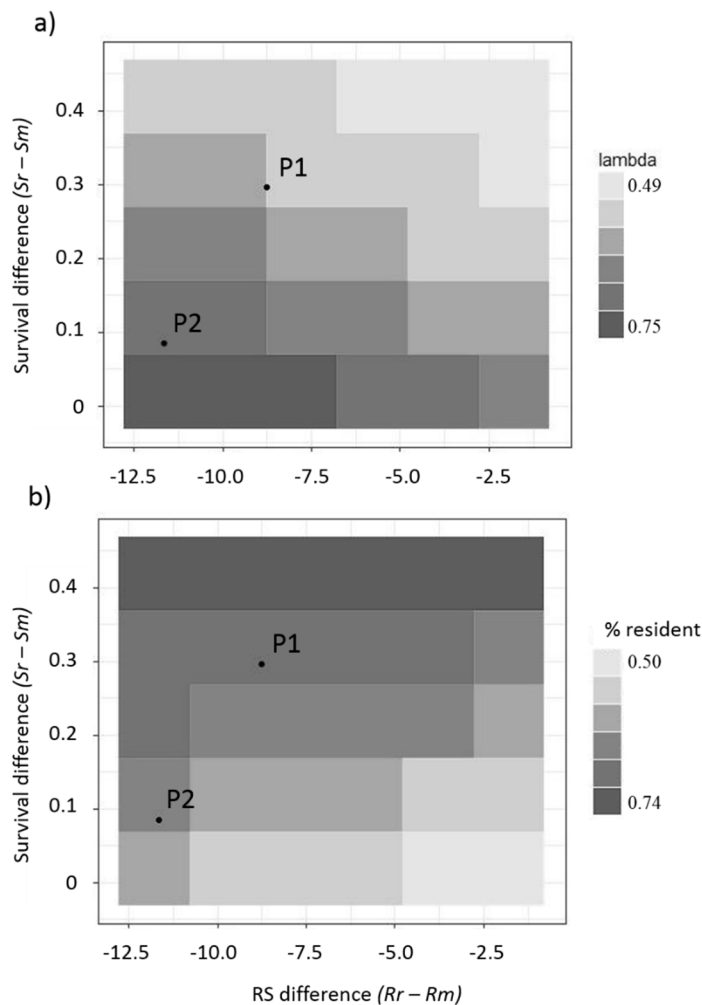


Figure 5. Population growth rate λ (a) and proportion of resident trout in the adult population (b), estimated from simulations of varying rates of migrant survival and reproductive success.

Discussion

The role of the migratory and resident tactics on brown trout population growth rate λ was uneven and varied over years. On average, λ was the most sensitive to resident female survival, but an increase in migrant female survival was behind the observed increase in λ from period 1 to period 2. Using simulations we observed that high survival and reproductive success in migrant trout would maximize λ and generate a balanced proportion of resident and migrant individuals in our study population.

Perturbation analyses showed that adult survival was the vital rate that drove the dynamics of this trout population. Similar results were found in iteroparous species with low fecundity but high survival (called 'long-lived species') (Gaillard et al. 2000, Caswell 2001, Eberhardt 2002). However, the elasticity of λ to reproductive success was also high, which suggests that salmonids are located in the middle of a continuum between long-lived and short-lived species (i.e. "slow-fast continuum") (Sæther and Bakke 2000). This may also illustrate the existing dependence between survival and reproduction, which are both highly correlated to body size in such a species with a continuous growth over its lifetime (Jonsson 1985).

When comparing migrant and resident tactics, the prospective analysis showed that a given proportional change in resident adult survival would have a higher effect on population viability than a similar change in migrant survival or migration probability. This means that the dynamics of migrant trout is highly dependent on resident trout. Although independent management of resident and migrant trout is the rule, these results highlight that integrated management actions would be more efficient to preserve population growth. In particular, the management of sea trout (i.e. migrant) fisheries in Europe may benefit from conservation actions of resident adult trout to ensure population and stock viability.

We relied on a change in the environment shared by both resident and migrant young trout, in the form of riverbank restoration, to define two periods within the study. A concomitant increase in young survival and density suggests that freshwater conditions improved following this restoration action. We also reported an increase in young migration between the two periods, which may result from competition exclusion in period 2 (Nelson 1995, Herrando-

Pérez et al. 2012) in accordance with studies showing strong density-dependence during the juvenile stage in salmonids (Einum et al. 2006). However, this change in young survival and migration did not contribute to the observed increase in population growth rate due to the low elasticity of λ to migration probability. Moreover, we detected no effect of riverbank restoration on resident survival that is the most influential vital rate on λ . Consequently, an improvement in the shared-environment by riverbank restoration actions appeared inefficient at the population level.

Actually, the observed increase in population growth was driven by an increase in migrant survival between the two periods. This contribution corresponded to the combined increase in i) mean migrant survival, and ii) the elasticity of λ to migrant survival (Stearns 1992, Pfister 1998, Gaillard and Yoccoz 2003). This result proves that the sensitivity of λ to vital rates is context-dependent, and we suspect that a change in the marine environment was responsible for this pattern. The number of migrant among adults appeared independent of the number of young trout migrating at sea, as illustrated by the low sensitivity of λ to migration probability. Instead, the number of migrant in the adult population seems regulated by migrant survival at sea. As a result, an improvement in marine conditions may be beneficial to the migratory tactic and increase the percentage of migrant trout in the population. Therefore, even if a change in the shared environment increased the number of migrating young, it was probably the conditions in the unshared environment, which mainly determined the structure of this brown trout population. The relative costs and benefits of resident and migrant tactics may have changed, leading to a reduction in fitness difference between resident and migrant individuals in period 2. Consequently, it seems crucial to develop adaptive population management approaches accounting for short-term (transient) dynamics to get efficient conservation plans in this species.

Simulation analyses confirm that an improvement in the unshared environment, which would minimise the difference in survival and maximise the difference in reproductive success between resident and migrant trout, would support the highest λ . Interestingly, our model returns a balanced proportion (~50%) of resident and migrant females in the population under this scenario. Accordingly, mortality risk is expected to be less variable in resident than in migrant females, which face higher exposure to predation, costs of metabolic changes, and

spatially heterogeneous threats (Hebblewhite and Merrill 2011, Vickery et al. 2014). Therefore, the resident tactic appears as a safe option but nonetheless unable to exploit highly favourable environments. In contrast, migrant individuals face higher mortality risks but they can exploit better feeding opportunities linked to a high growth potential when conditions are favourable in the unshared environment. This conclusion supports the hypothesis that populations with a complex structure should be more resilient towards environmental changes than populations with a single life history tactic (Carlson et al. 2011, González-Suárez and Revilla 2013).

Our study quantified the demographic influence of both main life-history tactics in a partially migratory population. Our results support the hypothesis that intraspecific tactic diversity confers an advantage to partially migratory populations compared to solely resident or solely migratory populations in a changing environment. In addition, we showed that the sensitivity of the population growth rate to vital rates is context-dependent. Consequently, conservation efforts in partial migration populations are more likely to succeed when considering the diversity in tactics and an adaptive management approach accounting for transient dynamics in a changing world (Ryman et al. 1995).

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AUTHORS' CONTRIBUTIONS

LM performed the analyses and drafted the manuscript. AO contributed to the model construction and data analyses. GE, LM and MN designed the study and AO, GE and MN contributed to manuscript preparation. All authors gave final approval for publication and

Supporting material

Appendix 5. Parametrization of the multi-event CR model

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3. Integral projection model – the influence of body size

3.1. Why a length-structured IPM?

The development of a length-structured IPM makes sense as numerous studies reported reductions in body size of many organisms (including salmonids), mainly due to changes in temperature and food quality associated with anthropogenic effects (Sheridan and Bickford 2011). Body size reduction has been reported for endotherms and ectotherms, terrestrial or aquatic species on several continents (e.g. Daufresne et al. 2009, Gardner et al. 2011, Sheridan and Bickford 2011). This phenomenon is considered as the third universal response to global warming (Daufresne et al 2009; Gardner et al 2011) (the others being changes in the phenology and distribution of species). A change in body size may have major implications for salmonids resilience to environmental change as it influences life history characteristics such as age at maturity, fecundity, egg size and survival. Thus, it seems crucial to quantify the influence of body size through the different life stages and the phenotype-demography relationships on the population growth rate. However, only few studies have applied IPMs to salmonid populations (the only references that we found were on Brook trout, Bassar et al. 2016, Carim et al. 2017) and they did not focus on partial migration issues.

Thereby, we adapted our female-based post-breeding census MPM (Article IV) into a length-structured, and density-independent integral projection model (IPM) (Ellner and Rees 2006; Easterlings et al. 2000). This IPM projects the distribution of a continuous body length based on demographic and trait transition functions, which allowed heterogeneity within a life-history stage (Ellner & Rees 2006). Thanks to this approach, we could use perturbation analyses developed for MPM.

3.2. Model structure

The mesh of the IPM matrix

First, we defined the IPM matrix based on the previous MPM (stages: young, i.e. 0+ old; resident; migrant, i.e. sea-trout); see life cycle in Article IV), with a body size mesh that represents the continuous scales of the body length. We set the upper and lower size limits

and defined the mesh points and size. Currently, the size range is 0.001 to 0.500 (m), with a mesh size of 50 (i.e. number of size segments), so with delta size of the mesh of 0.01 (m) (i.e. the size of a segment).

The demographic functions

We fitted the demographic functions relating body length to each demographic parameters and the growth functions to parameterize the IPM (Figure 23). Due to the importance of body size in each life stage in salmonids, we decided to define the demographic parameters of the juvenile, resident and migrant stages as a function of body length. The only parameter that was not defined as a function of body length was the young (0+ old) body length. Indeed, we did not include a relationship between mothers and young body length as we found no correlation in chapter 3 (Article III).

We characterized the migrant and resident growth by two different functions as growth depends on the unshared environment (different food quality and quantities available to migrant and resident). In contrast, we defined a unique reproductive success function for migrant and resident, because migrant and resident trout have equal reproductive success for a given body length (cf. Chapter 3, Article III). The parameterization of these functions were based on the data from Oir River system (from 1997 to 2015). We used estimates from chapter 3, and the female CR model used in the article IV using body length as a temporal covariate (mean young body length and mean adult body length) (Figure 23). We worked with log body length as advice by Rees et al. (2014); The reasons of this log-transformed size are given in appendix 6.

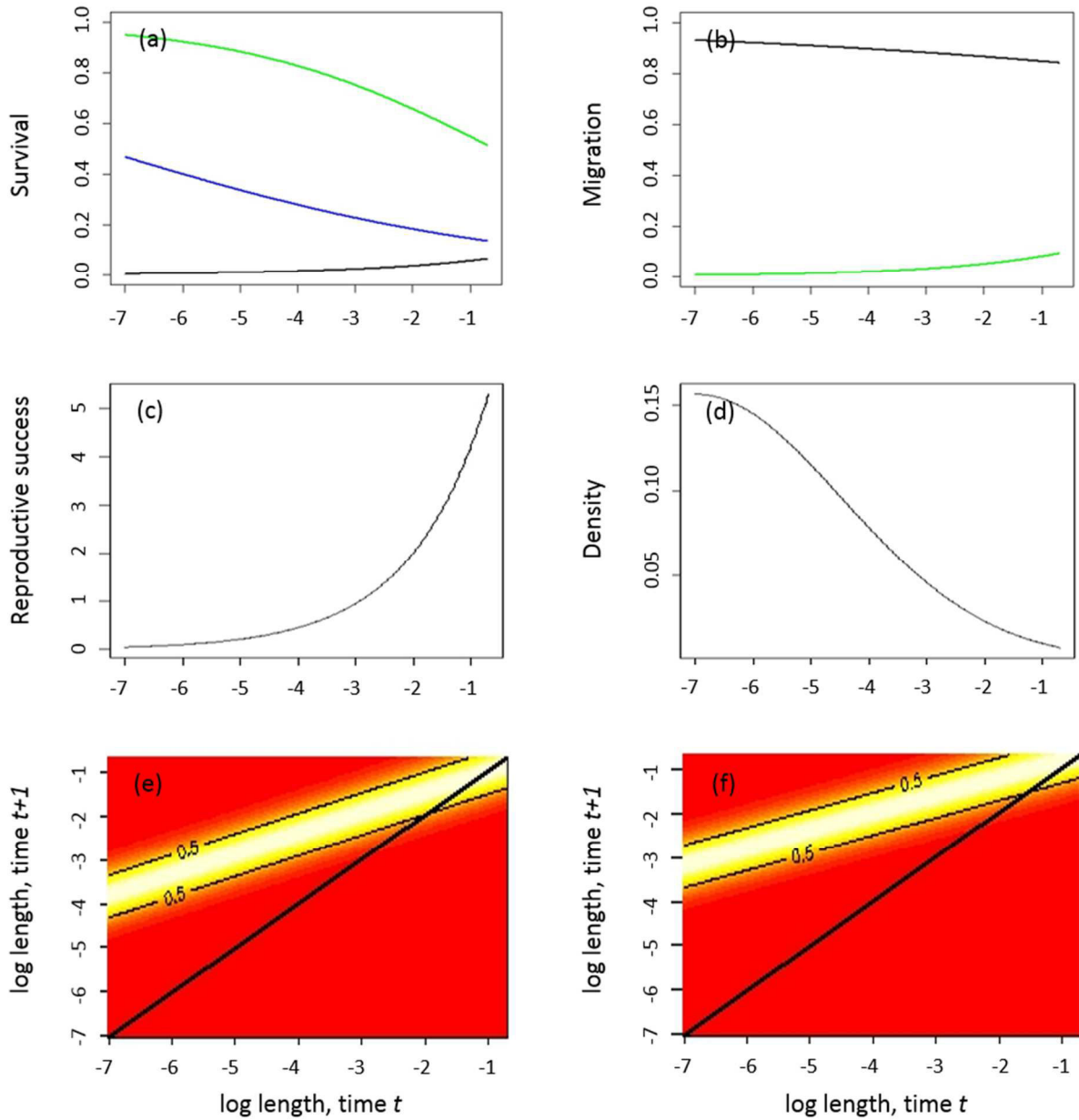


Figure 23. Demographic parameters function of body length incorporated in the IPM. *a*, the survival probability functions for Young stage (black line), Resident stage (green line), and Migrant stage (blue line); *b*, the migration probability functions for young 0+ old (black line), and 1+old (green line); *c*, reproductive success for both resident and migrant trout; *d*, the distribution of young (0+ old) body length; *e*, body length at next time step as a function of the current body length (i.e. growth function) for resident individuals (the surfaces represent the probability density with white for the upper limit); *f*, the growth function for migrant individuals. The black line represents a nul growth between t and $t+1$. No confidence interval are represented as there are not implemented in the model.

The Kernels, transitions matrix

We defined the kernel component functions (Table 8) that defined the transitions between each life cycle stage (see life cycle in article IV) including the demographic functions defined in Figure 23.

Table 8. Kernel definitions. S_y , young survival; S_r , resident survival; S_m , migrant survival; M_y , migration probability of young; M_r migration probability of 1+ old individual; R , reproductive success; G_r , resident growth; G_m , migrant growth; Q , offspring size; z , body length at t ; z' body length at $t+1$

Kernels	Component functions
Young (t) → Resident ($t+1$)	$S_y(z) * (1 - M_y(z)) * \sqrt{S_r(z)} * G_r(z', z)$
Young (t) → Migrant ($t+1$)	$S_y(z) * M_y(z) * \sqrt{S_m(z)} * G_m(z', z)$
Resident (t) → Resident ($t+1$)	$S_r(z) * (1 - M_r(z)) * G_r(z', z)$
Resident (t) → Migrant ($t+1$)	$S_r(z) * M_r(z) * G_m(z', z)$
Migrant (t) → Migrant ($t+1$)	$S_m(z) * G_m(z', z)$
Resident (t) → Young ($t+1$)	$S_r(z) * (1 - M_r(z)) * \frac{R(z)}{2} * Q(z') + S_r(z) * M_r(z) * \frac{R(z)}{2} * Q(z')$
Migrant (t) → Young ($t+1$)	$S_m(z) * \frac{R(z)}{2} * Q(z')$

Grouping of the IPM elements and use of the model

We grouped the transition matrices including the kernel and the IPM matrix (the body length mesh) to create the projection matrix. We ran the model and calculated the long-term population growth rate λ using standard MPM methods (Caswell 2001) with the *popbio* R package (Stubben et al. 2007). Then we analyzed the sensitivity and elasticity of λ to the kernels and the lower level parameters. With the sensitivity of λ to the intercept and to the slope of each demographic function, we could disentangle the influence of each demographic parameter itself from the influence of a change in body length distribution.

3.3. Preliminary results

Our first IPM model for the period from 1997 to 2015 estimated the asymptotic $\lambda = 0.51$ (no standard error was estimated as the demographic function contains no standard error value). This value is close from the estimation of λ estimated for the period 1997-2008 from the MPM

($\lambda = 0.557$, $SE = 0.067$; Article IV). As for the MPM, not accounting for immigration in our model resulted in this unrealistically low λ , in a population where we observed increasing recruitment between 1997 and 2015 (Article IV). Nevertheless, I completed preliminary perturbations and obtained elasticity results of the estimated population growth rate (Figure 24) consistent with the MPM results.

The prospective analysis showed that the calculated λ was the most sensitive to the IPM matrix elements related to the resident life history tactic (elasticity, Figure 24.e). The resident trout with body length ranging from 0.3 to 0.4 m at time t showed the highest elasticity value (Figure 24.e). This result suggests that the resident trout ranging from 0.3 to 0.4 m form the part of the population that ensures its viability over time. Now, we have to determine which demographic parameter related to the resident stage influences the most λ . Then, is it a change in body length distribution that influences λ the most through this identified demographic parameter (slope of the demographic parameter function) or is it a change in the demographic parameter independent of the body length (intercept of the demographic parameter function)? I am currently developing these analyses.

According to the MPM results, we expected that λ should be the most sensitive to the resident survival. In addition, we expected to observe larger slope sensitivity than those associated with the corresponding intercept sensitivity because perturbing a slope parameter affects larger individuals more than smaller individuals in this case and larger length classes have higher rates of survival and reproduction.

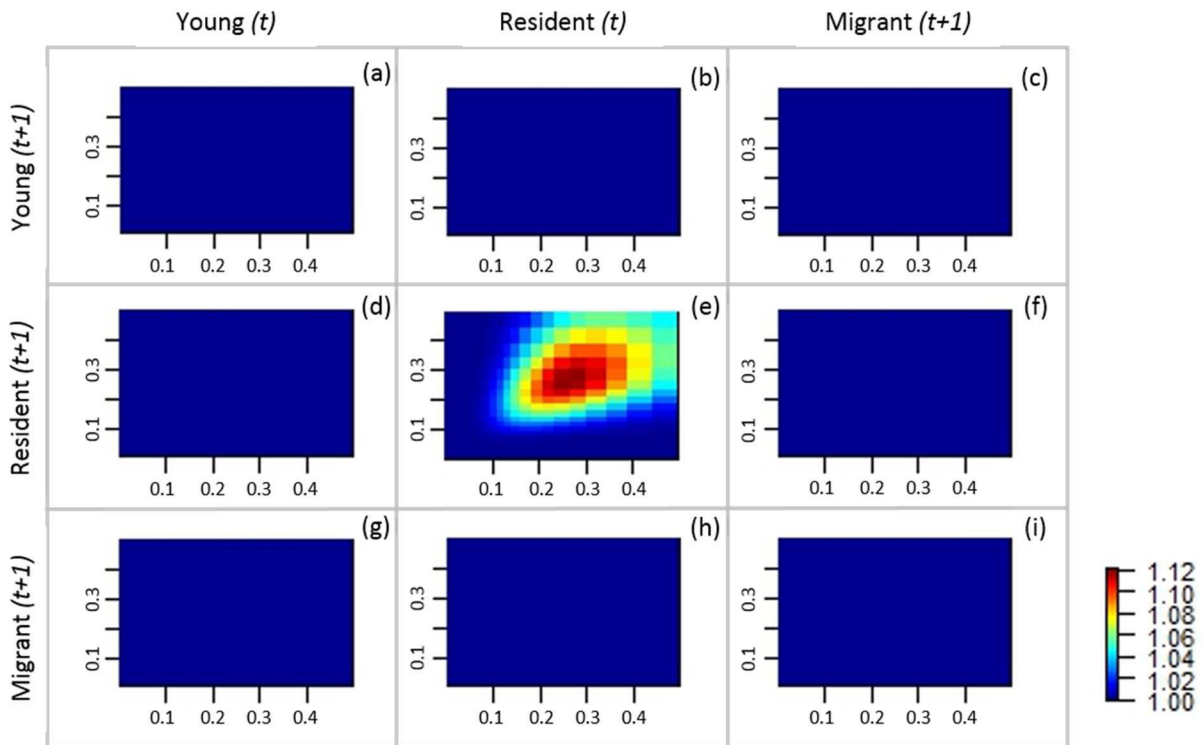


Figure 24. Elasticity of the population growth rate to the IPM matrix elements. *With stages and the body length (m) at time t in column and at time $t+1$ in rows. Some variations in elasticity were detected in panel b, c, d, g, h, and i between 1 and 1.0003 but are not represented at this scale.*

3.4. Suggestions for future developments

Our results (Chapter 1; Article I) and numerous studies on salmonids showed that the demographic parameters of juveniles (young survival, young body length, migration probability) are affected by competition. Consequently, a future development of our length-structured IPM should be the incorporation of these density-dependence processes to examine their consequences on the population dynamics.

Moreover, even if we did not detect any correlation between female body length and offspring body length in chapter 3, a significant heritability in migratory tactic has already been found in salmonids (Thériault et al. 2007). Thus, further analyses on the inheritance of the life history tactic would be useful to integrate this effect in our model. Furthermore, the estimation of reproduction parameters could be improved by disentangling fecundity from early life survival to determine the influence of these two parameters on the population dynamics. Currently, a non-invasive method is being developed in the ESE unit (INRA) to estimate the number and the size of ova by an ultrasound scan (Sonosite M-Turbo) (e.g. du Colombier et al. 2015) and

thus get data about fecundity in the field. However, the early life stage survival is difficult to estimate as data on fry are hard to obtain in the wild without inducing mortality.

When these improvements will be performed, a retrospective analysis of two IPMs (corresponding to two different periods with different λ , e.g. Article IV) could be done in addition to the prospective analyses (i.e. elasticity and sensitivity). The retrospective analysis will identify which demographic parameter function of body length contributed the most to the observed increase in λ and whether a variation in body length distribution is the driver of these changes.

4. Conclusion

Our investigation on the influence of the life history tactics on the population dynamics identified resident individuals as the most important part of the population for its viability. We highlight the necessity to assess the contribution of both migrant and resident tactics for the study and management of partially migratory populations. Our result supports the recommendation of the ICES working group on sea trout to better consider resident trout to manage population dynamics and sea-trout stocks. Nevertheless, we also highlighted that a brown trout population with an equal proportion of resident and sea-migrant should maximize the population growth rate. This finding supports the hypothesis that intraspecific tactic diversity confers an advantage to partially migratory populations compared to solely resident or solely migratory populations in a changing environment (Gilroy et al. 2016).

Furthermore, we developed a length-structured IPM that requires more work to fully understand the influence of body length distribution changes on the population dynamics but it should be very relevant for management aims as body length is much easier to measure than populations parameters. Moreover, IPM should allow the estimation of population growth rate of brown trout where no data exist to estimate demographic parameters by assuming common relationships between demographic parameters and body length, which could be a strong assumption as trout metabolism can vary among populations.

Major findings 4.

- The resident life history tactic appears as the most important to the viability of the brown trout population.
 - The tactics diversity promotes the higher resilience of partially migratory populations against environmental changes than solely resident or migrant populations.
-

DISCUSSION
&
CONCLUSION

Discussion and Conclusion



The objective of this thesis was to investigate the influence of the tactics diversity on the resilience of partially migratory populations to environmental changes. To do it, we analyzed the demographic responses of brown trout and Atlantic salmon to environmental variations during the juvenile stage, adult stage, and reproductive season. Through these analyses, we observed both common and contrasting demographic characteristics linked to their differences in partially migratory strategy. Then, by scaling up these results to the population-level, we determined how individual-level variations translate into the population dynamics and identified the role of the resident and migratory tactics of brown trout on the population growth rate. Through these analyses, we can now highlight the demographic characteristics that promote the resilience of partially migratory population to global change and discuss how tactics diversity influences it. From this discussion, we will be able to make predictions about the future of partially migratory populations considering the migration disappearance that is currently observed.

1. Advantages of partially migratory populations in a changing world

1.1. The plasticity in tactic determination

In Atlantic salmon and brown trout, resident and migrant individuals shape a common partially migratory species, where the tactic is determined at the juvenile stage during the shared season. These tactics are known to be partially determined by genetic factors and, we provided a new evidence that they are also influenced by juvenile environmental conditions, in brown trout (Chapter 1 + review in Ferguson et al. 2017). We showed that the resource availability in the juvenile environment (amount of surplus energy available to growth and space to avoid aggressiveness) negatively correlates with the migration probability of juvenile trout. Consequently, we suggested that the migration probability is a plastic trait enabling juvenile salmonids to respond to variations in juvenile environment.

By migrating out of limiting conditions, trout potentially maximize their fitness considering intrinsic and extrinsic factors (Chapter 1; Acolas et al. 2012, Sloat et al. 2014, Peiman et al. 2017). Nonetheless, an increase in the number of migratory juveniles may not produce more

migratory adults because fewer juveniles may survive to the smolt stage (Railsback et al. 2014). Migration probability can be seen as determined by adaptive plasticity if by choosing migration over residency when in poor condition results in higher overall lifetime reproductive success on average and *vice versa* when in good condition (Ferguson et al. 2017).

The plasticity in migratory tactic determination in brown trout might partly explain the variability in the proportion of sea-migratory individuals and residency with the latitude and among geographically adjacent populations (Jonsson and Jonsson 2009, Quéméré et al. 2016). This variability with latitude is not observed in Atlantic salmon (Klemetsen et al. 2003), which might suggest a lower level of plasticity in migratory tactic determination than in brown trout. In Atlantic salmon, food restriction at the juvenile stage appeared to increase the male migration probability and reduce the probability to mature in river (Olsson et al. 2006, Vainikka et al. 2012). Nevertheless, the tactic determination does not appear plastic for female Atlantic salmon (no female mature in freshwater) preventing the future juvenile production to be dependent on the past juvenile environment conditions.

Furthermore, as migration probability is mixed up with dispersion (Box 7), the plasticity in migration probability might have a considerable role in the successful colonization and establishment of brown trout around the world depending on the juvenile environment as in Kerguelen (Launey et al. 2010, Lecomte et al. 2013, Labonne et al. 2013), New Zealand (Townsend 1996) or the Rio Grande (O'Neal and Stanford 2011). In the Rio Grande, the population consisted solely of resident brown trout for at least two decades before fish began to migrate to the marine environment. This change in sea-migratory tactic might be induced by a reduction in food availability in river, limiting individual growth. Thereby, the plasticity in tactic determination is a clear advantage to the colonization of new environment and may allow partially migratory populations to adjust their distribution to cope with environmental changes.

In addition, the insensitivity of the population growth rate to the migration probability that we showed (Chapter 4) prevents the impact of its variability, induced by the plasticity in tactic determination under environmental variations, on the population dynamics. Thus, it might enable population adaptation through distribution changes while ensuring the demographic

stability of the population. In Atlantic salmon, as all female are anadromous, the populations may have a high dispersal probability and colonization ability but it should be less dependent on the juvenile freshwater conditions than in brown trout. Some simulation studies predict a shift northward of brown trout and Atlantic salmon as for other partially migratory diadromous species by the end of the century (Lassalle and Béguer 2009, Lassalle and Rochard 2009, Santiago et al. 2016).

Consequently, the tactic determination in partially migratory population is linked to three mechanisms by which population can persist when the juvenile shared environment changes: genetic adaptation to the new local conditions, phenotypic plasticity, or dispersal to track its preferred environment in space (Figure 25).

Box 7. Migration vs dispersal

By going in downstream river and at sea, juvenile salmonids can migrate or disperse. Nevertheless, we had no data enabling the distinction between these two processes. An individual that did not return to its native river may be a migrant fish that died or dispersed. Thereby, the migrant survival that we estimated in this thesis actually results in a mix of survival and dispersal probabilities. Masson et al. (2017) reported that sea trout dispersal is very rare under natural conditions. If it is not, the mix migration-dispersal involves potentially an underestimation of the survival probability at sea (and thus of the migrant survival). The increase in migrant survival that we observed in Chapter 4 can thus be the result of an actual increase in survival or a decrease in dispersal in favor of migration. If the underestimation of the migrant survival is large, we might underestimate the relative influence of the migratory tactic on the population dynamics. Nevertheless, the difference in sensitivity of the population growth rate to the resident and migratory tactic is so large, that this underestimation should not change the relative role of these two tactics on the population dynamics.

Estimating the dispersal probability would enable a better understanding of the ability to colonize new habitat and a better overview of the different mechanisms of salmonid populations to persist in a changing world.

1.2. The tactics diversity

In this thesis, we showed that the tactics diversity related to genetic and phenotypic differences within a population induces a diversity in individual responses to environmental variations (Chapter 2). The observed specificity in tactic responses to environmental changes might be due to the difference in energy allocation (among survival, growth, and reproduction) and in environments that they visit. This intraspecific response diversity illustrates a portfolio tactics that enables a part of the population to be affected by a change in the unshared environment, whereas another part is not and may prevent population extinction (Schindler et al. 2015).

Given tactics diversity, natural selection can select the tactic that has a low variability in demographic parameters and confers the highest individual fitness to buffer the impact of environmental variations on the population dynamics. (i.e environmental canalization; (Stearns and Kawecki 1994, Gibson and Wagner 2000, Gaillard and Yoccoz 2003, Péron et al. 2016). This process allows the reduction of the variability in population growth rate and prevents the risk of population collapse. We observed this process in Atlantic salmon where the trait showing the lowest temporal variability corresponded to the trait determining the female fecundity (body length) of the tactic contributing the most to the juvenile production (Multi-Sea-Winter) (Chapter 2 and 3). In brown trout, we suggested that natural selection has induced a high sensitivity of the population growth rate to the life history traits of resident females (Chapter 4). We identified that the survival of resident females was the most influential demographic parameter on the population growth rate. Theoretically, in a stochastic environment, this most influential parameter should be the least variable as it should have been evolutionary buffered against environmental fluctuations (Pfister 1998, Gaillard and Yoccoz 2003). We also showed that the sensitivity of the population growth rate to the life history traits could vary over different environmental conditions (Chapter 4). Changes in marine and/or river environment can modify individual fitness and/or the relative variability in traits related to the tactics, which might modify the influence of the tactic on the population dynamics. In these conditions, a trait related to another tactic could be canalized against environmental variations by natural selection and the most influential tactic on the population dynamics can change.

Our findings therefore support the statement from other studies on salmonids (reviewed in Fleming et al. 2014) that tactics diversity buffers overall population size fluctuation against environmental changes. This advantage of response diversity against environmental variations is not specific to fully partially migratory populations (Peterson et al. 1998, Bjornstad 2001, Vindenes et al. 2008) but it should be amplified with partial migration. Indeed, the less individuals share environment during their life the more they might show different responses to environmental variations. For instance, we highlighted response differences to environmental variations among sea-migratory tactics in Atlantic salmon by comparing Single-Sea Winter ('SSW') and Multi-Sea Winter ('MSW') salmon (Chapter 2). Nevertheless, Atlantic salmon with these migratory tactics shared longer common environment (during downstream migration, sea-entry, and upstream migration) than with resident males (i.e. precocious males). Thus, the response difference to environmental variations should be more marked between anadromous salmon and precocious males. Similarly, we expect marked response differences among resident and sea-migratory brown trout, where both males and females can be resident. By showing two 'extreme' tactics with different unshared environments during all the migration season in both sexes, partial migration in brown trout might enable a better buffering of overall population fluctuations against environmental variations than Atlantic salmon where females are solely migrant or population with solely migratory tactics or solely resident tactics. This advantage should be exacerbated in brown trout, where in addition to two 'extreme' tactics, a large panel of intermediate tactics shapes a continuum of life history tactics leading to a large tactics and response diversity (Box 8).

Consistently, we showed that a balanced proportion of resident and migrant brown trout on the spawning ground should maximize the population growth rate (Chapter 4). By having resident females with a high probability of living until the first reproduction, brown trout populations have a lower risk to have no reproductive female during the reproductive season than Atlantic salmon. We showed that this characteristic promotes the viability and stability of partially migratory populations (Chapter 3 and 4) in a changing world where environmental variation becomes less predictable (i.e. stochasticity). In contrast, the migratory tactics can boost the population growth rate under an improvement of marine conditions reducing the migration cost (i.e. increase in survival and access to the spawning ground, chapter 3) and increasing the migrant recruitment (Chapter 4). As migrants are better able to exploit very

productive ecosystems and maximize the growth and female fecundity, an increase in their number on the spawning ground should lead to a high annual juvenile production (through a higher number of eggs produced and higher potential offspring diversity) boosting the population dynamics.

Thereby, the two 'extreme' tactics present in partially migratory populations should exacerbate the response diversity (Figure 25). This tactics diversity enables the population to benefit from favorable environmental variations and to buffer the effects of unfavorable ones on the population dynamics. These two processes might promote a higher resilience of partially migratory populations to environmental change including anthropogenic effects (e.g. habitat destruction) than solely migratory or resident populations. Populations where all females are migrant as Atlantic salmon are less stable over time but take more advantage of marine environmental improvements than brown trout populations. This contrast in strategy benefit between brown trout and Atlantic salmon is well illustrated by the temporal variations in density of young-of-the-year of these both species (Chapter 1, Article I Fig.2.).

Box 8. Brown trout: not a dichotomy resident vs sea-migrant but a continuum of tactics

Aquatic ecosystems show a continuous gradient of environmental changes (river continuum concept; (Vannote et al. 1980). This gradient leads to a continuum in time and space of energy allocation in brown trout to optimize individual fitness, which shapes a continuum of life history tactics (Cucherousset et al. 2005). The gradual variation in costs and benefits of migration with the migration distance and duration is illustrated by a gradient in body size (e.g. in salmonids: increase in reproductive performances, decrease in survival probability; (Klemetsen et al. 2003, Jonsson and Jonsson 2006). This tactic continuum might have been selected by natural selection to promote population persistence (Cucherousset et al. 2005). Consequently, the tactic determination should not be limited to a dichotomy between resident and migratory tactics in brown trout. Nonetheless, as in numerous studies on salmonids, we did this dichotomy opposing only ‘extremes’ tactics (sea-migrant *versus* freshwater resident). By doing so, we simplified the continuum to get a first understanding of the population dynamics and help management actions with clear take-home messages. We provided a first demonstration of the key role of the resident and sea-migratory tactics in brown trout populations (Chapter 4) where classically only sea-trout are considered in management actions. Nevertheless, by considering all freshwater brown trout as resident trout we could not separate the effect of trout spending all their lives in their native river (in our study: La Roche brook) from those migrating in downstream river (e.g. Oir river) on the population growth rate as observed in Chapter 1. Oir river and La Roche brook showing different environmental conditions (food and space are more abundant in Oir river) the sensitivity of the population growth rate to the traits related to the “resident Oir river “ and the “resident La Roche brook” tactics should be different. By not considering this difference, we did not investigate the effect of the variation in juvenile migration in Oir river on the population dynamics. A consideration of it might promote more accurate and efficient management actions than an overall management advice from our current work.

The analysis of a continuum in life history tactics in a life cycle is hard to handle but we had the willingness to go over this dichotomy by developing an integral projection model that includes a continuum in demographic parameters based on the body length. It should allow to assess whether a management action through body length illustrating the continuum of life history tactic would be better than a management considering only two ‘extreme’ tactics.

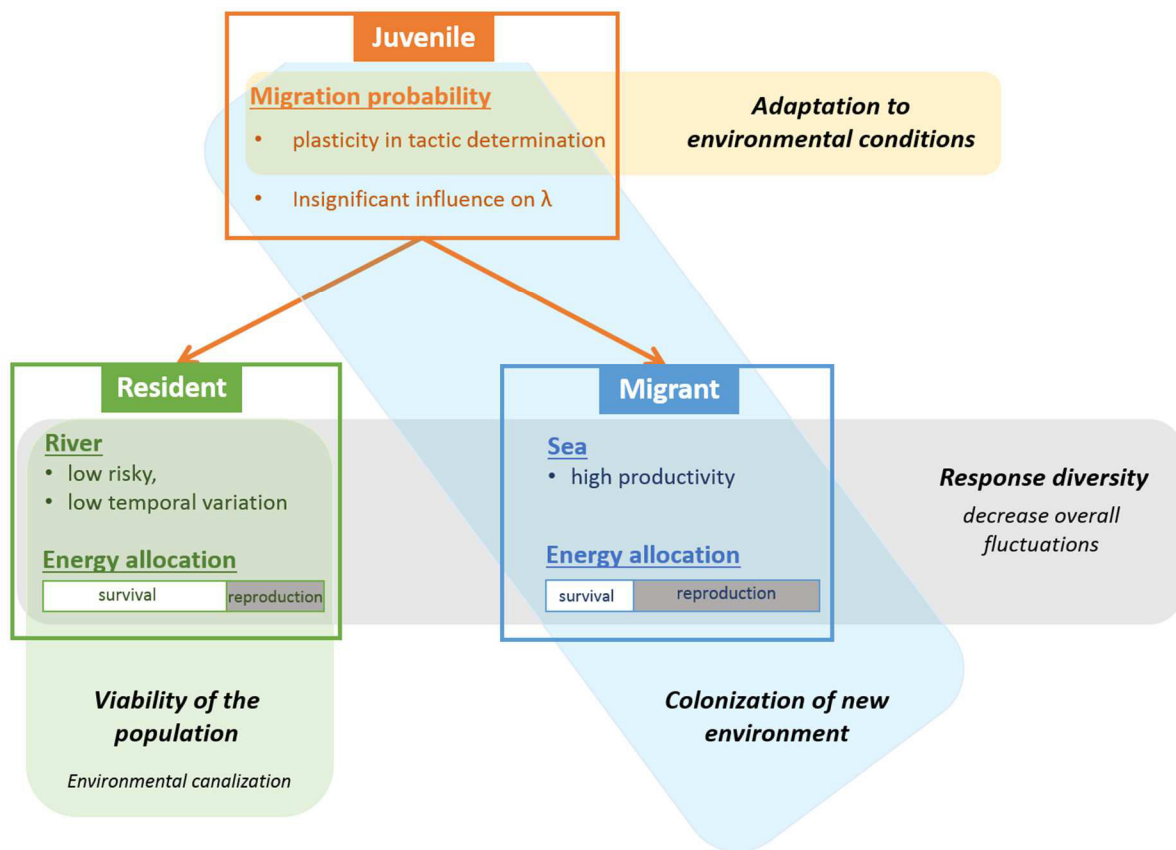


Figure 25. Summary of the advantages (in black) conferred by partial migration to population resilience in a changing world.

2. Migration disappearance

2.1. Demographic process

2.1.a. Faster life history

Many taxa including plants, fish, birds, and mammals tend to shift towards faster life histories (faster maturation, and reproduction) under climate change through evolutionary change or phenotypic plasticity (Sheridan and Bickford 2011, Aberle et al. 2012, Lancaster et al. 2017). This faster life history can partly be selected as it reduces the risk of mortality until reproduction under an increase in environmental stochasticity. Nevertheless, one of the most reported reasons explaining faster life history in ectotherms is the rising temperature (both in air and water) induced by anthropogenic climate change (Partridge and French 1996, Fischer and Fiedler 2002, Atkinson et al. 2003). Rising temperature increases the metabolic rate of ectotherms hence promoting a faster maturation and reproduction (Salminen 1997). By reducing the time to grow, an earlier reproduction induces a reduction in body size. The reduction in organism body size due to rising temperature has been commonly observed in vertebrates and is considered as the third universal response to global warming (Daufresne et al. 2009; Gardner et al. 2011). Body size changes can affect population stability through changes in energy acquisition, thermoregulation, life history transitions, and key demographic rates such as survival, growth, and reproduction (Calder 1984, Roff 2002, Kooijman 2010, Ozgul et al. 2014). However, is the reduction in body size a consequence or a cause of migration decline and faster life history?

In species with a continuous growth as salmonids, a decrease in age at first reproduction due to an increase in metabolic rate, should result in a lower body size inducing a reduction in reproductive capacity (i.e decreased fecundity). Several studies showed that Atlantic salmon mature earlier at a smaller size when the growth is stimulated by the increasing temperature at sea or in freshwater (Berrigan and Charnov 1994, Jonsson et al. 2013, Piou and Prevost 2013). This decrease in body size should deeply affect the population growth rate of semelparous populations (e.g. French Atlantic salmon populations), which have only one chance to pass on their genes. In iteroparous populations/species as brown trout, such a

decrease might be compensated by an increase in the number of reproductive events in a lifetime (i.e. bet-hedging, Childs et al. 2010).

In partially migratory salmonids, these changes should occur in both resident and migratory tactics. Nonetheless, a faster life history in migratory tactic results in a reduction in migration distance and duration. In addition, a temperature above the salmonids optimal thermal ranges might increase energetic costs, reduce oxygen circulation in the body inducing a reduction in freshwater and sea migratory performance (Richter and Kolmes 2005, Farrell et al. 2008, Hinch et al. 2012, Martins et al. 2012) hence further amplifying migration decline.

2.1.b. Increase in residency

Numerous studies on various vertebrates, including salmonids, reported a decline in migration duration, and in the proportion of migratory individuals (Ricker 1981, Bagliniere et al. 2004, Visser et al. 2009, Pulido and Berthold 2010, Gilroy et al. 2016, Gargan et al. 2016). In addition to a faster life history induced by climate change, the migration decline in partially migratory populations can result from an increase in the relative benefits of short-migration/residency (e.g. Finstad and Hein 2012). This increase can be due to an improvement of the conditions for resident individuals following climatic amelioration, or a deterioration of the conditions in the migratory environments, linked with anthropogenic disturbances (barrier and obstacle building, overexploitation, climate change,...; Berthold 1999, Maclean et al. 2008, Visser et al. 2009, Lok et al. 2013, Gilroy et al. 2016). As the mean migration duration of each migratory individual decreases, the proportion of non-migratory individuals may gradually increase. For instance in brown trout, a decrease in marine mortality or a reduction in the access of sea trout to spawning grounds would reduce the benefit of marine migration and may result in selection against anadromy. Berthold et al. (1990) showed on blackcap (*Sylvia atricapilla*) that given strong directional selection, full residency (as well as full migration) can evolve from a partially migratory population within a few generations. A similar process could transform a fully migratory population to a fully resident one (Pulido et al. 1996, Berthold 1999, Pulido 2007). Adaptive evolution of migration duration or the proportion of migrants is expected to

be very fast if the response to selection on these traits is reinforced by high, favorable genetic correlations (Pulido et al 1996, Berthold 1999, Pulido 2007).

2.2. Consequences of migration decline

2.2.a. Decrease in diversity

The decline in migration should generate a reduction in the portfolio of life history tactics, leading to a decrease in response diversity and thus, in the ability to buffer the effects of environmental variations on the population dynamics. In addition, the resulting greater similarity in tactics between individuals within a population may increase intraspecific competition and negative density-dependence effects. Moreover, reduced tactics diversity should reduce the gene flow that usually promotes genetic and phenotypic diversity in juveniles. Lower additive genetic variance increases extinction risks because less variable populations adapt more slowly and are thus less able to closely track changing trait optima (Bürger 1999). The reduction in gene flow could be amplified if mating is assortative (based on morphological or behavioral differences) and reduces interbreeding (Chapman et al. 2011). However, in our brown trout and Atlantic salmon populations, we observed random mating among ecotypes, which might prevent this amplification of gene flow reduction.

When response diversity and migration promote the coexistence of two populations with close ecological requirements as in our case study in La Roche brook, the loss of tactics diversity should increase the interspecific competition. The species showing the more rapid response to this novel source of selection may thus gain an evolutionary advantage over the other species. In our case, as we suggested a higher plasticity in tactic determination and a larger portfolio of tactics in brown trout, we might expect that brown trout would gain this advantage over Atlantic salmon.

2.2.b. Reduction in resiliency

In some populations, intrinsic factors can prevent the transition from partial migration to residency. In that case, the decline in migratory individuals will result in a population decline. For instance in Atlantic salmon, the population decline linked to a decrease in the proportion of Multi-Sea-Winter salmon illustrates the decrease in migration distance and duration

resulting from environmental change (e.g. Bagliniere et al. 2004). Nevertheless, this decrease is not compensated by a maturation of female in freshwater. Female physiology (i.e. energy required to produce gametes) may prevent the evolution of residency and induce a rapid decline of the population. In the opposite, by showing a continuum of migratory tactics, the disappearance of migration in a brown trout population might progressively transform it in an isolated resident population. We may expect a complete disappearance of anadromous trout compensated by an increase in freshwater resident individuals. Nonetheless, intraspecific density-dependence processes might maintain the existence of migration in freshwater as migration from La Roche brook to Oir river in our population.

Our results suggest that a brown trout population can be viable without anadromous individuals (Chapter 4). Several studies reported that persistence of salmonid populations isolated in a freshwater environment may rely on faster somatic growth rates, and younger age of maturity (Letcher et al. 2007, Morita et al. 2009). However, these findings indicate that populations may persist under isolation if there is sufficient genetic diversity to adapt to future environmental and anthropogenic pressures (Carim et al. 2017). Many brown trout populations that have encountered loss of intraspecific diversity due to environmental degradation or fishing are now faced with a medium-term high risk of extinction (Laikre et al. 1999, Dudgeon et al. 2006, Caudron et al. 2011). Indeed, in isolated populations, genetic diversity can be lost rapidly due to genetic drift and lack of gene flow, potentially penalizing populations to environmental changes and causing a higher risk of inbreeding depression (Kovach et al. 2015, Carim et al. 2017).

Consequently, we can suggest that by losing the migratory tactics and becoming solely resident, populations as brown trout might persist in the medium-term against environmental change but their viability may be under threat on the long-term (Gilroy et al. 2016).

3. Conclusion and perspectives

This thesis investigated the characteristics that promote the resilience in partially migratory populations in a brown trout population in comparison to an almost solely migratory Atlantic salmon population. By combining complementary datasets, methodological tools and ecological approaches we bring some key insights proving that i) the resident tactic drives the long-term viability of the population and ii) the tactic diversity enables to cope with or benefit from environmental changes. Our work supports the hypothesis that partially migratory populations are more resilient than solely migratory populations (Gilroy et al. 2016). Nonetheless, even if the risk of population collapse is reduced by partial migration, we highlighted that this risk still exists under the current global trend of migration disappearance.

Based on our findings on the influence of the tactic diversity and the resident tactic we can provide new recommendations for a better management of salmonids and prevent their collapse. We found evidence supporting the necessity to ensure the ecological continuity (i.e. stream connectivity) for both partially migratory and solely migratory populations. Based on our results, the ecological continuity should promote the resilience of partially migratory populations by maximizing diversity in migratory tactics and response diversity to environmental changes. This management action may not increase tactics diversity in (almost) solely migratory population as Atlantic salmon but is crucial to ensure sustainable recruitment rates.

Even if the tactic diversity tends to maximize the resilience of population dynamics, we identified that MSW individuals in Atlantic salmon and the resident tactic in brown trout ensure the viability of the population and thus should be the most protected components of the population to stabilize the population abundance over the years. These advices are concordant with the current management actions on Atlantic salmon but not on brown trout. Even if the demographic link between resident and sea-trout must be common to all brown trout populations, it is important to note that our results might be specific to our river. Thereby, the elasticity of the population growth rate to resident and migratory tactics should be estimated in other populations (including partially migratory populations with river resident and lake migrant) to determine if these management advices can be generalized. To

do so, a first step should result in an improvement of the data sets by promoting capture declarations of brown trout in France and monitoring resident individuals in European populations. Nonetheless, for brown trout, our study presents the first evidence that sea trout abundance is driven by the resident dynamics and the protection of resident brown trout may promote the viability in European sea-trout stocks. Given the influence of resident trout on brown trout population dynamics, the potential adverse effect of the release of hatchery resident trout (stocking) occurring in some rivers on the population dynamics and population functioning should be investigated.

Furthermore, one of the best way to apply efficient management and conservation efforts in the actual context of global environmental change would be to estimate the risk of population collapse. Models have been developed to give such predictions as Early Warning Signals ('EWS', Clements and Ozgul 2016). EWS combines long-term data on abundance (or density) and body size to detect the statistical signal predicting a future collapse of a population (Clements and Ozgul 2016, e.g. on whale stocks, Clements et al. 2017). In collaboration with Ozgul and Clements from the University of Zurich, we tested this model on our brown trout data from Oir river, using the density of juvenile 0+ and their body size. We detected a signal in 2010 predicting a future collapse. Interestingly, a collapse in juvenile density took place in 2015. When estimating the temporal variation in female resident and sea-migrant survival, we observed a decrease in female resident survival from 2011. Nevertheless, these observations raise more questions than answers. Indeed, does this signal meant that the juvenile reached a minimum body size threshold in 2010? Why is there a time lag between the signal and the collapse? Is the body size of juvenile a good candidate variable despite the low sensitivity of this trait to population growth rate (chapter 4)? Should we run the EWS with the mean body size of mature resident trout instead? EWS has a great potential for future investigation, which could help salmonids management. By coupling this signal investigation with our length-structure Integral Projected Model ('IPM') we could better understand the resilience of this population and detect critical points that could lead to population decline. By doing so, this coupling could enable a revision of the body length limit of the captured fish to improve management efficiency.

In addition to management advice, this thesis raises several new questions to fully understand and predict the population dynamics of salmonids and partially migratory populations. For instance, we did not investigate the demographic consequences of a change in the number of reproductive events that may be important as a safeguard against occasional reproductive failure (Saunders and Schom 1985), whereas the environment may influence the occurrence of repeat spawners (Niemelä et al. 2006). Moreover, our findings certainly result from a mix of ecological and evolutionary mechanisms that we did not clearly disentangle (DeLong et al. 2016). What is the contribution of plasticity, genetic or both on the observed changes in life history traits? Partitioning the relative contribution of plastic and evolutionary changes in demographic traits will enable an understanding of the influence of evolution on ecology and vice-versa (Thompson 1998).

Such understanding might allow to determine the speed of migration decline vs colonization and predict future resilience to environmental change. Indeed, our study highlighted the high capacity of brown trout to colonize new habitat suggesting a possible shift in the species distribution range in response to long-term environmental change. One can expect a northward distribution shift as already observed in some temperate salmonids populations (e.g. pink and Atlantic salmon; Jonsson and Jonsson 2009, Dunmall et al. 2013). We should observe a high rate of fish species invasions (in a broad definition that includes any species that become established outside of its native range; Richardson et al. 2000, Rejmánek et al. 2002) in high-latitude regions and a potentially high rate of local extinction in the tropics and semi-enclosed seas in the 21st century (Cheung et al. 2009). Using simulations, Lassale and Rochard 2008 predicted that brown trout should lose all its suitable habitat in the southern part of its distribution area but likely continue being abundant in northern basins.

However, what would be the consequence of such a massive redistribution and abundance change on the colonized ecosystems? Will this redistribution change the resilience of population to environmental change? Will the migration decline limit this phenomenon? Will the interaction with other species limit these latitudinal shifts, as suggested by Fernandes et al. (2013)?

For instance, currently, Arctic charr *Salmo alpinus* is better able to exploit marginal northern habitats than brown trout because of its high growth efficiency at low water temperature and

low food abundance (Larsson and Berglund 2005). With climate change, the increase in productivity and temperature of Arctic systems will offer new opportunities for brown trout extension northward (Lassalle and Béguer 2009). Brown trout being more aggressive, its invasion in habitat usually occupied by Arctic charr might affect population of the latter (Jonsson and Jonsson 2009).

The projected massive changes in distributions and community structure of species may affect the resilience of populations, the fishing activities and have socio-economic impacts on vulnerable communities (Allison et al. 2009).

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APPENDICES

Appendices



1. APPENDIX 1

Manuscript under review in Journal of Fish Biology

Fishes in a changing world: learning from the past to promote sustainability of fish populations

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Abstract

Populations of fishes provide valuable services for billions of people, but face diverse and interacting threats that jeopardise their sustainability. Human population growth and intensifying resource use for food, energy and goods are compromising fish populations through a variety of mechanisms, including over-fishing and declines in water quality. The important challenges raised by these issues have been recognised and have led to considerable advances over the past decades in managing and mitigating threats to fishes worldwide. In this review, we identify the major threats faced by fish populations alongside recent advances that are helping to address these issues. Many societies are striving to ensure a sustainable future for the world's fish and fisheries and those who rely on them; although considerable challenges remain, by drawing attention to successful mitigation of threats to fish and fisheries, we hope to provide the encouragement and direction that will allow these challenges to be overcome in the future.

Introduction

Fish populations are of immense global value, shaping ecosystem services for billions of people worldwide (Holmlund & Hammer, 1999; Worm *et al.*, 2006). However, our planet is currently facing unprecedented environmental and societal changes, which are having dramatic impacts on fish and fisheries (Waters *et al.*, 2016). Understanding the likely scope of these changes is crucial in allowing us to develop mitigation strategies, manage fish populations, and minimise negative impacts for those who rely on them. Moreover, the pivotal position of fish in aquatic ecosystems renders them important indicators of environmental health. Effective assessment and proactive management at the ecosystem level has the potential to considerably improve the resilience of aquatic ecosystems to global change, preventing potentially disastrous declines in fish populations (McCauley *et al.*, 2015; Scheffer *et al.*, 2015). The success of such management relies on the ability to identify current and future threats to fishes and using past successes to develop effective tools for future mitigation strategies.

This paper was envisioned by a team of 30 biologists, during the 50th anniversary conference of the Fisheries Society of the British Isles, who were challenged to think about the greatest threats fish populations are facing and how we might ensure sustainability in the future. The paper was written as a collaborative endeavour, whereby authors highlighted ideas focused

on what threats fishes face today, what can be learnt from previous successes, and how to best address future challenges. These ideas were then collated and key points selected to form the basis of this review paper.

Issues facing fishes today

Fishes today face a multitude of threats ultimately driven by increasing human populations (projected to reach 9.7 billion by 2050; United Nations 2017) and intensifying resource use including for food provision (fishing, irrigation, agriculture, livestock production), energy production (hydropower, wind turbines, oil and gas drilling, fracking, biomass harvesting) and other goods (mining, forestry, river channelling). The accumulation of threats has resulted in unprecedented impacts on ecosystems, with widespread population declines of fauna and extinctions across many taxa (Foley *et al.*, 2011, Mueller *et al.*, 2012; Young *et al.*, 2016; Ceballos *et al.*, 2017). These threats are manifested through multiple biological, chemical, physical and climatic mechanisms (Figure 1). Threats occur across a wide range of spatial and temporal scales; therefore, they need to be understood in the context of a combination of local (spatially and temporally variable) and global (with little spatial and temporal variation) pressures. A combination of local and global mitigation methods will therefore be required to restore and sustain the health of aquatic systems.

Physical threats to aquatic systems include habitat degradation, fragmentation or destruction (e.g. Valiela *et al.*, 2001, Waycott *et al.*, 2009) and freshwater flow modification (e.g. water extraction for societal use), caused by developments of energy infrastructure (e.g. dams for hydropower) and changes in land use (Dudgeon *et al.*, 2005; Ziv *et al.*, 2012; Pittock *et al.*, 2015). Stressors such as anthropogenic noise (e.g. commercial shipping, recreational motorboats) have been shown to affect both the physiology and behaviour of fish and have direct impacts on fitness (Slabbekoorn *et al.*, 2010; Simpson *et al.*, 2016). Overexploitation of fish stocks beyond sustainable limits is one of the most severe threats to fish populations (Pauly *et al.*, 1998; Allan *et al.*, 2005; Pauly & Zeller, 2016), with direct impacts ranging from mortality through to fishing-induced life-history changes on populations (Jørgensen *et al.*, 2007; Kuparinen & Festa-Bianchet, 2017). Expansion of severely hypoxic water masses, caused by global warming (Diaz & Rosenberg 2008), compresses habitable areas for fish (Gallo & Levin, 2016). Such human-induced biological changes may persist over time through a range of genetic and epigenetic mechanisms (Feil & Fraga, 2012; Paris *et al.*, 2015; Uusi-Heikkilä *et*

al., 2017). Biological threats such as invasive non-native species and aquaculture have emerged as significant pressures on biodiversity in aquatic environments and can have profound ecological impacts both directly (e.g. predation) and indirectly (e.g. habitat alterations, pathogens) (Gallardo *et al.*, 2015; Middlemas *et al.*, 2013). Water pollution is a major threat, acting via a diverse array of mechanisms. Chemicals from industrial and domestic wastewater discharges and run-off from agriculture and aquaculture can persist in aquatic environments and have a wide range of biological impacts on organisms and populations, ranging from lethal (over toxicity and mortalities) to non-lethal physiological changes such as disruption of the endocrine system (Jobling *et al.*, 1998; Jones & de Voogt, 1999; Hamilton *et al.*, 2016). Additionally, agricultural and aquacultural run-off can cause eutrophication of aquatic systems leading to local reductions in oxygen concentrations, which may be further exacerbated by climatic changes (Smith *et al.*, 1999; Jenny *et al.*, 2016). Conversely, human exploitation of upland areas, including disruption of river continuity due to hydroelectricity production coupled with stocking of migratory fishes, can cause shortages in nutrient availability (Nislow *et al.*, 2004).

Threats that are temporally persistent and geographically extensive will have the most widespread impacts on ecosystems. For instance, rising atmospheric carbon dioxide (CO₂) levels and associated acidification, together with warming and expansion of hypoxic zones in aquatic environments, have a range of individual-, population-, community- and ecosystem-level impacts on fishes globally (Perry *et al.*, 2005; Stramma *et al.*, 2012; Deutsch *et al.*, 2011; Jenny *et al.*, 2016). The increase in severely hypoxic water masses (<0.5 mL/L O₂) has become a major cause of concern (Diaz & Rosenberg, 2008), due to the lethal or sub-lethal effects on organisms and the compression of habitable areas (Gallo & Levin, 2016; Townhill *et al.*, 2017). Mobile organisms can escape or adapt behaviourally, physiologically or morphologically (Gallo & Levin, 2016), whereas stationary, hypoxia-intolerant organisms may be more susceptible to hypoxic events. Some marine fishes may be more resilient to changes in temperature due to their potential for poleward range shifts (e.g. Simpson *et al.*, 2011a; Fosheim *et al.*, 2015), whilst non-diadromous freshwater fishes are more likely to be constrained by enclosed ecosystems, making such compensatory range shifts less feasible (Strayer & Dudgeon, 2010; Rolls *et al.*, 2017). Extreme weather events associated with climate change are leading to mismatches between seasonal temperature patterns and photoperiodic cues, which can have

population- and ecosystem-wide effects at high latitudes (Stevenson *et al.*, 2015; Jørgensen *et al.*, 2014). Elevated CO₂ threatens fishes through associated reductions in pH and carbonate levels, causing physiological and behavioural changes that may have severe consequences for both marine and freshwater populations (Munday *et al.*, 2012; Simpson *et al.*, 2011b; Tix *et al.*, 2017). Additionally, climate change can dramatically impact hydrological regimes and increase the frequency and intensity of droughts and floods (Reynard *et al.*, 2017 ; Milly *et al.*, 2005; Arthington *et al.*, 2010). Such dramatic changes for freshwater habitats can have impacts on riverine fish distributions and abundance (Arthington *et al.*, 2010).

Aquaculture of fish and other organisms is an important and growing source of food for people and may relieve pressure on natural fish stocks. Conversely, without careful management, aquaculture has the potential to cause damage, for example due to harvesting of wild fish for food, proliferation of parasites, destruction of physical habitat, localised pollution and distortion of native gene pools through escapes of strains selected for performance in captive conditions (Naylor *et al.*, 2000, Tornero & Hanke, 2016). Aquaculture also faces its own challenges that are often difficult to tease apart, as extracting signals of environmental change from natural environmental variability is difficult. Recent research shows that due to their coastal locations, aquaculture sites have been, and are likely to be, heavily impacted by environmental changes such as increased storms, rising sea temperature and levels, acidification and coastal pollution (Callaway *et al.*, 2012, Karvonen *et al.*, 2010).

The threats faced by fishes are rarely, if ever, experienced in isolation (Halpern *et al.*, 2008). Threats to aquatic ecosystems can occur concurrently and/or consecutively within the lifetime of a fish, with resulting antagonistic, additive or synergistic effects which may significantly alter the impacts of the individual stressors (Crain *et al.*, 2008; Darling & Côté, 2008), and the consequences of exposure to multiple stressors are often highly complex and context dependent. For example, coral reef habitats and the fishes that occupy them are simultaneously threatened by both local overfishing and pollution as well as changes to global ocean pH and temperatures (Hughes *et al.*, 2017). When acting together, temperature and hypoxia act synergistically in some cases, such that small shifts in one stressor result in large effects on organismal performance when fish are exposed to both in combination (McBryan *et al.*, 2013). In contrast, hypoxia can protect fish embryos from copper toxicity, but this effect

is reversed after hatching (Fitzgerald *et al.*, 2016; 2017). In marine upwelling ecosystems hypoxia can reduce predation pressure on hypoxia-tolerant prey fish (Salvanes *et al.*, 2015). In freshwater lakes, climate-change induced increases in temperature and precipitation influence both eutrophication and deep-water hypoxia, altering fish habitat availability (Graham & Harrod, 2009; Rolls *et al.*, 2017). The increasing frequency of droughts can have a synergistic effect with other anthropogenic stressors, for example by increasing the concentration of chemical pollutants in freshwaters (Woodward *et al.*, 2010). Diadromous species experience environmental change across multiple habitats. Symbiotic interactions further complicate the impacts of ecosystem threats, as sub-lethal impacts on one species can have lethal effects on another species with which it interacts (e.g. eutrophication: Mills & Reynolds, 2004; warming: Beldade *et al.*, 2017). Such interactions introduce considerable complexity to the analysis of the issues that fishes face, increasing the difficulty to predict levels of threat, causal relationships and likely consequences for survival.

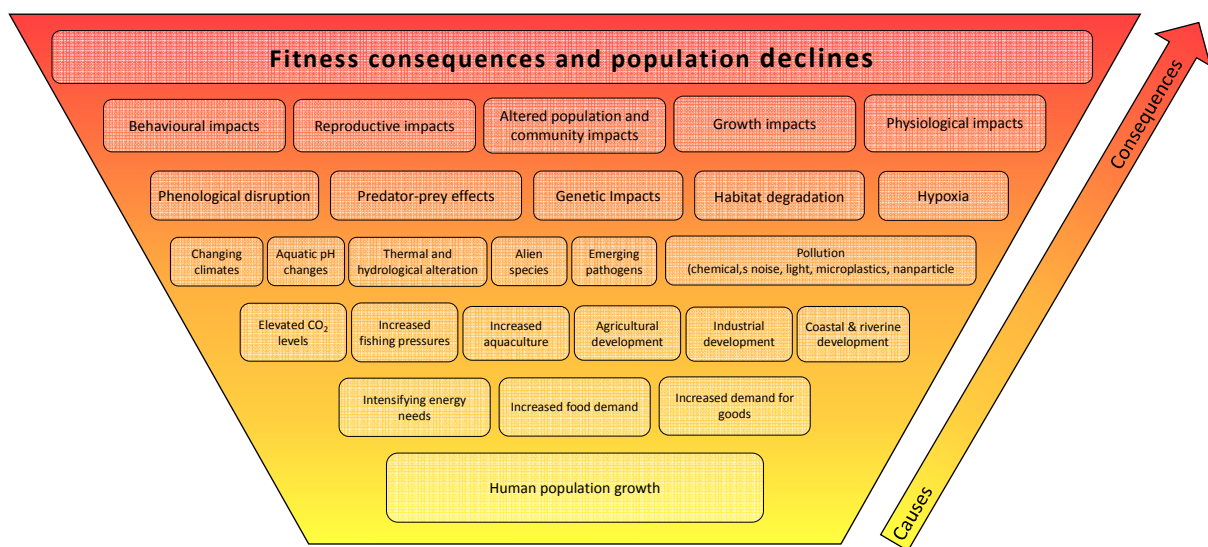


Figure 1: Hierarchical structure of threats facing fishes globally. Human population growth as a driver leads to altered resource use and subsequently to fitness consequences and population declines by a wide range of varied and inter-linking mechanisms.

Learning from previous successes

In confronting the significant challenges faced by fishes in globally changing ecosystems, it is important to reflect on the significant progress that has been made in addressing such issues over past decades. Revolutionary new conceptual, experimental, computational and technological advances have dramatically changed approaches in aquatic ecology, facilitating

the development of strategies for dealing with future challenges. For example, modern genetics and genomics methods have revealed the fine-scale genetic diversity within and among fish populations, modern modelling tools have allowed incorporating multiple individual-level processes in simulation models used to address realistic large-scale management scenarios, and technological developments in survey equipment have enhanced our ability to study and conserve deep-water ecosystems (e.g. Dunlop *et al.*, 2009; Favaro *et al.*, 2011; Fernandes *et al.*, 2016; Valenzuela-Quiñonez, 2016) and to fill gaps in our knowledge for some species of great concern (e.g. Beguer-Pon *et al.*, 2015). The following examples are not intended to be comprehensive, but provide case studies of how increases in understanding or new technologies have improved the management of fish populations.

Chemical pollution

Advances in ecotoxicology have demonstrated that even very small concentrations of pharmaceutical and industrial chemicals can have extensive impacts upon fish populations through sub-lethal effects (Hamilton *et al.*, 2016). For example, synthetic oestrogens present in waste waters can result in widespread endocrine disruption in wild fish, with potentially negative impacts on populations (Jobling *et al.*, 1998; Jobling *et al.*, 2006; Kidd *et al.*, 2007). Further, lessons from large oil spills (e.g. Exxon Valdez in 1989; Deepwater Horizon in 2010) have revealed variability across life-stages in the response of fishes to pollutants, along with the time scales associated with stock recovery, the time lags associated with secondary effects such as disease and malnutrition, and the interactions of oil pollutants with natural environmental conditions (Pearson *et al.*, 1999; Thorne & Thomas, 2008; Whitehead, 2013; Incardona *et al.*, 2014). Additionally, recent experimental findings show that petroleum-based pollutants at environmentally-relevant concentrations disrupt behaviours that are crucial to larval survival and settlement in coral reef fishes (Johansen *et al.*, 2017). These recent developments in our understanding of the consequences of exposure to pollutants enhance our ability to predict and mitigate the impacts of such events in the future. This ability has important implications for governmental decision-making, for example regarding waste water treatments, oil exploration, drilling and construction near sensitive ecosystems. As a result, examples of ecosystem recovery have been reported following introduction of improved treatment of wastewaters and reduction of discharges, including for the River Aire (Sheahan

et al., 2002) and the Mersey estuary (Jones, 2006) in the UK, demonstrating the effectiveness and benefits of improved management of wastewaters.

Climate change

Growing concerns surrounding the impacts of anthropogenic climate change have resulted in a dramatic increase in related research. For many decades researchers have been looking for simple correlations between climatic variables and fish recruitment. More recently, a wealth of predictive models have been developed to help determine future patterns of fish distribution and productivity, with increasing competitive abilities(?) and physiological challenges (e.g. Piou *et al.*, 2015, Cheung *et al.*, 2013). Furthermore, despite the problem of ocean acidification having only been recognized within the last decade or so, there is now significant progress towards understanding the impacts of temperature and changing ocean pH, both as individual stressors and in the context of a complex suite of other environmental pressures (Orr *et al.*, 2005; Kroeker *et al.*, 2017). Additionally, our understanding of the impacts of climate change on freshwater ecosystems has increased. For example, fish in riverine systems have been shown to shift their spatial distributions with altering isotherms, although not currently at a rate fast enough for future projections (Comte & Grenouillet, 2013). Previously research had centred upon spatial predictions and exposure; our recently increased understanding of impacts can now be used in detailed vulnerability frameworks (including species-specific sensitivities, adaptive capacity and exposure) to aid in the conservation and management of fish populations by determining the best type of strategy and the urgency with which it should be applied (Dawson *et al.*, 2011). For example, understanding a species' vulnerability may inform managers that an intensive approach is required involving assisted migrations outside of a species' native range (Dawson *et al.*, 2011; Lunt *et al.*, 2013), although such assistance is still debated due to potential unintended consequences (Ricciardi & Simberloff, 2009). Within freshwater environments there is potential for mitigation against thermal increase, for example by planting trees to provide shading where temperatures are predicted to exceed optimum or critically high levels for growth and survival of fish species (Jackson *et al.*, 2016). Understanding the capacity of farmed species to cope with changes to the environment (Castanheira *et al.*, 2017) and the potential to select species suited to future conditions (Callaway *et al.*, 2012) could buffer some of the detrimental impacts of climate change both on food production and the environment. Active research in these areas will enable management of the risks.

Overexploitation

Overexploitation of fish stocks, in addition to the removal of individuals, can induce phenotypic shifts in life-history traits of remaining fish and thus disrupt size-dependent community and ecosystem functioning (Pauly *et al.*, 1998; Branch *et al.*, 2010; Kuparinen *et al.*, 2016; Graham *et al.*, 2017). To achieve more ecologically and socially sustainable management schemes, especially in the wider context of increasing climate-induced pressures, balanced harvesting strategies (Garcia *et al.* 2012) and spatially or evolutionarily explicit, ecosystem-based approaches have emerged as alternatives to traditional individual-species management (Pikitch *et al.*, 2004; Laugen *et al.*, 2014; Möllmann *et al.*, 2014; Patrick & Link, 2015). These ecosystem-based approaches have started to be implemented around the world, but largely remain in their infancy, and are designed to prioritize management of the ecosystem first through defined biological and societal objectives, ultimately supporting target fisheries (Pikitch *et al.*, 2004; Garcia & Cochrane, 2005; Ruckelshaus *et al.*, 2008). Recent models have shown that such approaches should be very effective management strategies to achieve many social, economic and ecological objectives (Fulton *et al.* 2014). The adoption of an ecosystem-based management regime represents the best option for a sustainable management. However, it is a complex process involving many organisations, communities and stakeholders, making it a challenge to implement, but it has been shown to be achievable (Garcia & Cochrane, 2005; Olsson *et al.*, 2008). For example, management of the Great Barrier Reef Marine Park transitioned from protection of individual reefs to the wider-scale seascape through reorganization of the park authority, which enabled better collaboration with scientists and increased public awareness of threats (Olsson *et al.*, 2008).

Protected areas

Marine (and freshwater) protected areas (i.e. aquatic areas where fishing or other activities are limited or prohibited) represent an important tool for recovery and replenishment of exploited stocks and potentially adaptation to climate change if implemented, managed and enforced appropriately [Huntington 2010, Edgar, 2014, Roberts *et al.*, 2017]. Development in the design and implementation of aquatic protected areas has focused on integrating and improving resilience to climate change and enhancing socio-ecological capacities (Cinner *et al.*, 2009). Additionally, an improvement in reserve design and consideration of global marine reserve connectivity and larval supply can serve to better direct reserve benefits to both

people and the environment (Chollett *et al.*, 2016; Krueck *et al.*, 2017a; Andrello *et al.*, 2017). This can optimize the trade-off between conservation and fisheries production (Gaines *et al.*, 2010; Brown *et al.*, 2015; Chollet *et al.*, 2016). In freshwater systems, management using protected areas has improved through enhancing the connectivity of important sections of rivers, lakes and estuaries (Harrison *et al.*, 2016).

Genetics

Recent technological advances also hold enormous potential for balancing the demands of global economies and the need for viable fisheries and biodiversity conservation. DNA barcoding now allows global tracking of seafood fraud (Pardo *et al.*, 2016), and next-generation sequencing-based eDNA metabarcoding can be used to effectively detect non-native and endangered species when this was hitherto impractical (Bohmann *et al.*, 2014). Use of eDNA is arguably on the verge of revolutionizing fish community monitoring (Valentini *et al.*, 2016) and is becoming an effective tool for biomonitoring of aquatic ecosystem health states (Chariton *et al.*, 2015; Aylagas *et al.*, 2016). In an Australian riverine system, eDNA has been used to improve management and control of the invasive redfin perch (*Perca fluviatilis*) through great sensitivity of detection, allowing more accurate placement of exclusion barriers (Bylemans *et al.*, 2016).

Big data

The growing availability of free or low-cost data from a wide range remote sensing platforms, combined with miniaturisation of data storage devices, has provided the ability to collect large amounts of data which can be shared internationally between multi-disciplinary groups (Sbrocco *et al.*, 2013, Yeager *et al.*, 2017). This is allowing development of 'Big Data' approaches in fish science, which have the potential to help tackle issues related to monitoring and mitigating changes in large-scale systems (Hampton *et al.*, 2013). Future technological developments may lead to further dramatic improvements in the ability of scientists and environmental management to assess and manage the impacts of global change on fishes.

Modelling

Major progress has been made in advanced modelling techniques, allowing society to transfer understanding of impacts of environmental change on individual fish to population and

community levels. For example, developments in computing and software have allowed for a range of food web models, such as Ecopath (ref e.g. Moloney *et al.*, 2005). Advanced modelling techniques facilitate greater understanding of key features of population dynamics, including energy budgets, reproduction, larval dispersal, recruitment, genetic changes and productivity of fisheries (Dunlop *et al.*, 2009; Cheung *et al.*, 2010; Sibly *et al.* 2013; Krueck *et al.*, 2017a), leading to improved utility for management and conservation. This potentially allows scientific advice to play a greater role in policy, as evidenced by successes such as the establishment of multi-disciplinary management indicators adopted by the EU Water Framework Directive (European Commission, 2016). Nevertheless, much of this advice can be further improved. The use of mandatory Environmental Impact Assessments (EIA) in Europe has extended, beneficially, to many forms of aquatic development planning. Yet, the ability to predict robustly the outcomes of development and to engage effectively in post-scheme monitoring and adaptive management still constrains the practical application of EIA (Rose, 2000; Milner, 2015). Hydrological and ecological models have been used successfully in restoration of riverine habitats that have been affected by water extraction and associated altered flow regimes, which bodes well for future uses in similar systems. Such models, combined with empirical research, were used to inform management decisions on flow regulation to increase fish spawning and recruitment on a flood plain on the River Murray, Australia (Arthington *et al.*, 2010; King *et al.*, 2010).

Interdisciplinary and holistic thinking

The severity of problems facing fishes and the difficulty of studying long-term anthropogenic changes have necessitated the development of new integrative and holistic ways of thinking in environmental biology. Multi-disciplinary, ecosystem-based approaches have emerged as particularly promising novel frameworks, resulting in significant advances in both research and management applications. For instance, local societal and ecological changes have been linked to global climate change (Karnauskas *et al.*, 2015), biophysical modelling has been integrated with population genetics (Selkoe *et al.*, 2008), ecosystem service ideas have been expanded to include relational values (Chan *et al.*, 2016), and fisheries sustainability has been added to biodiversity in considering the effectiveness of marine protected areas (Krueck *et al.*, 2017b). Further, recent ideas promote decision-making based upon expected future ecosystem states, as opposed to past baselines, to increase the efficacy of future management strategies (Rogers

et al., 2015). Calls for anticipative management of this nature have led to increased understanding of the subtle variations characterizing degraded environments as well as the novel fish assemblages that arise from warming-induced range shifts and abundance changes (Harborne & Mumby, 2011; Simpson *et al.*, 2011a; Mumby, 2017; Salvanes *et al.*, 2015).

Addressing future challenges

Despite significant recent advances in assessing the responses of fishes to global change, several key challenges remain. Ultimately, many of the most pervasive problems facing global fish populations today can only be mitigated through collaborative efforts involving both scientists and wider society (e.g. Lynch *et al.*, 2015). Future efforts must, therefore, use both scientific and societal approaches in order to most effectively secure a future for fishes worldwide.

Scientific challenges

Ultimate impacts

Understanding how individual-level responses to environmental change affect individual fitness, and subsequent population- and ecosystem-scale effects, is a major challenge (e.g. Rolls *et al.*, 2017; Windsor *et al.*, 2017). This includes the development of suitable techniques for understanding multiple stressor effects in ecologically realistic settings at the broadest scales of biological organisation (Dafforn *et al.*, 2015). Furthermore, identifying and quantifying links between observed ecological effects and provision of ecosystem services is important for demonstrating the relevance of this research to a wider societal audience and for effective action (Hering *et al.*, 2015).

Indirect effects

Indirect effects of environmental change are also important in defining consequences for ecosystems. For example, the generation of novel habitats through environmental modification might provide new niches but also serious challenges for fish communities if these modifications impede migration pathways and reduce connectivity among crucial habitats (Acreman *et al.*, 2014; Graham *et al.*, 2014). Predicting the constituents of these altered habitats and the likely responses of existing fish communities to these changes represents a considerable current knowledge gap.

Understanding acclimation and adaptation

The potential for acclimation and adaptation to environmental change and disturbances is a crucial determinant of fish persistence and productivity (Munday *et al.*, 2017). These mechanisms are fundamental to ecosystem resilience, and are therefore central in identifying the actual ecological risks presented by a range of environmental stressors. Intra-specific variation in responses is often overlooked, despite potentially important implications for the ability of fish populations to exhibit short-term and evolutionary responses to stressors (Radford *et al.*, 2016, Ellis *et al.*, 2017). Understanding the mechanisms underpinning population responses and their variability and integrating this knowledge into predictive models (e.g. Piou *et al.*, 2015) are important to appropriately manage fish populations and communities under stress.

Long-term datasets

Determining the effects of global change on fishes is problematic without extensive, long-term datasets (Soranno & Schimel, 2014). In many cases, the data required to answer certain macro-scale questions are not available, and the expansion of existing data-sharing practices in conjunction with data collection networks is required to facilitate long-term ecosystem-scale analysis (e.g. Laney *et al.*, 2015). In cases where technological advances have allowed collection of large datasets, current computational capabilities are not always sufficient for appropriate storage, sharing and analysis of these data (i.e., dealing with the 'data deluge'), and greater investment in infrastructure and computational tools is required (e.g. Hallgren *et al.*, 2016). A further aspect of engaging with big data and tackling large-scale questions revolves around contributing to global, interdisciplinary initiatives (Hampton *et al.*, 2013). For instance, understanding fully the potential environmental risk of microplastics in freshwater systems will require a collaborative effort from multiple disciplines including chemistry, hydrology and ecotoxicology (Wagner *et al.*, 2014) and similar approaches will be required to address other large-scale threats, including those arising from other pollutants and climate change. Therefore, fostering collaborations between disciplines is of vital importance for determining the likely consequences of global change upon ecosystems (Holm *et al.*, 2013).

Societal challenges

Widening participation

Effective communication of the problems facing fish and fisheries, scientific solutions and risks and potential options for the future, is of fundamental importance. Support for research and management can be enhanced by instilling and nurturing an ethos of care and value among communities of people. Wider societal participation within environmental science can promote the progression of research and management of fish in a changing world. Emphasising the involvement of the non-scientific community in data collection and decision making is important in gaining momentum towards positive change (Wiber *et al.*, 2009). A number of 'citizen science' projects focussing on data collection for fishes already exist (see Hyder *et al.*, 2015). Despite this, the absence of best practice regarding these processes is hindering progress and positive change through public engagement. Improving transparency and feedback within communication pathways between scientists and non-academics may enhance participation in management of fish populations (Dickinson *et al.*, 2012). Improved stakeholder interaction and better use of citizen science also requires development of novel information technology tools and mobile applications that allow for the collection and use of data by the public (Hyder *et al.*, 2015).

Spatial boundaries

Practical solutions are necessary to overcome existing issues regarding the use of ecologically arbitrary spatial boundaries to separate the dynamic environment of open water bodies (e.g. Exclusive Economic Zones), which can prevent current management strategies from reaching their full potential (Song *et al.*, 2017). Ultimately, sympathetic and inclusive management at a range of spatial scales (local to global) is needed and this can aid with compliance in strategy implementation (see Ramírez-Monsalve *et al.*, 2016).

Political landscapes

The global political landscape provides a major challenge to researching and managing fish populations. Destabilisation of both domestic and international politics threatens to affect the international scientific community worldwide and the translation of discoveries into advice for management; examples include uncertainty surrounding the impact of Brexit on fisheries and nature conservation policies (Rush & Solandt, 2017), potential changes in European

marine environmental protection policy (Boyes & Elliott, 2016) and breakdowns in transboundary agreements regarding the management of South China Sea fish stocks (Teh *et al.*, 2017). In the face of a world facing dramatic changes to ecological, societal and political environments, maintaining consistency and employing robust management strategies, such that political uncertainty does not result in degraded ecosystems, will be a major challenge for the future.

Public concern for fish welfare

Public concern for fish welfare in aquaculture (e.g. presence of sea lice) and both commercial and recreational fishing appears to lag behind that for terrestrial farming systems, but voices of concern are growing and evidence is accumulating on this contentious and challenging issue (Huntingford *et al.*, 2006). However, current data and knowledge are insufficient for representatively assessing the current state of fish welfare and supporting significant improvements in this area (Röcklinsberg, 2015). Continued research on fish welfare topics should address this knowledge gap.

Prioritisation of resources

It may be necessary to prioritise specific avenues for research, management or regulation in the face of a rapidly changing global environment and limited resources. Problem areas that may benefit from rapid intervention to address emergent threats should be given a higher priority compared to others where immediate action may not be necessary and/or effective. Such prioritisation should be based not only on scientific merit, but also inclusion of societal requirements, conservation and management strategies (Gullestad *et al.*, 2017). For example, proposed habitat developments (e.g. hydropower) should increasingly weigh up the cost to biodiversity and fish productivity against societal requirement, to avoid negative consequences for aquatic conservation (Ziv *et al.*, 2012). Alternatively, aquatic infrastructure can potentially be eco-engineered to provide benefits to a range of taxa (e.g. Perkins *et al.*, 2015). Increasingly, compromises must be made in assessing the volume of scientific information that is required to competently answer research questions yet also provide timely advice to inform decision-making and management strategies (i.e. a quest for “the perfect” should not be an “enemy of the good”). There is increasing concern regarding the rate of global change and the risk of overly cautious scientific conclusions limiting the speed, onset

and potential benefits of effective management decisions. Some management decisions need to be made on priority issues with 'best current knowledge' using precautionary principles, in the knowledge that in the future decisions may be adjusted as new data emerge. This bolder management approach can accelerate the management of new challenges and prevent deterioration of the environment.

Conclusion

Fish populations worldwide face a multitude of threats ultimately stemming from human population growth and altered resource use. These threats present dramatic challenges for both science and society today, but a range of successes over the past decades provide a roadmap for many of these challenges to be met effectively. For example, major scientific, technological and conceptual advances associated with the challenges of making better use of 'Big Data' and harnessing the power of new electronic and genetic techniques, have increased our ability to effectively manage fish populations, at least in the developed world. Significant ecological, political and societal challenges must be met to secure a future for the world's fishes (and in doing so, their entire supporting ecosystems), requiring global and collaborative efforts to achieve effective solutions for sustainable fisheries and ecosystems. The rate of global change threatening fishes worldwide is such that time has become the most precious commodity in mitigating the threats faced by fish populations. Urgent and bolder action is needed for the effective protection of ecosystems and the services on which humans rely.

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2. APPENDIX 2

ARTICLE I. Model details and Transition matrices from GEPAT in E SURGE.

All individuals were marked as young-trout in La Roche brook in autumn, thus the initial state of individuals (i.e. tagging) was constrained in the model as $L_r = 1$. Then the probability for an individual to move from states at time t (rows of the matrices) to states at time $t+1$ (columns of the matrices) (i.e. transition probability), was decomposed into migration and survival probabilities. Based on the ecology of young trout and because the tagging occasion happened just before the migration period, we chose to model the migration probability as the first transition step. The second step was the survival probability given migration probability. By modelling migration before survival, we were thus able to estimate the survival probability of resident young-trout, i.e. trout that did not migrate during their first winter. The transitions between successively occupied states were assumed to obey a Markov chain (Pradel 2005).

Aarestrup et al. (Aarestrup et al. 2017) showed that seaward migration of juvenile trout can occur outside the peak period (i.e. spring). However, in our study system, migration from La Roche brook (L_r) to Oir river (S_m) and to sea (L_m) were rarely observed in summer (46 on 707 migrations records over the study period). Consequently, we assumed that these transitions were negligible in summer and fixed these transitions to zero in the model. We may thus slightly underestimate migration probabilities.

The encounter probability, i.e. the probability for an individual to be recorded in one event given its underlying state, was decomposed into two steps: detection probability and identification probability of the life history tactic given the detection. For instance, if we consider an individual detected by the antennas in Oir river with unknown type, the individual can be either a short-distance migrant individual or a long-distance migrant individual. A further example, if we consider an individual captured by electrofishing and recorded as non-anadromous type in La Roche brook, actually the individual can be either a resident, a short-distance, or a long-distance individual due to uncertainty in the identification of the type, whereas if we consider an individual captured by the upstream fish trap, it can be only a long-distance migrant individual (see appendix S1 in supporting material). We defined a biannual time step to model the two periods within a year that correspond to different migration

transitions: the juvenile downstream migration from autumn to next spring; and the adult upstream migration from spring to autumn. Data collected from the three monitoring protocols were grouped into two occasions per year: spring (records from March to June), and autumn (records from September to December).

The first occasion was autumn 1997. If an individual was recorded more than once in a time step, we selected the data that gave the most certain information on the individual type. For example, if in a same time step, an individual was captured by electrofishing in Oir River and recorded anadromous type and also detected by the antennas in the Oir River, we selected the information from the electrofishing as event for this time step. There is currently no goodness-of-fit test applicable to multi-event models (Kendall 2009). Therefore, we used the Jolly Move (JMV) umbrella model with observables states (Lr, Sm, Lm) (Pradel 2005) with the software U-Care v2.3.2 (Choquet et al. 2009b). The umbrella model was chosen to be $[\beta(f) \phi(f) p(f) \omega(f)]$ where each parameter was modelled as a function of states (f) with the previous constraints cited.

Initial state	Lr	Sm	Lm	Dead
	*	-	-	-

Migration	Lr	Sm	Lm	Dead
Lr	*	y	y	-
Sm	y	*	y	-
Lm	-	-	*	-
Dead	-	-	-	*

Survival	Lr	Sm	Lm	Dead
Lr	y	-	-	*
Sm	-	y	-	*
Lm	-	-	y	*
Dead	-	-	-	*

Detection	Not seen	pLR	pOir	Ant_LR	Ant_Oir	PM	PD
LR	*	y	-	y	-	-	-
Oir	*	-	y	-	y	-	-
Aval	*	y	y	y	y	y	y
Dead	*	-	-	-	-	-	-

	Not seen	pLR_R	pLR_A	pOir_R	pOir_A	Ant_LR	Ant_Oir	PM	PD	Ant_LR+PM	Ant_Oir+PM
Not seen	*	-	-	-	-	-	-	-	-	-	-
pLR	-	*	y	-	-	-	-	-	-	-	-
pOir	-	-	-	*	y	-	-	-	-	-	-
Ant_LR	-	-	-	-	-	*	-	-	-	y	-
Ant_Oir	-	-	-	-	-	-	*	-	-	-	y
PM	-	-	-	-	-	-	-	*	-	-	-
PD	-	-	-	-	-	-	-	-	*	-	-

Lr = resident trout, Sm = short-distance migrant, Lm = long-distance migrant (i.e. anadromous). pLR = captured by electrofishing in La Roche brook, pOir = captured by electrofishing in Oir river, Ant_LR = detected by the antenna downstream La Roche brook, Ant_Oir = detected by the antenna in Oir river, PM = by the upstream fish trap, PD = by the downstream fish trap, pLR_R = "captured by electrofishing and recorded as non-anadromous type in La Roche brook", pLR_A = "captured by electrofishing and recorded as anadromous type in La Roche brook", pOir_R = "captured by electrofishing and recorded as non-anadromous type in Oir river", pOir_A = "captured by electrofishing and recorded as anadromous type in Oir river", Ant_LR+PM = "captured by the upstream fish trap and detected during the same occasion by the antenna downstream La Roche brook", Ant_Oir+PM = "captured by the upstream fish trap and detected during the same occasion by the antennas in Oir river", "-" represents the absence of possible transition and "*" is the complementary.

3. APPENDIX 3

ARTICLE II. Supplementary figures

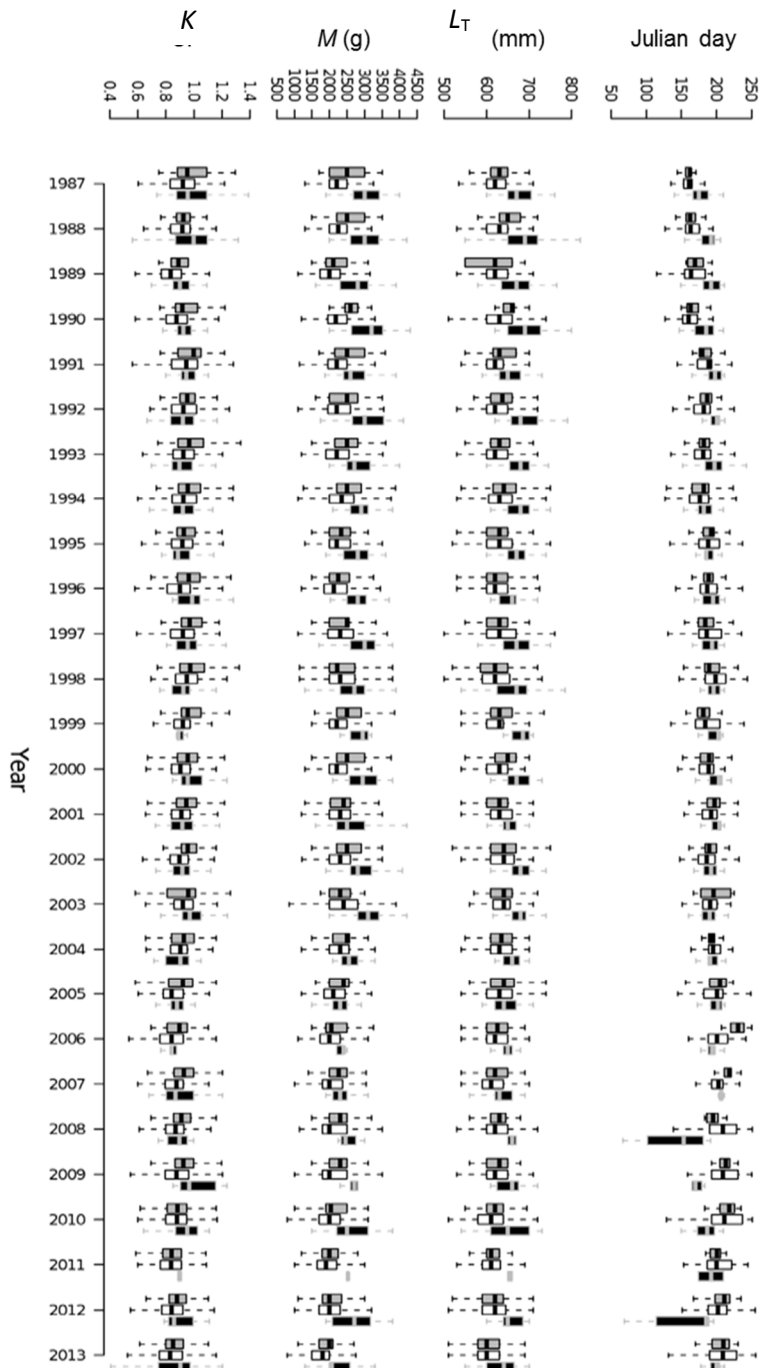


Fig. S1. Box plots of raw data for the date of river entry, total length (L_T), fish mass (M) and Fulton's condition factor (K) in one sea-winter (1SW) *Salmo salar* caught by the French hook-and-line recreational fishery (spring and summer catches) from Normandy (■), Brittany (□) and Aquitaine (▣)

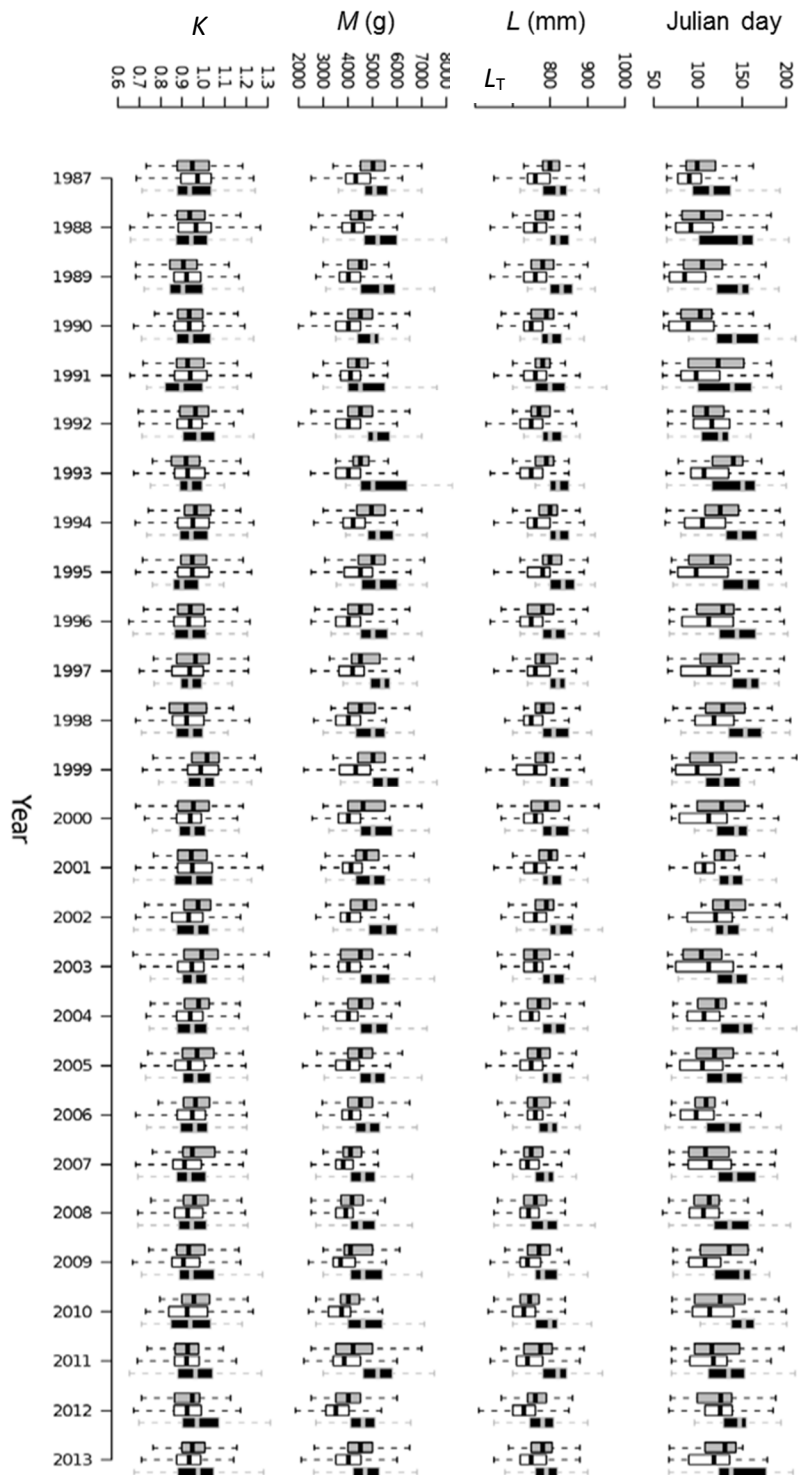


Fig. S2. Box plots of raw data for the date of river entry, total length (L_T), fish mass (M) and Fulton's condition factor (K) in two sea-winter (2SW) *Salmo salar* caught by the French hook-and-line recreational fishery (spring and summer catches) from Normandy (■), Brittany (□) and Aquitaine (▣).

4. APPENDIX 4

ARTICLE III. Supplementary figure

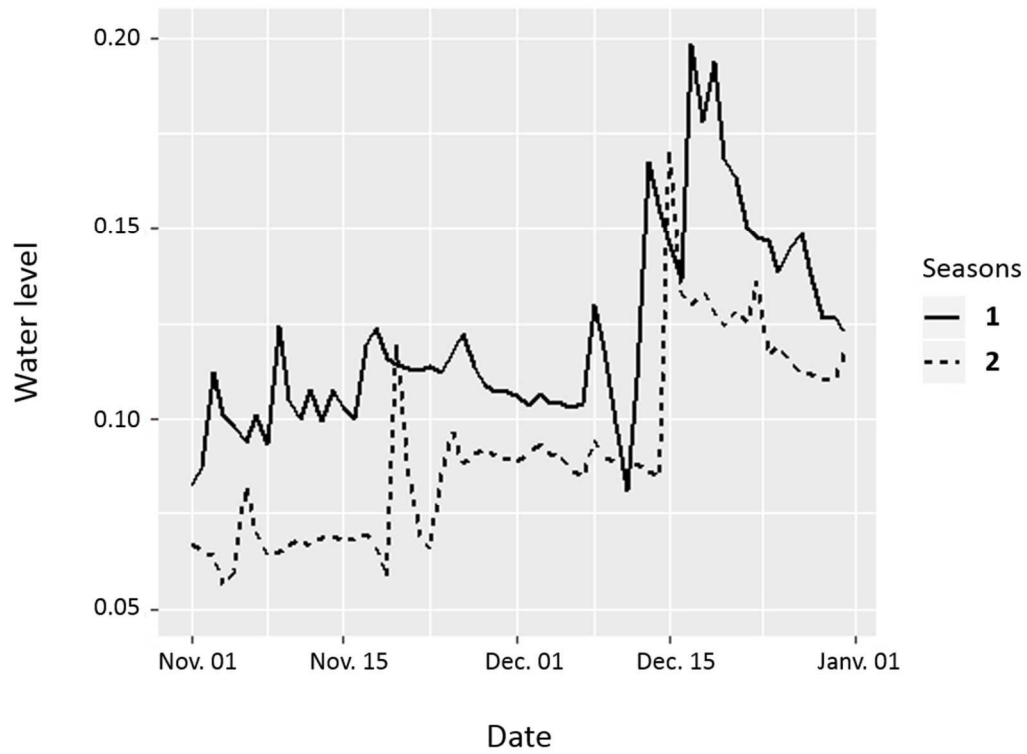


Fig.1. Water level on La Roche brook during the reproductive season 1 (2014-2015) and 2 (2015-2016) data from U3E-INRA monitoring.

5. APPENDIX 5

ARTICLE IV. Parametrization of the mutli-event CR model

The CR model consisted in six states depending on the reproductive strategy and the sex of trout: young female, “Yf”; young male, “Ym”; resident female, “Rf”; resident male, “Rm”; migrant female, “Mf”; and migrant male, “Mm”. We defined 22 events to account for all possible combinations of field records.

Event number	Event description
1	not seen
2	captured by electrofishing and recorded as non-anadromous type in La Roche brook
3	captured by electrofishing and recorded as non-anadromous type and male in La Roche brook (according to morphological features)
4	captured by electrofishing and recorded as non-anadromous type and female in La Roche brook
5	captured by electrofishing and recorded as non-anadromous type in La Roche brook (unknown sex)
6	captured by electrofishing and recorded as anadromous type and male in La Roche brook
7	captured by electrofishing and recorded as anadromous type and female in La Roche brook
8	captured by electrofishing and recorded as anadromous type in La Roche brook (unknown sex)
9	captured by electrofishing and recorded as non-anadromous type and male in Oir river
10	captured by electrofishing and recorded as non-anadromous type and female in Oir river
11	captured by electrofishing and recorded as non-anadromous type in Oir river (unknown sex)
12	captured by electrofishing and recorded as anadromous type and male in Oir river
13	captured by electrofishing and recorded as anadromous type and female in Oir river
14	captured by electrofishing and recorded as anadromous type in Oir river (unknown sex)
15	detected by the antenna downstream La Roche brook with unknown type
16	detected by the antenna in Oir river with unknown type
17	captured by the upstream fish trap and recorded as male
18	captured by the upstream fish trap and recorded as female
19	captured by the upstream fish trap (unknown sex)
20	captured by the downstream fish trap and recorded as male
21	captured by the downstream fish trap and recorded as female
22	captured by the downstream fish trap (unknown sex)

In this model the transition probability, i.e. the probability for an individual to move from one state to another between two consecutive occasions, was decomposed into two conditional steps: survival

probability (ϕ) and migration probability given survival (β). The transitions between successively occupied states were assumed to obey a Markov chain (Pradel 2005). The encounter probability, i.e. the probability for an individual to be recorded in one event given its underlying state, was decomposed into two steps: detection probability (p) and identification probability (I).

All individuals entered the studied population as young in La Roche brook in October but their sex was unknown. Therefore, we assumed a balanced sex ratio at this stage, and constrained the initial state of individuals (i.e. at tagging) in the model as $Y_f = 0.5$.

Transition matrices from GEPAT in E_SURGE, from states at time t (rows of the matrices) to states at time $t+1$ (columns of the matrices). “-” represents the absence of possible transition and “*” is the complementary. p_{LR} = captured by electrofishing in La Roche brook, p_{Oir} = captured by electrofishing in Oir river, Ant_{LR} = detected by the antenna downstream La Roche brook, Ant_{Oir} = detected by the antenna in Oir river, PM = by the upstream fish trap, PD = by the downstream fish trap.

Survival ϕ

$t / t+1$	Ym	Yf	Rm	Rf	Mm	Mf	Dead
Ym	y	-	-	-	-	-	*
Yf	-	y	-	-	-	-	*
Rm	-	-	y	-	-	-	*
Rf	-	-	-	y	-	-	*
Mm	-	-	-	-	y	-	*
Mf	-	-	-	-	-	y	*
Dead	-	-	-	-	-	-	*

Migration β

$t / t+1$	Ym	Yf	Rm	Rf	Fm	Ff	Dead
Ym	-	-	*	-	y	-	-
Yf	-	-	-	*	-	y	-
Rm	-	-	*	-	y	-	-
Rf	-	-	-	*	-	y	-
Mm	-	-	-	-	*	-	-
Mf	-	-	-	-	-	*	-
Dead	-	-	-	-	-	-	*

Detection p

	Not seen	pLR	pOir	Ant_LR	Ant_Oir	PM	PD
Ym	*	y	-	-	-	-	-
Yf	*	y	-	-	-	-	-
Rm	*	y	y	y	y	-	-
Rf	*	y	y	y	y	-	-
Mm	*	-	-	y	y	y	y
Mf	*	-	-	y	y	y	y
DEAD	*	-	-	-	-	-	-

Identification I

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Not seen	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
pLR	-	*	y	y	y	y	y	y	-	-	-	-	-	-	-	-	-	-	-	-	-	-
pOir	-	-	-	-	-	-	-	-	*	y	y	y	y	y	-	-	-	-	-	-	-	-
Ant_LR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-	-
Ant_Oir	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-	-
PM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	y	y	-	-	-
PD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	y	y

6. APPENDIX 6

IPM. Why IPMs often use log-transformed size. From Rees et al. 2014

It is common practise to adopt a log transformation of size when building a new IPM. Why is this? The short answer is that it very often “works”, in that log transformation results in a linear growth model in which the error variance (i.e., the variation in growth) ends up independent of size. This is an assumption of linear regression that ensures the estimated parameters are as precise as they can be. More importantly, it means that to model growth we do not have to resort to more sophisticated methods that require additional parameters to model the size-variance relationship. And in cases where growth variance still depends on size after log transformation, the dependence is often weak, so that a simple linear or exponential model with just one additional parameter is adequate. Another practical advantage of using a log transformation is that it avoids the possibility that the IPM generates individuals with negative sizes: you always have a positive size no matter where you lie on a log transformed scale.

The log transformation also makes biological sense when using a linear model to describe growth. For the moment let u denote some absolute measure of size and $z = \log u$, and assume that growth is completely deterministic. Fitting a linear model using absolute size, $u' = A + Bu$, the growth increment $\Delta u = u' - u$ is a strictly decreasing or increasing function of size. That is, $\Delta u = A + (B - 1)u$. This is a decreasing function of size if individuals exhibit determinate growth ($B < 1$). However, in many species we observe a humped relationship between the absolute growth increment and size, so the relationship between size and age is sigmoidal. This is precisely the relationship that emerges if we instead assume that the expected change in log size is a linear function of log size and therefore fit a linear regression to successive values of log size, $z' = a + bz$. For species with determinate growth ($b < 1$), this implies that the relative growth rate $\log(u') - \log(u) = z' - z = a + (b - 1)z$ is a decreasing function of size. For this model the relationship between the absolute growth increment and size is $\Delta u = e^{a+bu} - u$. This is hump-shaped when $b < 1$.

Growth is a complex phenomenon, reflecting patterns of resource availability, competition and life history allocation decisions. However, one fairly general explanation for the hump-shaped pattern arises from a consideration of energy acquisition and maintenance costs. All else being

equal, larger individuals typically acquire more resources than smaller conspecifics, which means they have more energy available to spend on growth, reproduction and maintenance. When individuals are small, maintenance costs increase slowly with size relative to acquisition, resulting in a positive relationship between size and absolute growth rate. Later in life when individuals are large, maintenance costs increase more rapidly with size relative to acquisition, leading to a negative relationship between size and growth. Such ideas can be formalized using dynamic energy budget theory.

Scientific activities

Scientific publications

- Bal, Montorio, Rivot, Prévost, Baglinière, and Nevoux. **2017**. Evidence for long-term change in length, mass and migration phenology of anadromous spawners in French Atlantic salmon *Salmo salar*. ***Journal of Fish Biology***
- Montorio, Evanno, and Nevoux. Intra- and interspecific density shape different life history traits in a salmonid population. ***In major revision in Oecologia***
- Montorio, Ozgul, Evanno, and Nevoux. Diversity in life history tactics promotes population viability in a partially migratory fish. ***Under review in Oikos***
- Gordon, Harding, Clever, Davison, Montgomery, Nedelec, Weatherhead, Windsor, Armstrong, Bardonnnet, Bergman, Britton, Coté, D'Agostino, Greenberg, Harborne, Kahilainen, Metcalfe, Mills, Milner, Mittermayer, Montorio, Prokkola, Rutherford, Salvanes, Simpson, Vainikka, Pinnegar, Santos. Fishes in a changing world: learning from the past to promote sustainability of fish populations. ***Under review in Journal of Fish Biology***
- Montorio, Nevoux, Besnard, Jousseume, Le Cor, Tremblay, and Evanno. The migrant and resident reproductive success: the tactic and trait that drive the population juvenile production in a changing world. ***In preparation***

Oral communications

- Ma thèse en 180 sec. Rennes, February 2015
- Bal, Montorio, Prévost, Baglinière, Nevoux, and Rivot. Individual characteristics impacts and buffering to environmental variability emerge from synchronous changes in adult salmon migratory characteristics. 11th Ecology & Behaviour meeting. Toulouse, FR. May 17 - 21, 2015.
- Montorio, Evanno, and Nevoux. Contrasted impact of density increase on life history strategies in a population of wild trout (*Salmo trutta*). ***101st Ecological Society of America annual meeting***. Fort Lauderdale, USA. August 7 – 12, 2016.
- Montorio, Ozgul, Evanno, and Nevoux. The effect of the partial migration on the population dynamics. ***Ecobio meeting***. Rennes, FR. April 3th, 2017.
- Montorio, Nevoux, and Evanno. The determination of the reproductive success of resident and anadromous forms of brown trout. ***SPAM meeting***. Saint-Pée sur Nivelles, FR. May 9-11, 2017.

- Montorio, Ozgul, Evanno, and Nevoux. The sensitivity of the population growth to vital rates of resident and anadromous individuals in a brown trout population. **50th Anniversary Symposium of the Fisheries Society of the British Isles**. Exeter, UK. July 3-7, 2017.

Posters

- Montorio, Ozgul, Evanno, and Nevoux. The sensitivity of the population growth to vital rates of resident and anadromous individuals in a brown trout population. **50th Anniversary Symposium of the Fisheries Society of the British Isles**. Exeter, UK. July 3-7, 2017.

Teaching experience

- Courses of Diversity and organization of life, and Nutrition-Reproduction to Bachelor students, University of Rennes I – 66h, 2015-2016.

Intern supervision

- Co-supervision of a Master 2 thesis: The effect of the life history tactics on the reproductive success of Atlantic salmon, *Salmo salar*.

International mobility

Research fellowship at the University of Zurich, Department of Evolutionary Biology and Environmental studies, Population Ecology Group supervised by A. Ozgul (Switzerland). October – December 2016.

Training

- Les Doctoriales de Bretagnes 2015. UBL. Rennes, FR. February, 2015.
- Animal experiment training (level 2). ONIRIS. Nantes, FR. June, 2015.
- Communication English-French. UBL. Rennes, FR. May, 2016.
- Bayesian integrated population modeling using BUGS and JAGS. Swiss Ornithological Institute, Sempach, CH. December, 2016.
- Sustainable and Efficient Food Systems: Food, Water and Energy Nexus. EIR-A. Montpellier, FR. April, 2016.
- Forests in the territories : issues and risks. EIR-A. Nancy, FR. April, 2015.
- Integrity and Ethics in research. EIR-A. Nancy, FR. April, 2015.

Member of Agreenium International Research School (EIR-A) since 2014. (<http://www.agreenium.org/>)

ABSTRACT

This thesis investigates the influence of the tactic diversity on population dynamics in two partially migratory salmonids: Atlantic salmon, *Salmo salar* and brown trout, *Salmo trutta*. These two species have high ecological and economic values but the role of migrant and resident individuals on population dynamics and resilience to environmental changes is currently largely unknown. I undertook a multidisciplinary approach combining demographic, genetic, and modeling tools to address these issues in populations from France. I found that tactic determination is partly plastic as juveniles can respond to environmental variations by migrating. In addition, this thesis showed that tactics diversity in partially migratory populations enables a better use of favorable environmental conditions and buffer the effects of unfavorable conditions on their dynamics. These two processes might promote a higher resilience of partially migratory populations to environmental change, including anthropogenic effects, than in solely migratory or resident populations. Nonetheless, given the different strategies in Atlantic salmon and brown trout, my results suggested that brown trout should have better abilities to response to environmental changes and a higher level of resilience than Atlantic salmon.

Key words: partial migration, *Salmo*, resilience, life history tactic, demographic parameters, population model.

RESUME

Cette thèse étudie l'influence de la diversité des tactiques d'histoire de vie sur la dynamique des populations de deux salmonidés à migration partielle: le saumon Atlantique, *Salmo salar* et la truite commune, *Salmo trutta*. Ces deux espèces ont de fortes valeurs écologique et économique, mais les rôles respectifs des individus résidents et migrateurs sur la dynamique et la résilience des populations à des changements environnementaux demeurent méconnus. Nous avons abordé ces questions par des approches démographiques, génétiques et de modélisation. Nous avons démontré que la détermination de la tactique d'histoire de vie est en partie plastique et permet aux individus juvéniles de migrer en réponse à un changement de l'environnement. De plus, cette thèse démontre que la diversité des tactiques permet aux populations à migration partielle de bénéficier d'un changement favorable de l'environnement et de réduire l'effet d'un changement défavorable sur la dynamique de population. Ces deux processus pourraient expliquer la plus forte résilience des populations à migration partielle face aux variations environnementales par rapport aux populations strictement résidentes ou migratrices. Toutefois, étant donné les différences de stratégies chez le saumon Atlantique et la truite commune, nos résultats suggèrent que la truite a une meilleure capacité de réponse aux changements environnementaux et un niveau de résilience plus élevé que le saumon Atlantique.

Mots clés: migration partielle, *Salmo*, résilience, tactique d'histoire de vie, paramètre démographique, modèle de population.

RÉSUMÉ

ABSTRACT

Impact des changements environnementaux sur l'histoire de vie, la démographie et la dynamique de population chez les salmonidés

Cette thèse étudie l'influence de la diversité des tactiques d'histoire de vie sur la dynamique des populations de deux salmonidés à migration partielle: le saumon Atlantique, *Salmo salar* et la truite commune, *Salmo trutta*. Ces deux espèces ont de fortes valeurs écologique et économique, mais les rôles respectifs des individus résidents et migrants sur la dynamique et la résilience des populations à des changements environnementaux demeurent méconnus. Nous avons abordé ces questions par des approches démographiques, génétiques et de modélisation. Nous avons démontré que la détermination de la tactique d'histoire de vie est en partie plastique et permet aux individus juvéniles de migrer en réponse à un changement de l'environnement. De plus, cette thèse démontre que la diversité des tactiques permet aux populations à migration partielle de bénéficier d'un changement favorable de l'environnement et de réduire l'effet d'un changement défavorable sur la dynamique de population. Ces deux processus pourraient expliquer la plus forte résilience des populations à migration partielle face aux variations environnementales par rapport aux populations strictement résidentes ou migratrices. Toutefois, étant donné les différences de stratégies chez le saumon Atlantique et la truite commune, nos résultats suggèrent que la truite a une meilleure capacité de réponse aux changements environnementaux et un niveau de résilience plus élevé que le saumon Atlantique.

Mots-clefs : migration partielle, *Salmo*, résilience, tactique d'histoire de vie, paramètre démographique, modèle de population.

Impact of environmental changes on life history, demography and population dynamics in salmonids

*This thesis investigates the influence of the tactic diversity on population dynamics in two partially migratory salmonids: Atlantic salmon, *Salmo salar* and brown trout, *Salmo trutta*. These two species have high ecological and economic values but the role of migrant and resident individuals on population dynamics and resilience to environmental changes is currently largely unknown. I undertook a multidisciplinary approach combining demographic, genetic, and modeling tools to address these issues in populations from France. I found that tactic determination is partly plastic as juveniles can respond to environmental variations by migrating. In addition, this thesis showed that tactics diversity in partially migratory populations enables a better use of favorable environmental conditions and buffer the effects of unfavorable conditions on their dynamics. These two processes might promote a higher resilience of partially migratory populations to environmental change, including anthropogenic effects, than in solely migratory or resident populations. Nonetheless, given the different strategies in Atlantic salmon and brown trout, my results suggested that brown trout should have better abilities to response to environmental changes and a higher level of resilience than Atlantic salmon.*

Keywords: partial migration, *Salmo*, resilience, life history tactic, demographic parameters, population model.



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