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Variability in dispersal, stocking practices, and life strategies of Atlantic salmon coexisting populations using otolith chemistry

Anthony Fontaine

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UNIVERSITÉ DE PAU ET DES PAYS DE L'ADOUR
ÉCOLE DOCTORALE 211 - SCIENCES EXACTES ET LEURS APPLICATIONS

VARIABILITY IN DISPERSAL, STOCKING PRACTICES, AND LIFE STRATEGIES OF ATLANTIC SALMON COEXISTING POPULATIONS USING OTOLITH CHEMISTRY

Defended on November 15th, 2024, by

Anthony FONTAINE

to obtain the title of **Philosophiæ Doctor (PhD)**

In population biology and ecology

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ABSTRACT

In our very volatile world, which experiences rapid and drastic global changes, there is a crucial need for a better understanding of the responses of threatened species from a conservation perspective. Migratory fish species such as Atlantic salmon (*Salmo salar*) are particularly vulnerable, as they face numerous environmental (e.g. climate change) and anthropogenic (e.g. habitat alterations) pressures along the freshwater-estuarine-sea continuum. Indeed, although the eco-evolutionary dynamics of this species have led to considerable life-history diversity, which spans diverse spatial and temporal scales, a general reduction in the portfolio effect is reported across the northern hemisphere. Salmon populations from the southern Bay of Biscay represent the southern limit of the species' range on the eastern Atlantic coast, yet little is known about the structure (i.e. connectivity, life history diversity, and proportion of hatchery-origin individuals in adult returns) of these populations, which are particularly at risk considering their location. Therefore, from this context, we used the different properties of otolith chemistry to (i) quantify the temporal patterns of connectivity levels in the southern Bay of Biscay, (ii) investigate the role of stocking programs in the proportion of hatchery-origin adult returns and (iii) assess the spatio-temporal variation of life history diversity in a natural gradient of coexisting populations (from strongly dependent to completely independent of stocking programs). Our results demonstrated a complex metapopulation structure, with asymmetric migratory flows between a set of local populations. Exchanges of individuals mostly originated from proximate populations, but also included some from distant populations (with more variable contributions over time), depending on the receiving population, and this apparent biocomplexity was relatively stable over a 10-year period. In coexisting populations, we observed an asymptotic effect of released reared-fish biomass and a “bigger is better” pattern with stage-at-release in the proportion of hatchery-origin returning adults. This thesis also revealed strong spatial synchrony between Atlantic salmon

populations from southern France, especially considering the juvenile (freshwater) stage, with a net increase in the proportion of one-river winter (1RW) in adult returns. Overall, my thesis emphasizes the importance of better understanding the complex mechanisms driving the metapopulation dynamic, as it is composed of local populations that are managed independently, which exhibit evidence of spatial autocorrelation. Since Atlantic salmon are exposed to many stressors along their ontogenic migrations, occurring at different life stages, and acting independently or synergistically, identifying the key factors contributing to weakened portfolios and increased spatial synchrony is critical. Finally, this thesis reinforces the urgent need for collaborative work to promote natural biocomplexity and connectivity (regarding life history diversity but also habitat functionality), as it will enhance population stability and persistence in a very uncertain future.

Keywords: metapopulation, portfolio effect, biocomplexity, connectivity, otolith chemistry, management, conservation, synchrony, stocking programs, coexisting population

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LIST OF ABBREVIATIONS

1RW: One-river winter

1SW: One-sea winter

2RW: Two-river winter

2SW: Two-sea winter

3SW: Three-sea winter

3Y: Three years old

4Y: Four years old

$^{87}\text{Sr}/^{86}\text{Sr}$: Isotopic ratio of strontium

AD: Adour

ALL: Allier

Ar: Argon

ARI: Ariège

Ba: Barium

BGM: *Bretagne Grands Migrateurs*

BID: Bidasoa

BRE-GAL: Bretagne-Galicia

Ca: Calcium

CaCO_3 : Calcium carbonate

CL: Conservation limit

CMR: Capture-Mark-Recapture

CNICS: *Centre national d'interprétation des captures de salmonidés migrants*

CNRS: *Centre National de la Recherche Scientifique*

CNSS: *Conservatoire National du Saumon Sauvage*

CO₂: Carbon dioxide

COGEPOMIs: *COmités de Gestion des POissons Migrateurs*

CRM: Certified Reference Material

CWT: Coded Wire Tag

DOR: Dordogne

DTW: Dynamic Time Warping

EM: Expectation-Maximization

ER: Emigration rate

ESA: Electrostatic sector

EU: European Union

FL: Fork length

FR: Fidelity rate

GAM: Generalized Additive Model

GAR: Garonne

GIR: Gironde

GWLs: Global warming levels

HDDC: High dimensional data clustering

He: Helium

HR: Homing rate

I3: Inorganic Isotopic Imaging

ICES: International Council for the Exploration of the Sea

IOS: International Otolith Symposium

IPCC: Intergovernmental Panel on Climate Change

IR: Immigration rate

IRMS: Isotope ratio mass spectrometry

IUCN Red List: International Union for Conservation of Nature's Red List of Threatened Species

LA-ICPMS: Laser ablation – inductively coupled plasma mass spectrometry

LC: Least Concern

LDA: Linear Discriminant Analysis

Loess: Locally estimated scatterplot smoothing

LOGRAMI: *Loire Grands Migrateurs*

M/Z: Mass/Charge ratio

MC-ICPMS: Multi-collector – inductively coupled plasma mass spectrometry

MDS: Multidimensional Scaling

Mg: Magnesium

MIGADO: *Migrateurs Garonne Dordogne Charente Seudre*

Mn: Manganese

MSW: Multi-sea winter

NASCO: North Atlantic Salmon Conservation Organization

NIV: Nives

NT: Near Threatened

NVL: Nivelle

OFB: *Office Français de la Biodiversité*

OLO: Oloron

OOB: Out-of-Bag

OR: Otolith radius

P: Phosphorus

PAMAL: *Plateforme d'Analyse des Métaux Traces par Ablation Laser*

PIXE: Particle induced x-ray emission

PLAGEPOMIs: *PLAns de GEstion des POissons Migrateurs*

QDA: Quadratic Discriminant Analysis

RF: Random Forest

RLM: Robust Linear Model

RNA: *Région Nouvelle-Aquitaine*

SIMS: Secondary ion mass spectrometry

SD: Standard Deviation

Sm: Smoothing method

Sr: Strontium

TAC: *Total Admissible de Capture* / Total Allowable Catch

TOF: Time of flight

UPPA: *Université de Pau et des Pays de l'Adour*

VEZ: Vézère

Zn: Zinc

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“The pessimist complains about the wind; the optimist expects it to change; the realist adjusts the sails.”

William Arthur Ward

1 GENERAL INTRODUCTION

CONTEXT

For centuries, the global economy has been based on a traditional agrarian system over the world. Human populations would then live from local cultures and proximate trades. The worldwide industrial revolution (Ashton, 1997), which our planet experienced for roughly seventy years (1760-1830), marked an unequivocal turning point for the economy (Xu et al., 2018), but not only. The development of international trades, the multiplication of operating sites, and innovations towards faster, more efficient technologies for large-scale production have considerably modified our environment. Where traditional methods were limited by the human calorie, the industrial revolution has opened up new prospects for expanding and intensifying production, on both continents and seas, leading to unprecedented environmental consequences. From 1985 to 1990, Jean Jouzel and Claude Lorius published a series of papers demonstrating for the first time the significant relationship between carbon dioxide (CO₂) emissions and climate change (Lorius et al., 1985; Jouzel et al., 1987; Lorius et al., 1990). Ever since, climatologists and paleoclimatologists have identified considerable effects between human activities, greenhouse gas emissions, and the overwhelming number of environmental consequences (Appendices 1, 2). Among them, an abnormally rapid rise in the Earth's surface temperature, the premature melting of the largest glacial zones, and the increase and intensification of extreme climatic events have been predicted for more than 30 years now in the first report of the Intergovernmental Panel on Climate Change (IPCC) (IPCC, 1992). However, global change does not only affect the climate itself but also the vast majority of biotopes and biocenoses we know on Earth (IPCC, 2023a). Based on the work from Soulé (1991), the United States National Research Council suggested 5 components of global change: (1) degradation and fragmentation of natural environments; (2)

overexploitation of wild species through overfishing, deforestation, poaching; (3) modification of biogeochemical and hydrological cycles and pollution of water, soil and air; (4) introduction of invasive exotic species and; (5) climate change (United States National Research Council, 2000). Undoubtedly, one of the major issues with global change is the exceptional speed at which it is occurring in our contemporary world (IPCC, 2023b) and how it sharply contrasts with eco-evolutionary processes that have taken place throughout the millennia. As a result, many evolved strategies that follow seasonal variations are now extremely disturbed or jeopardized by global change.

From ants to whales, migration phenomena are widespread across the animal kingdom (Milner-Gulland et al., 2011) and represent one of the most fascinating and complex (Maggini et al., 2022) life strategies in response to biotic and abiotic cues. As described in Shaw (2012), there are three reasons for an animal to benefit from a migration: to seek refuge, to breed, or to track environmental resources. However, because migration is mainly driven by environmental conditions (*e.g.* temperature, photoperiod, food availability, or predation), it is critical to understand the extent to which climate change is affecting the “selective pressures on movement behavior” (Shaw, 2016). In aquatic ecosystems, diadromous fish can be categorized according to three life strategies: (i) the anadromous fish where adults migrate from the ocean, where they have completed their somatic growth, to freshwater to spawn, (ii) the catadromous fish which follow the opposite cycle and (iii) the amphidromous fish, which undergo regular migrations between freshwater and marine environments independently of their reproductive cycle (Myers, 1949; McDowall, 1988). Although diadromy is quite scarce among fish species with about 250 documented species (McDowall, 2008), which represents only 0.8% of the ray-finned fish species (Corush, 2019), many of them are well known because of their high economic and cultural values around the world (Lassalle et al., 2009a). Additionally, recent studies have demonstrated the high potential of ecosystem services (Appendix 3) that can be provided by diadromous species (see

DiadES project: <https://diades.eu/>), strengthening their ecological importance. Yet, in the last five decades, diadromous fish have undergone a massive decline (Limburg and Waldman, 2009; Tamario et al., 2019; Almeida et al., 2023) (Figure 1-1), mostly due to anthropogenic pressures (e.g. habitat alterations such as dams and anthropic barriers, overexploitation, climate change, pollution). Given the particular complexity of diadromous life cycles and the negative effect of global change on natural ecosystems, improving our understanding of fish life strategies and implementing adapted management actions are key (McDowall, 1999) to maintain these species, although very challenging (Gallagher et al., 2022).

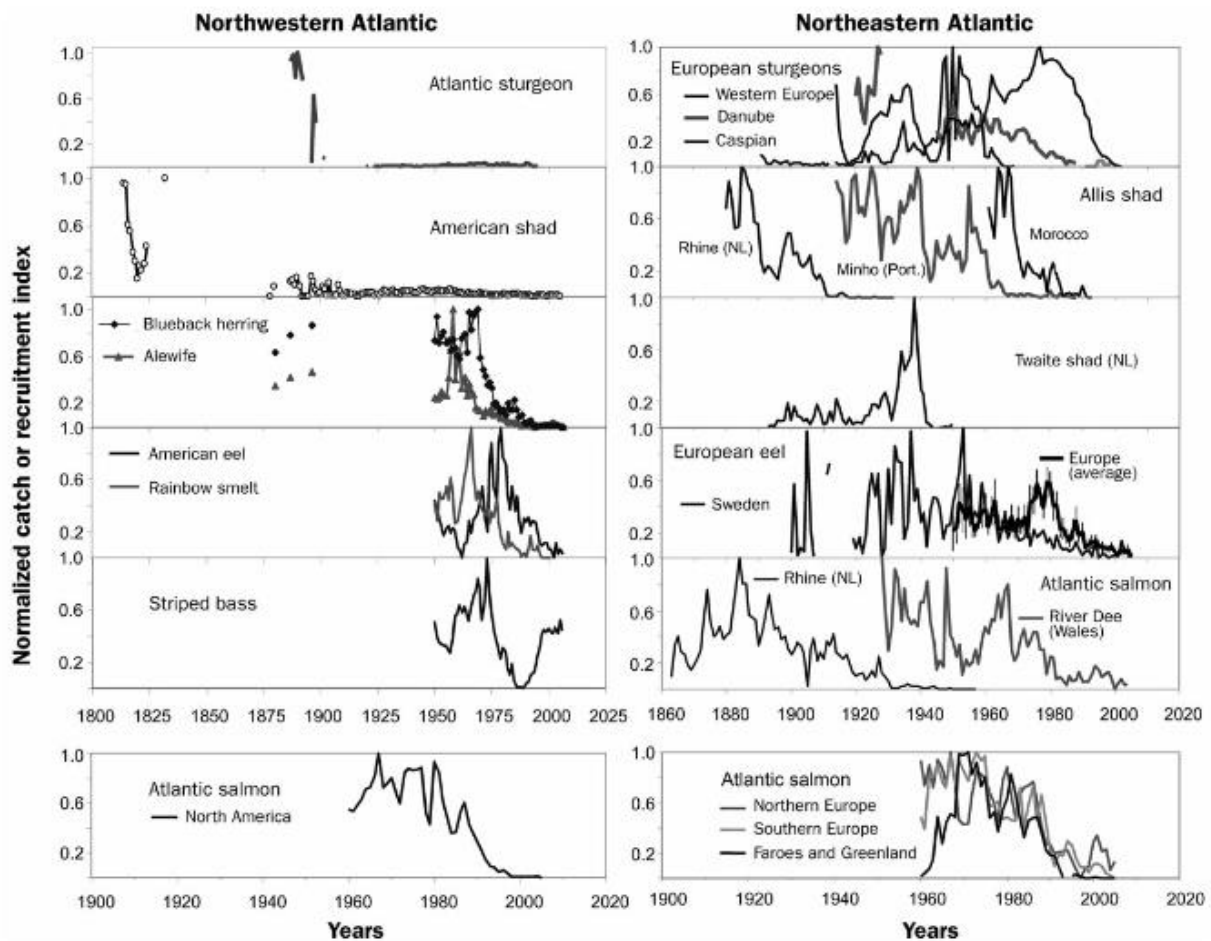


Figure 1-1: Normalized time series of indices of abundance of selected north Atlantic diadromous species, from Limburg and Waldman (2009).

The Atlantic salmon (*Salmo salar*, Linnaeus 1758) is perhaps the most valuable diadromous fish in the North Atlantic with a very high cultural, economic, recreational, and subsistence importance (Thorstad et al., 2021). Like many other diadromous species, Atlantic salmon populations have been strongly decreasing in the last 50 years, with worldwide nominal catches crashing by around 80% between 1975 and 2000 (ICES, 2021). Although this important decline is thought to be mostly driven by reduced marine survival (Chaput, 2012; ICES, 2021), it is still not clear how environmental stressors are affecting Atlantic salmon populations. In fact, each life stage can be affected separately (Figure 1-2) by interacting stressors, possibly resulting in individual and populational impairments (Forseth et al., 2017; Crozier and Siegel, 2023; Vehanen et al., 2023). Thus, it remains very challenging to underpin the consequences of combined natural and anthropic pressures, that vary across life stages, meaning both spatially and temporally, especially in a changing world (Crozier and Siegel, 2023).

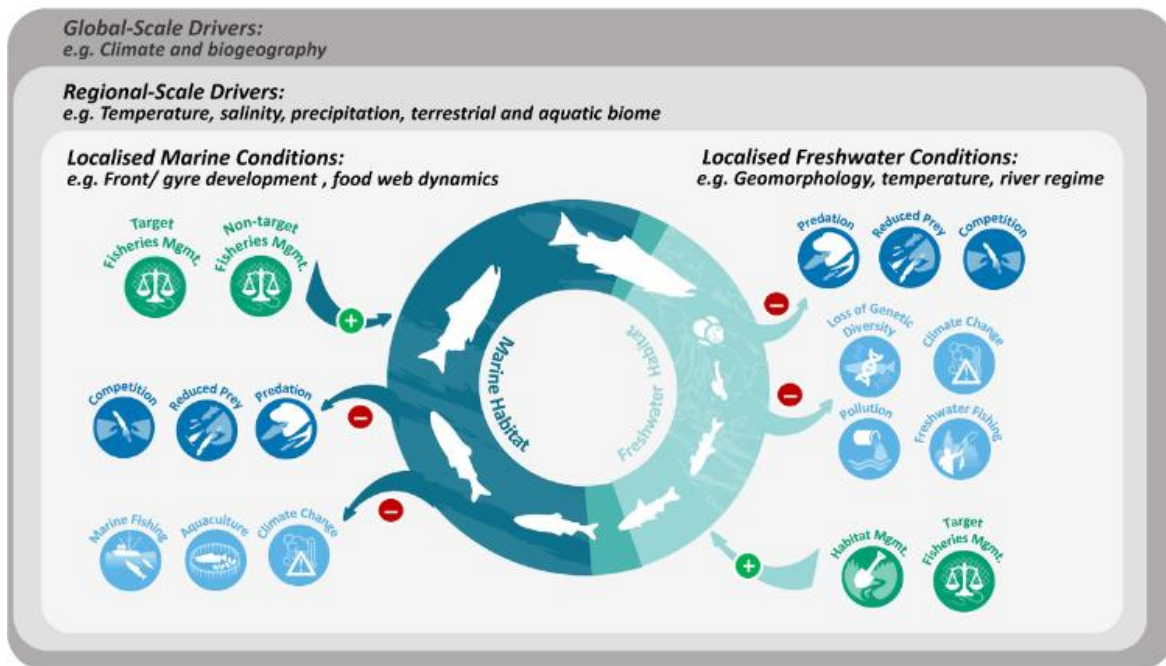


Figure 1-2: Conceptual overview of the life cycle of the Atlantic salmon showing hierarchical scaling of primary environmental drivers influencing stock dynamics across the marine and freshwater life stages, from Bull et al. (2022).

In Atlantic salmon, the upstream migration to spawning grounds is characterized by a strong homing behavior, with generally from 90 to 95% of individuals returning to their natal stream in wild populations (Jonsson et al., 2003; Keefer and Caudill, 2014; Lamarins and Buoro, 2023). As a result, this elevated “fidelity” promotes locally-adapted populations and has preferably justified regional or river-scale management (Thorstad et al., 2021) to maintain fitness benefits for the next generations. This is especially true for massive stocking programs that have been adopted in many North Atlantic rivers where salmon spawn or used to spawn (ICES, 2021), in response to population collapse (Chaput, 2012; ICES, 2019). Aside, dispersal is also fundamental for *Salmo salar*, highly influenced by proximate (e.g. habitat quality) and ultimate (e.g. habitat stochasticity) environmental cues (reviewed in Lamarins (2022)). Thus, salmon populations often exhibit a metapopulation structure, via the exchange of individuals (Schtickzelle and Quinn, 2007), which may vary spatially and/or temporally, both in terms of direction and intensity. The sustainability of this complex natural mosaic (*i.e.* biocomplexity) in life histories is essential for reducing population synchrony, which can erode the portfolio effect (Greene et al., 2010; Schindler et al., 2010; Satterthwaite and Carlson, 2015; Sturrock et al., 2015), particularly in a global change context (Anderson et al., 2015; Herbold et al., 2018; Crozier and Siegel, 2023). While a substantial amount of work on dispersal and connectivity has been conducted on Pacific salmon (Candy and Beacham, 2000; Brenner et al., 2012; Willmes et al., 2021) and in the northern ranges of Atlantic salmon distribution (Jonsson et al., 2003; Pedersen et al., 2007), we still lack information on its south-western area of distribution, especially considering spatial and temporal variations, in addition to the potential adverse effects of hatchery releases (Jonsson et al., 2003; Horreo et al., 2012; Ford et al., 2015; Jonsson and Jonsson, 2017).

In this context and based on otolith chemistry, this thesis aims to (i) investigate and quantify the inter-annual variability in dispersal behaviors of Atlantic salmon populations in the southern Bay of Biscay, (ii) examine the role of stocking programs in adult returns and (iii) to better

understand the life strategies and potentially the key drivers of returning mature salmon in coexisting populations.

THE ATLANTIC SALMON: A FASCINATING TRAVELLER IN A CHANGING WORLD

1.1 Life cycle

Native to European and North American basins that flow into the northern Atlantic Ocean, as well as the Barents and Baltic Seas (Figure 1-3), the Atlantic salmon is an anadromous fish whose demonstrates a wide diversity of life strategies (Birnie-Gauvin et al., 2019). Indeed, although the vast majority of individuals migrate between freshwater and marine water, other non-anadromous forms can occur (*i.e.* precocious maturation, complete freshwater residence in lakes or rivers) (Klemetsen et al., 2003; Thorstad et al., 2010; Åsheim et al., 2023).

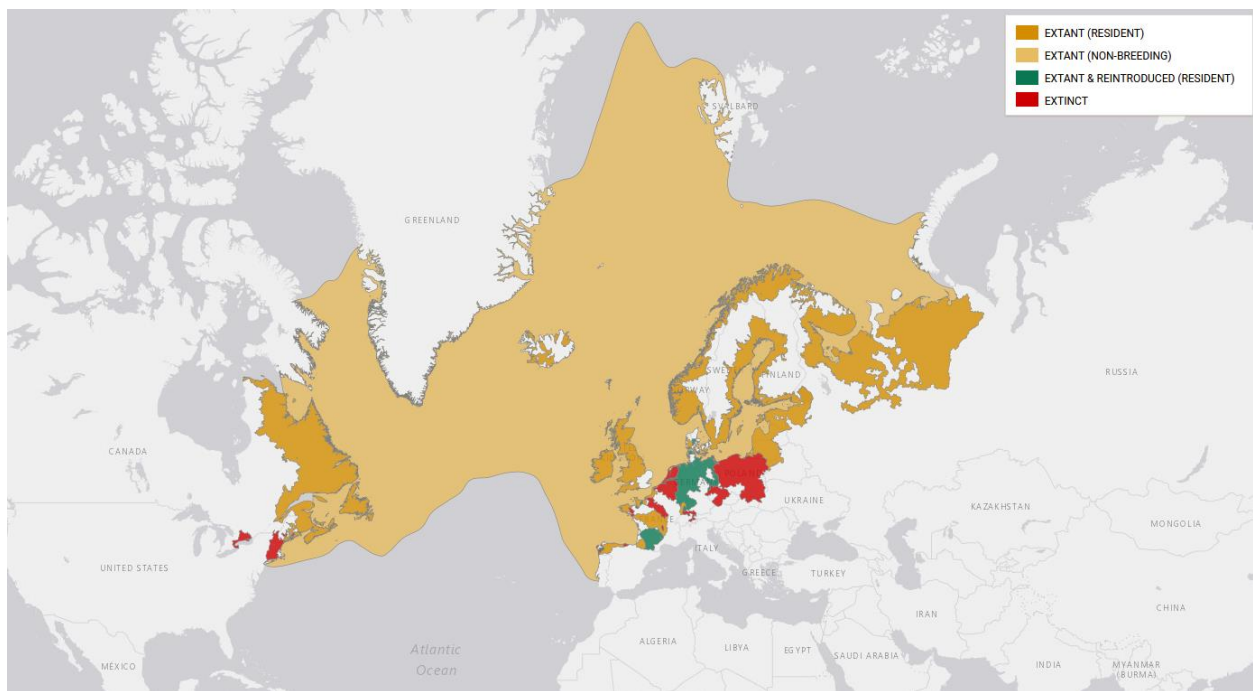


Figure 1-3: Map of the past and present worldwide distribution ranges of the Atlantic salmon (*Salmo salar*).

Source: <https://www.iucnredlist.org/species/19855/67373433#geographic-range>.

Typically, mature adults spawn in rivers during the winter and the eggs deposited on specific gravel beds (the nests can be referred to as “redds”) will hatch in the spring. The

incubation time is often estimated in degree-days and may roughly vary between 450 and 500°C/day (Jonsson and Jonsson, 2009). According to a combination of factors (e.g. the latitude and the associated water temperature, the genetic make-up), the alevins will feed on their endogenous reserves, *i.e.* the yolk sac, for 3-8 weeks before they emerge from the gravel as fry and start an exogenous feeding (Thorstad et al., 2010). The juveniles or “parrs” will most commonly spend 1-4 years in freshwater before starting their downstream migration where they experience strong behavioral, physiological, and morphological transformation defined as “smoltification” (McCormick et al., 1998). This transition from parr to smolt enables young salmon to prepare for marine conditions, and is considered as a key stage for individual survival (Teichert et al., 2020). Once at sea, adults from temperate regions will usually feed for 1-5 years before initiating their breeding migration (Klemetsen et al., 2003; Thorstad et al., 2010). Fish that experience only one marine winter are called “one-sea winter” (1SW) or “grilse” while adults that grow for at least two successive years at sea are referred to as “multi-sea winter” (MSW). After the spawning period, although the majority of individuals die in the river (*i.e.* semelparous), some can survive the breeding season and spawn multiple times (*i.e.* iteroparous, or “kelts”, or “repeat spawners”) (Kaland et al., 2023; Simmons et al., 2024). Here again, multiple strategies are observed in the wild for iteroparous individuals, with fish staying from days to months in riverine or estuarine habitats before migrating to the ocean (Birnie-Gauvin et al., 2019). The latter is a perfect example of the wide diversity of tactics that Atlantic salmon can express (Figure 1-4), as demonstrated by Erkinaro et al. (2019) with no less than 120 different life histories observed over a 40-year period.

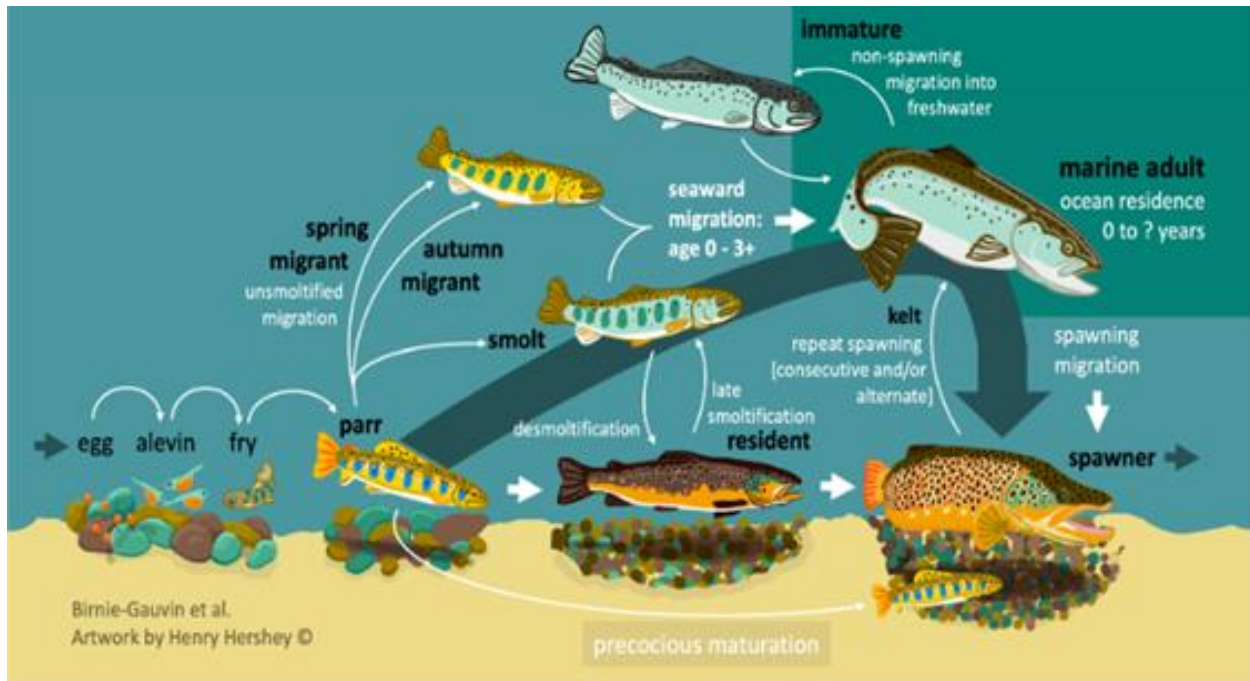


Figure 1-4: An improved life cycle of Atlantic salmon (*Salmo salar*) from Birnie-Gauvin et al. (2019). The most commonly described anadromous lifecycle (and perhaps the most commonly observed strategy) is highlighted by the dark blue arrow.

1.2 Status of *Salmo salar*

Worldwide populations of Atlantic salmon have strongly diminished in the last 40 to 50 years (NASCO, 2020a), and despite a drastic effort to reduce marine and estuarine captures (ICES, 2021), most of the natural populations are still displaying signs of decline (Figure 1-5). This collapse has resulted in the recent change of category in the International Union of Nature’s Red List of Threatened Species (IUCN Red List) from least concern (LC) to near threatened (NT). Because salmon inhabit various habitats along the freshwater-estuary-sea continuum at different life stages, they are continuously exposed to a wide variety of environmental risks (Crozier and Siegel, 2023; Murdoch et al., 2024). “Drivers influencing state, duration, and functional traits of the different life stages can operate across multiple scales, often in interaction (Brook et al., 2008), and several may be operating either in synchrony or asynchronously—as stressors rarely occur

singly in space or time (Jackson et al., 2021)”, as presented in Bull et al. (2022). Therefore, from a conservation perspective, there is an urgent need to increase our knowledge of each life stage response to environmental stressors, with emphasis on both space and time, and share the acquired information via the various institutions and stakeholders (*i.e.* scientists, regional agencies, managers, policymakers, local communities) to achieve the most efficient management possible (Gillis et al., 2023).

1.3 Major causes of decline

In order to consider and understand the influence of previous life-history traits and “their interactive and legacy effects” (Gregory et al., 2019) on subsequent life stages, a brief overview of the main environmental threats by life stage is presented in the following section.

Eggs and alevins

The primary issues identified with the first life stages are related to water flow and temperature (Jonsson and Jonsson, 2009; Crozier and Siegel, 2023; Gillis et al., 2023). As incubation time is directly related to an estimated temperature sum, which varies by location, a large or sudden increase in river temperature can be lethal to an egg’s survival (Smialek et al., 2021). Negative effects of elevated temperatures on hatching time (which will subsequently affect the environmental conditions encountered for alevins and fry– match/mismatch) and embryo sizes are also described in the literature (Jonsson and Jonsson, 2009; Crozier and Siegel, 2023). In addition, water discharge and quality (*i.e.* oxygen concentration and sedimentation level) also play an important role in an egg’s viability and/or development (Smialek et al., 2021).

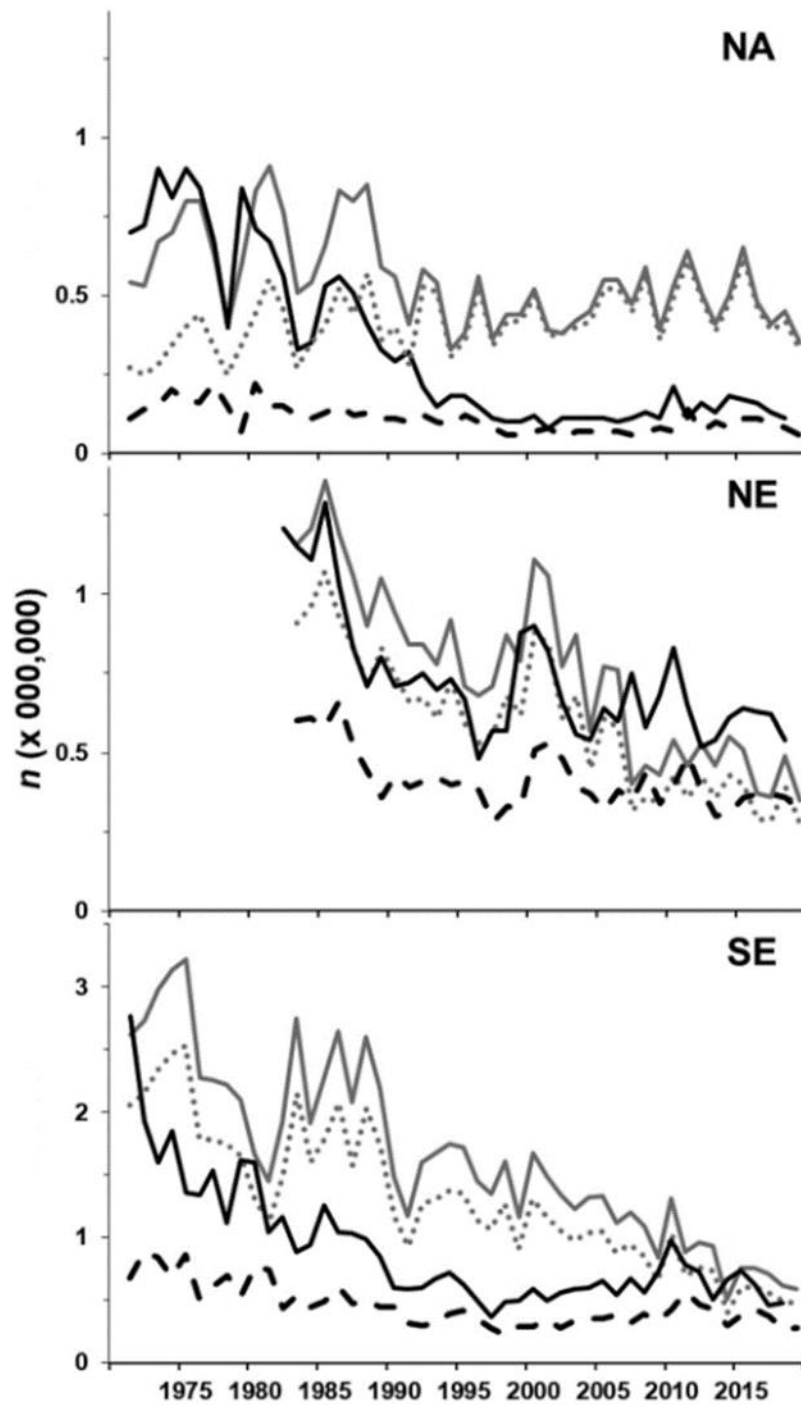


Figure 1-5: Estimated prefishery abundance (solid lines) and adult returns (dotted or dashed lines) of wild 1SW (gray) and 2SW (black) Atlantic salmon in millions from North American (NA), Northern Europe (NE) and Southern Europe (SE) stock complexes in the North Atlantic during 1971–2019, from Dadswell et al. (2022).

Fry and parr

As for eggs and alevins, and commonly to every freshwater stage, water discharge and temperature are key environmental drivers for fry and parr survival (Crozier and Siegel, 2023; Andrew et al., 2024; Pander et al., 2024), even if fry display the highest thermal tolerance compared to the others stages (Gillis et al., 2023). Indirect effects of disturbances in water temperature or discharge are also identified with changes in prey abundance and diversity, which can in turn alter young salmon growth (Crozier and Siegel, 2023). Because the parr are highly mobile, they need various habitats and resources during their downstream migration. For example, regarding food availability, this has been described as the concept of “foodscapes” (Rossi et al., 2023). A significant amount of studies on both Pacific and Atlantic salmon species also demonstrate the importance of habitat diversity and their dynamics for growth and survival (Phillis et al., 2018; Brennan et al., 2019; Cordoleani et al., 2021; Coleman et al., 2022; Cordoleani et al., 2024), especially in a global change context (Gillis et al., 2023; Iacarella and Weller, 2024). Of course, human-induced modifications such as dams or weirs, which reduce the connectivity between free-flowing rivers (Grill et al., 2019), can severely increase fry and parr mortality (Croze, 2008). Other environmental stressors such as pollution (OECD, 2017), density-dependence, intra- or inter-species competition (Crozier and Siegel, 2023), or thiamine deficiency (Suffridge et al., 2024) have also been identified for salmon species.

Smolt

In addition to every possible subsequent effect from the previous stages, survival of smolts is undoubtedly driven by the timing at sea departure (Teichert et al., 2020; Crozier and Siegel, 2023; Frechette et al., 2023; Gillis et al., 2023; Vehanen et al., 2023). Indeed, smolt migration to marine environments has been identified as one of the most, if not the most critical phase for individual survival in the scientific literature (Dauphin et al., 2023 and references therein). As described in

Vehanen et al. (2023), migration timing of smolt has evolved to ensure favorable conditions at sea entrance (e.g. avoidance of predators, food availability, suitable physico-chemical conditions). Therefore, a mismatch with biotic or abiotic requirements or an individual poorer condition when entering a marine environment (Armstrong et al., 2018; Gregory et al., 2019; Simmons et al., 2022), potentially caused by the interactions of stressors previously described (Russell et al., 2012; Otero et al., 2014), could result in reduced fitness and increase marine mortality.

Marine adults

Sea mortality is supposed to be the primary factor of the observed decline in worldwide populations of Atlantic salmon (Chaput, 2012), although the drivers of mortality are not clear. Carried-over effects from the previous stages and more particularly the timing and condition of smolts are thought to be one of the main reasons (Russell et al., 2012; Harvey et al., 2020; Lilly et al., 2023). In Pacific salmon, the match-mismatch dynamic has been pointed out as an important factor of salmon survival for both wild and hatchery individuals (Satterthwaite et al., 2014; Wilson et al., 2023). Similarly to freshwater stages, a reduction in food availability or resource diversity is deleterious for Atlantic salmon populations, as the variety and abundance of salmon's prey, over diverse marine feeding areas is essential for individual survival (O'Sullivan et al., 2022; Utne et al., 2022). In addition to the overwhelming climate-induced effects on life history traits and population biocomplexity (Piou and Prévost, 2013; Piou et al., 2015; Olmos et al., 2020; Munsch et al., 2022; Tréhin et al., 2023), overfishing at sea, both legal and illegal, is also pointed out as a cause of populations decline (Dadswell et al., 2022).

Spawners

Because the feeding activity of returning adults is negligible, the majority of their energetic reserves being attributed to the reproduction effort, they are very sensitive to environmental

stressors such as repeated thermal stress or extreme (high or low) water discharge events (Crozier and Siegel, 2023; Gillis et al., 2023; Howard and von Biela, 2023). Habitat modifications (e.g. dams, alterations of cold-water refuges, and spawning grounds) are also important causes of reduced reproductive success, potentially acting synergistically with other stressors, increasing bioenergetics constraints for spawners. Other sources of mortality such as diseases, parasite load, overfishing (in estuaries or freshwaters), and pollution are also mentioned in the literature (Jonsson and Jonsson, 2009; Thorstad et al., 2021; Crozier and Siegel, 2023).

1.4 Management of Atlantic salmon – a daunting task

As we have seen that Atlantic salmon occupy different habitats and must cope with numerous environmental pressures during their ontogenic migration (Secor, 2015), from local rivers or tributaries to the open ocean, they have “their counterparts in current stock management measures” (Bull et al., 2022), where regional, national and international institutions cooperate (André et al., 2021).

1.4.1 International measures

Created in 1983, the North Atlantic Salmon Conservation Organization (NASCO) is an international cooperation, including six governments and the European Union (EU), aiming at linking scientific advances and proper management actions to restore and enhance Atlantic salmon populations throughout their distributional range (Thorstad et al., 2021). In 1998, members of NASCO adopted a precautionary approach, prioritizing conservation in population management (Prévost and Lebot, 2022). Therefore, in agreement with the International Council for the Exploration of the Sea (ICES), NASCO recommends that management actions should be based on a unique reference, the conservation limit (CL). The CL represents a threshold of returning adults (*i.e.* potential spawners) under which the population is threatened from a

conservation perspective (André et al., 2021). Because a CL is set at the population level, it needs to be decided at a national or a regional scale (White et al., 2023).

1.4.2 The Bay of Biscay

The Bay of Biscay (Appendix 4) represents the southern range of European Atlantic salmon distribution (NASCO, 2020a), and includes the western part of France and the northern part of Spain. In France, migratory species are managed by nine regional committees (Appendix 5), *i.e.* the *COmités de GEstion des POissons Migrateurs* (COGEPOMIs), which gather national, regional and local entities (André et al., 2021; Prévost and Lebot, 2022). In this collaborative guidance, stakeholders meet every six years to establish management plans, *i.e.* the *PLAns de GEstion des POissons Migrateurs* (PLAGEPOMIs), following NASCO recommendations. In Spain, salmon management is also coordinated on a local basis, mainly via regional governments, in cooperation with other institutions such as provincial councils and water agencies (Álvarez et al., 2010; García et al., 2014). However, it should be noted that information on Spanish salmon populations is fairly scarce, including management decisions or available data to evaluate stock status as presented in Smialek et al. (2021). Yet, numerous researches have been conducted to describe the evolution of the genetic structure of Spanish populations, especially in response to human actions (Horreo et al., 2011a, 2011b; Almodóvar et al., 2020, 2023).

1.5 Population characteristics in the Bay of Biscay

On a genetic basis, the Bay of Biscay holds seven regional populations of Atlantic salmon (from north to south): Bretagne, Allier, Gironde, Adour, Bidasoa, Asturias-Cantabrias and Galicia (Blanco et al., 2005; Saura et al., 2006; Perrier et al., 2013b). However, from a management and conservation perspective, a larger number of populations can be considered, partially because of the diversity of habitats and the population dynamics within the same region. For example, the

Adour population identified by Perrier et al. (2011) gathers two distinct watersheds; the Nivelle and the Adour *per se*. Yet, in another study by Perrier et al. (2014), the authors demonstrated significant differences in the genetic structure between the Nivelle and the Adour populations. Therefore, throughout this thesis, because of (i) the genetic structure of populations (Blanco et al., 2005; Saura et al., 2006; Perrier et al., 2011b, 2014), (ii) the composition of management units (<https://www.ofb.gouv.fr/en/international-year-salmon-2019>) and (iii) the physico-chemical, geological and hydromorphological characteristics among watersheds, we present and interpret the data according to nine regional areas (Figure 1-6). We then particularly focus our study on the southern Bay of Biscay (*i.e.* the Nouvelle-Aquitaine region), which includes the receiving catchments of the Gironde (Garonne-Dordogne), the Adour, and the Nivelle.

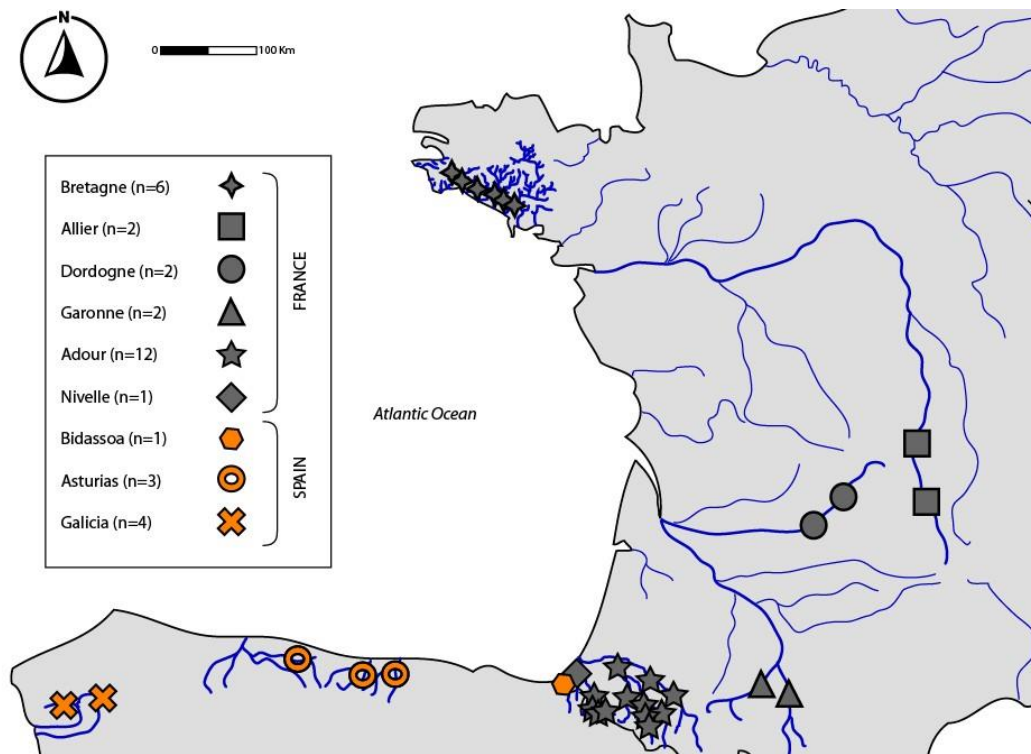


Figure 1-6: Map of the thesis study sites from the Bay of Biscay. The number of rivers available from each watershed is specified in brackets.

1.5.1 The southern Bay of Biscay

Gironde

The Gironde system (Figure 1-7) is shaped by two sub-basins (Garonne and Dordogne) and is of particular interest for salmon's management as the population completely disappeared in the early 20th century (Thibault, 1994), mainly because of dam's constructions (Labedan, 2016). In the 1980's, in order to reintroduce a natural population, three distinct phases of fish releases (in terms of origin) succeeded one another: 1) from Canada, Scotland, and Norway, 2) from the Allier (adjacent basin to the north) and the Adour (adjacent basin to the south) and 3) from a captive broodstock, since 1995, which is governed by MIGADO (a regional association that supervises migratory fish species in the Garonne-Dordogne area) (Vandeputte et al., 2021). Although only one population is considered in the Gironde, both the Dordogne and the Garonne sub-basins are substantially different (Table 1-1). Geographically, while the Dordogne originates from the Massif Central, the Garonne rises in the Pyrénées (Figure 1-7), which implies distinct hydraulic regimes and geological substrates (Parra et al., 1999; Semhi et al., 2000). Even if the Garonne is a longer system, an important portion of it is not accessible to migratory species because of river dams and artificial barriers (Carry et al., 2023). Therefore, for most downstream spawning grounds, potential breeders must at least pass several migration facilities, and a system of "trap/transport" has been deployed since 2014 for most upstream spawning sites (Cornu et al., 2019). In the Dordogne, returning adults also have to cross several obstacles before reaching their breeding sites, which are themselves located downstream of impassable dams and weirs (Caut and Delavaux, 2022). In addition, both sub-basins are managed independently as fish released in the Dordogne are mostly from the Castels and Fialicie hatcheries while individuals released in the Garonne are mainly from the Pont Cruzet hatchery (Figure 1-7). However, despite strong efforts in stocking programs, habitat restoration plans and measures to limit fish captures, the Garonne-

Dordogne population still needs to be highly monitored (Cornu et al., 2019; Caut and Delavaux, 2022). For example, a recent study using parentage assignments showed that 31.3% of the returning adults were wild-born (Vandeputte et al., 2021), indicating that the natural Gironde population firmly rely on fish from hatcheries. Globally, if the Gironde population showed a slight positive dynamic in the 21st century, this trend is mainly observed in the Dordogne sub-population (Figure 1-8, ~ from 200 to 400 individuals), while the Garonne sub-population remains almost stable with low return levels (Figure 1-8, ~ from 100 to 130 adults).

Table 1-1: Type of substrate and maximal length of every location (from north to south) hosting Atlantic salmon (*Salmo salar*) in the Bay of Biscay.

Geographic area	Sub-basin	Substrate type	Maximum length (km)
Bretagne		Mainly crystalline	149
Allier		Mixed crystalline and volcanic	1,006
Gironde	Dordogne	Mixed crystalline and sedimentary	483
	Garonne	Mixed crystalline and sedimentary	525
Adour	Nives	Mixed crystalline and sedimentary	79
	Oloron	Sedimentary	149
	Pau	Mixed crystalline and sedimentary	193
Nivelle		Sedimentary	39
Bidasoa		Sedimentary	66
Asturias-Cantabrias		Sedimentary	145
Galicia		Mainly crystalline	340

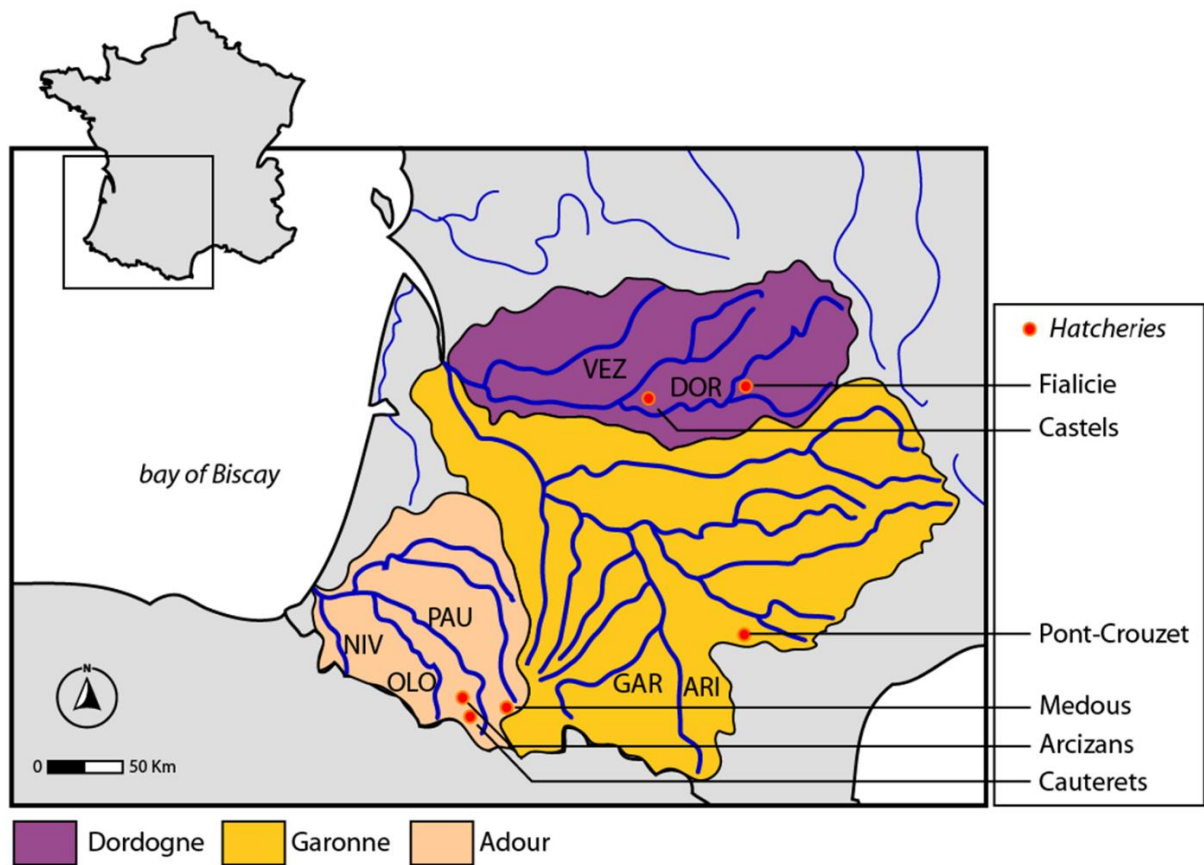


Figure 1-7: Map of the Gironde (or Garonne-Dordogne) and Adour watersheds. Hatcheries are represented by a red circle. Abbreviations: ARI, Ariège; DOR, Dordogne; GAR, Garonne; NIV, Nives; OLO, Oloron; VEZ, Vézère.

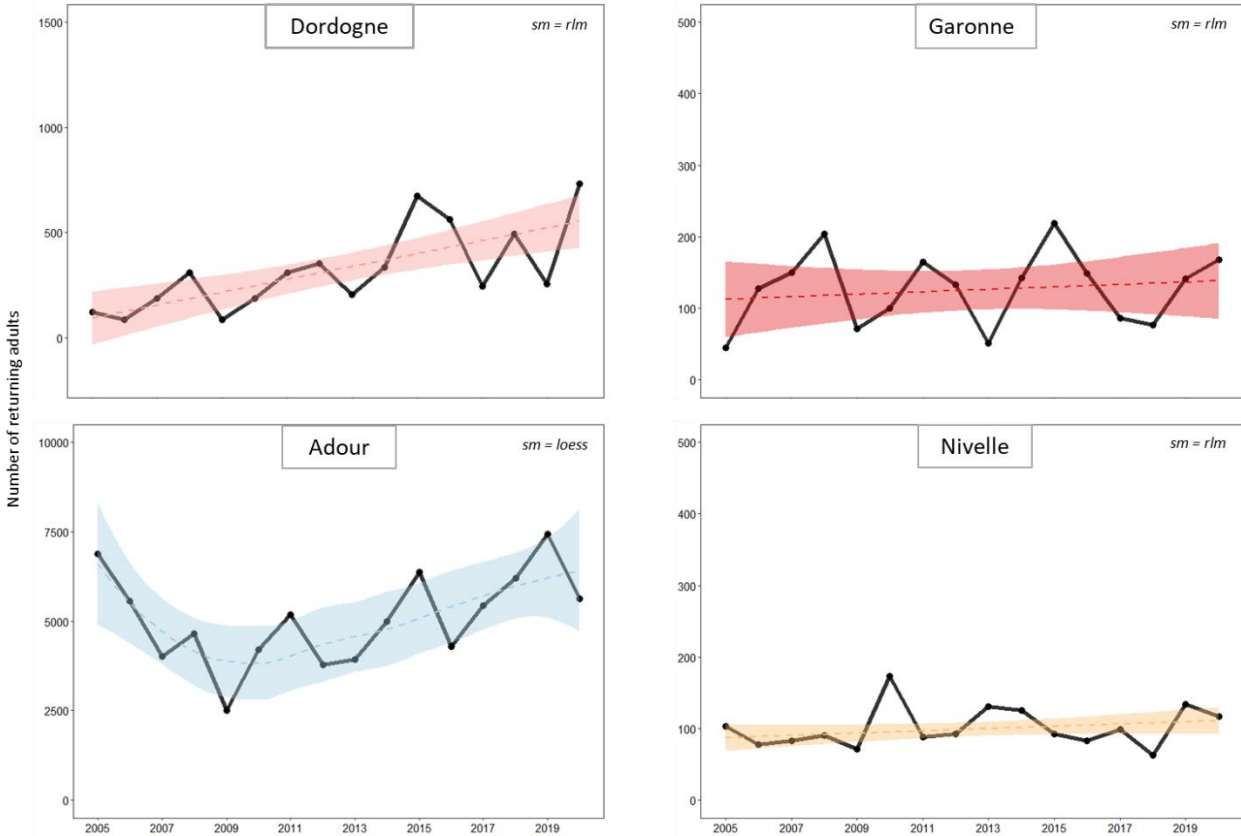


Figure 1-8: Number of returning adults (including individuals from both wild and hatchery origin) from the main locations (in the southern Bay of Biscay) investigated in this thesis, from 2005 to 2020. To facilitate the visual assessment of the temporal dynamics over the period of interest, a robust linear model (*rlm*) or a locally estimated scatterplot smoothing (*loess*) has been applied as a smoothing method (*sm*) for every location \pm standard error (shaded area, IC: 95%). In the case of the Adour, which is significantly influenced by fishing activities, these data incorporate catch reports from both commercial and recreational fishermen. Sources: <https://www.migado.fr>; <https://www.migradour.com>.

Adour

The Adour system represents a medium-size watershed (Table 1-1) which can be separated into three sub-basins: Nives, Oloron, and Pau (Figure 1-7). While Pau and Oloron sub-basins experiment a hydrological regime characterized by important spring and fall flows due to heavy precipitations and intense snowmelt for the spring period (Mouliia, 2021; Mullet et al., 2021), the Nives sub-basin is mostly defined by a rainfall regime under strong influence of oceanic conditions

(Picoulet and Marty, 2020a). The Adour basin hosts the largest population of the southern part of France (Figure 1-8) and returning mature adults can be found in thirteen rivers. Nevertheless, the population is not equally distributed across sub-basins as approximately 70% of the mature salmon that have escaped the fisheries would ascend to the Oloron sub-basin, 20% to Pau and only 10% to the Nives (Bareille et al., 2017). As most salmon-frequented basins in the Bay of Biscay, the Adour population has strongly decreased during the second half of the 20th century. However, restoration programs are bearing fruit, in particular through improved ecological continuity (Picoulet and Marty, 2020b), as the Adour population has shown a significant positive dynamic over the last fifteen years (Figure 1-8, ~ from 4000 to 6000 individuals), which is very encouraging. In addition to habitat restoration and the enhancement of ecological continuity, monitoring programs are also carried out since 1979 in the Adour system (Picoulet and Marty, 2020b). Since the primary aim of these stocking programs is to ensure the autonomy and the sustainability of a natural population, which has been successfully evaluated in the Nives and Oloron sub-basins (Picoulet and Marty, 2020b), only the Pau sub-basin is still subject to hatchery-releases since 2011. Here again, encouraging results are observed as the number of returning adults in the Pau sub-basin has doubled between 2015 and 2021 (Appendix 6).

Nivelle

The Nivelle is a small coastal river (Table 1-1), mainly described by a rainfall regime (Picoulet and Marty, 2020), which flows directly into the Bay of Biscay very close to the Adour estuary (approximately 10km to the south, Figure 1-6). The river drains predominantly marine Mesozoic carbonate formations from the western part of the Pyrénées (Coynel et al., 2005) and carries the smallest, native, and self-sustaining French Atlantic salmon population (Figure 1-8). Indeed, the population, although composed of a few dozen adults, is considered self-sufficient since the last releases of hatchery-fish in 1991 (Picoulet and Marty, 2020a) and has been relatively stable over the last 15 years (Figure 1-8).

1.5.2 Other locations: Bretagne, Allier, Bidasoa, Asturias-Cantabrias and Galicia

At the northern extreme of the Bay, the Bretagne (Figure 1-6) holds the largest population of the Bay of Biscay (Figure 1-9). Salmon rivers are relatively short, generally less than 100km (Bal et al., 2017), and as a result, these systems with numerous small coastal rivers (approximately 20 to 30 rivers are frequented by Atlantic salmon) are often inter-connected via exchanges of individuals, with a large proportion of 1SW individuals compared to MSW fish (Prévost and Lebot, 2022). Limited stocking programs have been undertaken in Bretagne (Perrier et al., 2013b), with salmon management almost solely based on the annual definition of a CL and the associated Total Allowable Catch (TAC, or *Total Admissible de Capture* in French) (<https://www.observatoire-poissons-migrateurs-bretagne.fr/>). Adult returns of Atlantic salmon in the Bretagne region oscillated during the last two decades (Figure 1-9), with lower levels (<10,000 salmon) during the 2007-2009 and 2018-2020 periods and higher levels (~ 12,000 individuals) before 2007 and from 2010 to 2017.

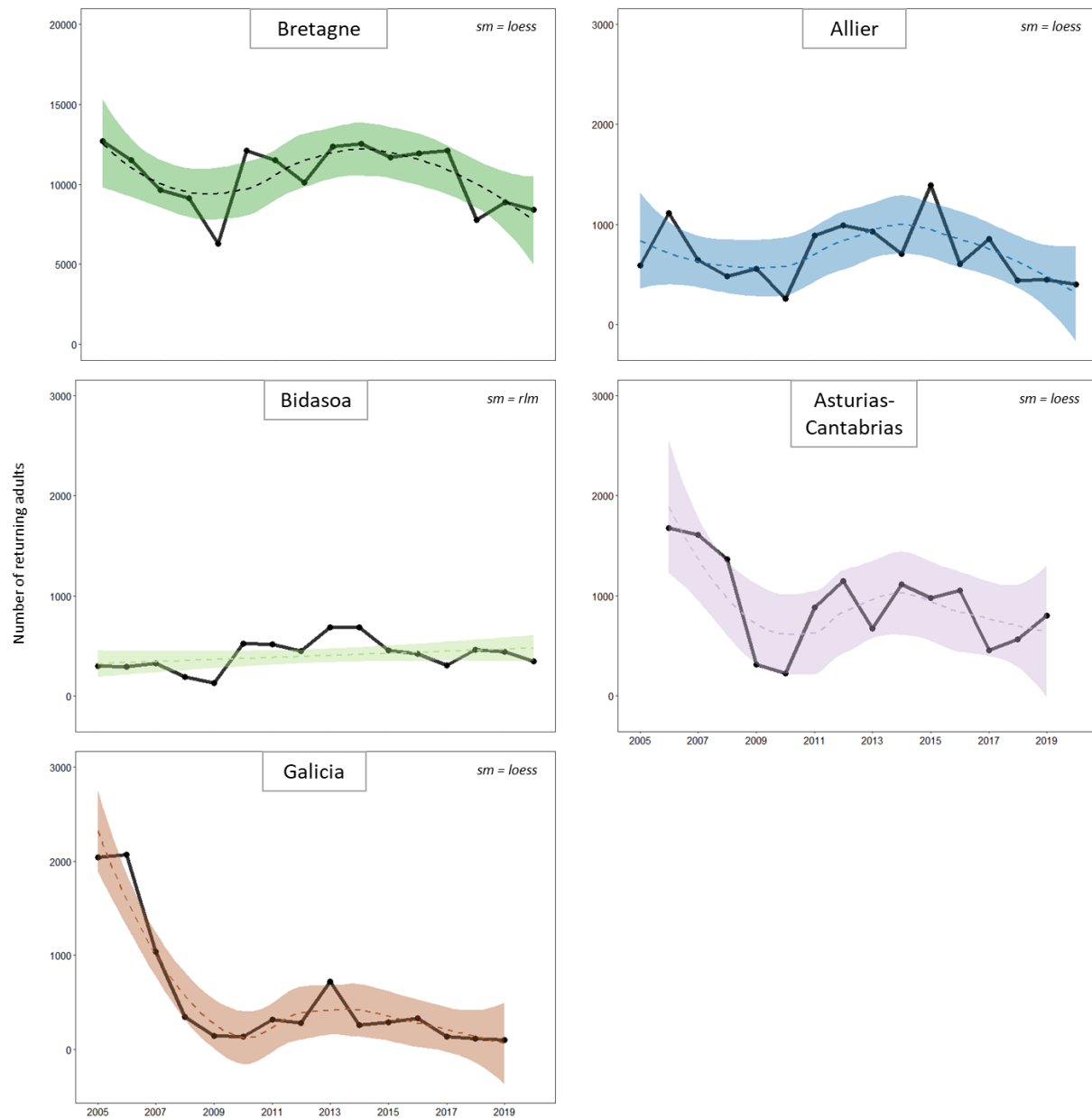


Figure 1-9: Number of returning adults from the other locations investigated in this thesis, as potential donors of individuals from the Bay of Biscay, from 2005 to 2020. To facilitate the visual assessment of the temporal dynamics, a robust linear model (*rlm*) or a locally estimated scatterplot smoothing (*loess*) has been applied as a smoothing method (*sm*) for every location \pm standard error (shaded area, IC: 95%). Estimations were obtained by Bayesian modelling (Bretagne), camera counts (Allier), trap counts (Bidasoa) and based on fishing captures (Asturias-Cantabrias, Galicia). No robust estimations could be provided in 2005 for the Asturias-Cantabrias, in addition to 2020 for the Asturias-Cantabrias and the Galicia regions. Sources: Lebot and Rivot (In press); <https://www.logrami.fr>; Navarre government; NASCO (2020b); Courtesy of the Galicia government.

Located south of Bretagne and north of Gironde (Figure 1-6), the Allier basin is the longest salmon-fed stretch in the Bay of Biscay (Table 1-1). Its main river, the Loire, is the last European river to support a population of “large salmon”, capable of migrating over 10,000km and reaching impressive sizes (over a meter, see <https://www.migrateurs-loire.fr/les-indicateurs/saumon/>). As in the Garonne-Dordogne system and probably because of the important number of obstacles (mostly hydroelectric dams) and other habitat degradations, the Atlantic salmon population from the Allier area is still very concerning, despite strong efforts in stocking programs (Legrand et al., 2023). As presented in the Figure 1-9, the Allier population showed an interesting positive trend in adult returns until 2015, decreasing significantly from then until 2020.

At the most southern range of the Bay of Biscay, the Atlantic salmon is found in three main systems: the Bidasoa (in the Gipuzkoa province), the Asturias-Cantabrias, and the Galicia (Figure 1-6). Historical records and data show a considerable abundance of Atlantic salmon north of the Iberian Peninsula, up to several tens of thousands of individuals (Álvarez et al., 2010). Here, too, strong environmental pressures have led to a sharp decline in the North Iberian Atlantic salmon populations (Álvarez et al., 2010), which are particularly vulnerable to climate change effects (Valiente et al., 2010; Nicola et al., 2018) as they represent the southernmost range of the eastern Atlantic coast (NASCO, 2020a). In response, massive stocking programs were launched between the 1970's and the 1990's, followed by a supportive breeding strategy, based on artificial reproduction from native adults (Horreo et al., 2011a; Almodóvar et al., 2020). However, as in many locations where populations experienced a severe collapse, side effects on populational phenotypic characteristics were also observed such as the reduction in length and mass of returning adults, shifts in the timing of smolt emigration or adult's migration to breeding sites, or changes in the age structure and genetic diversity (Garcia de Leaniz et al., 2007; Horreo et al., 2011a, 2011b; Almodóvar et al., 2020, 2023). From 2005 to 2020, the Asturias-Cantabrias and

Galicia populations experienced an important decline, while the Bidasoa population showed a slight increase, especially in the 2010-2015 period (Figure 1-9).

In summary, contrasting regional patterns in adult salmon returns were observed in the Bay of Biscay from 2005 to 2020. First, some populations present recent (~ the last 10 years) signs of decline, whether they are composed of wild fish (*i.e.* Bretagne) or highly sustained by stocking practices (*i.e.* Allier, Galicia, Asturias-Cantabria). Second, in other populations or sub-populations, generally small (*i.e.* Garonne, Nivelle, and Bidasoa), the annual number of returning adults is relatively stable over the last 15 years. Finally, two populations clearly show, in average, an increase in the number of mature salmon during the 2005-2020 period, namely the Dordogne sub-basin and the Adour basin (Figure 1-10).



Figure 1-10: First knowledge gap identified in the thesis, with the associated hypothesis of research work.

DISPERSAL AND CONNECTIVITY

In the previous section, we have shown that Atlantic salmon populations are essentially managed regionally, following national and international guidelines. This is mostly because salmon populations express strong local adaptations to their natal environment, as a result of an eco-evolutionary mechanism to maximize fitness benefits (Thorstad et al., 2010; Keefer and Caudill, 2014).

1.6 Natal philopatry

1.6.1 Mechanisms of philopatric behavior

Natal philopatry (or “homing”) defines a fundamental behavior by which mature adults migrate to their natal area, sometimes the same breeding site where they had hatched as fry (Vähä et al., 2007; Hamann and Kennedy, 2012), to spawn. Resultingly, this will largely increase the chances of finding suitable mates, expressing genetical and phenological adaptations to their ecosystems, in favorable environments for both the spawners and the future generations (Dittman and Quinn, 1996; Garcia de Leaniz et al., 2007). Therefore, this remarkable life trait shapes distinct populations in an eco-evolutionary dynamic (Lamarins, 2022). The main mechanisms involved in successful homing include sequential juvenile imprinting during the downstream migration in freshwater and the use of geomagnetic gradients at sea or nearshore to locate their upmigration route (Dittman and Quinn, 1996; Thorstad et al., 2010; Berdahl et al., 2016). In freshwater, an olfactory imprinting, also referred to as “odor bouquets”, is the primary mechanism subsequently used by mature adults. This olfactive memory relies on multiple organic and inorganic substances such as pheromones, amino acids, or a combination of geological signatures (Keefer and Caudill, 2014). Another hypothesis to explain philopatry has been proposed in scientific literature and

suggests that returning adults identify their home by responding to environmental odors released by their young conspecifics (Keefer and Caudill (2014) and references therein). Although juvenile imprinting is generally acknowledged in fishery sciences, this second theory should not be seen as an alternative, but rather as a complementary explanation, particularly in view of the massive rearing programs that have been undertaken (see section 1.5). Regarding the marine phase, in addition to the geomagnetic field, schooling effects have also been discussed as a factor influencing successful homeward migration (Berdahl et al., 2016).

1.6.2 Are we on the same page?

Multiple terms are found in the literature to define natal philopatry, including “homing” and “fidelity” most frequently. While they probably all refer to a similar behavior (*i.e.* the upstream migration of returning mature adults to their natal waters), depending on the method used to estimate the homing rate (*e.g.* modeling, otolith chemistry, genetics, tagging, telemetry, capture–mark–recapture (CMR)) and the spatial scale of interest (*e.g.* spawning grounds, rivers or tributaries, sub-basins, watersheds), the estimations and their associated ecological implications might significantly differ. In my perspective, philopatry refers to the ecological concept that describes an individual's ability to migrate back to their river of origin, while homing is a similar notion, but one that most often refers to a population rather than an individual level. In fact, the term "homing rate" is largely used to discuss populational effects, whereas "philopatric rate" is much rarer or absent from the literature. Similarly, fidelity is sometimes used to designate homing, even though the very notion of fidelity implies quantifying, or at least considering, infidelity. Therefore, whereas philopatry and homing can be approximated with a given population and therefore a single locality (according to the spatial scale previously defined), fidelity is by definition dependent on several localities, *i.e.* all the other potential destinations of “unfaithful fish”. This is

why, depending on the method, the design of the study but also and above all the ecological question we wish to answer, it is essential to define the terms and their meanings (Table 1-2).

Table 1-2: Glossary of the terms and their associated definitions used in this thesis.

Terms	Definitions
Allee effect	Ecological mechanism by which the reduction of population density (potential spawners), especially in small populations, results in the reduction of population growth
Biocomplexity	A combination of genetical, phenotypical, and ecological diversity within and among populations resulting in a variety of life history traits
Carry-over effect	Downstream consequences associated with upstream environmental pressures, stressors, or an individual's "decision"
Connectivity	A network system that gathers spatially and genetically distinct populations by the exchange of individuals
Dispersal	The movement of one or more individual(s) from their natal area to non-natal freshwater locations
Donor population	Also referred to as the source population, a population that provides individual(s) to another
Emigration rate	Based on the absolute size of one given population, the proportion of individuals that would disperse into other populations
Fidelity	Based on the absolute size of one given population, the proportion of individuals that would reach their natal waters. In theory, the fidelity and the emigration rate are complementary and cover the entire absolute population if every possibility (<i>i.e.</i> the receiving populations, or localities), is monitored
Homing	In migratory species, defines the behavior by which adults will migrate back to their natal sites to breed. In opposition to the fidelity, the homing often refers to one given location, and examines, out of the absolute number of returning adults, the proportion of individuals that had hatched in this location

Immigration rate	Directly linked to the homing rate, the immigration rate considers, in one specific population (or locality), the proportion of individuals that are non-native to the location, whatever their geographical origin
Match – Mismatch	In opposition to match, “[...] mismatches are said to occur when the time in the annual cycle when resource demands of the consumer species (<i>i.e.</i> predators, herbivores) are highest does not match with the period when its resource (<i>i.e.</i> prey, plants) is most abundant” (Visser and Gienapp, 2019). In fisheries science, the terms asynchronous and synchronous are also often employed for mismatch and match conditions, respectively
Metapopulation	A metapopulation gathers spatially distinct populations, that are interconnected, in a spatio-temporal dynamic, by the exchange of individuals through migratory flows
Natal philopatry	Similar to homing, defines the migratory behavior by which an individual returns to his natal area to reproduce. While the homing is often applied to a populational level, the natal philopatry is more adapted for individual interpretations
Phenology	Individual and/or populational response to an environmental signal
Portfolio effect	Based on financial portfolios, in ecology the portfolio effect describes “how ecosystems are organized, how species interact, and how evolutionary strategies develop” (Schindler et al., 2015) to maintain and favor the stability of the overall system
Receiving population	Also referred to as the sink population, a population that receives individuals from distinct populations through dispersal mechanisms
Rescue effect	Either genetic, phenotypic, or demographic, describes a positive effect of dispersal on the receiving population by maintaining local diversity/demography or even contributing to the sink population growth
Straying	A synonym of dispersal, mostly associated with a negative connotation. Strayers (<i>i.e.</i> individuals that express straying movements) are often viewed as failures, and straying “suggests an unintentional error and thus disqualifying dispersal as a life history strategy with significant implications” (Lamarins and Buoro, 2023)

1.7 Dispersal

1.7.1 Definition of dispersal

Dispersal (or “straying”) defines the movement of one or more individual(s) from their natal waters to non-natal spawning areas, with potential gene flow (*i.e.* effective dispersal). Here again, terminology must be clearly defined. Although straying and dispersal are synonyms, most of the time “straying” carries a negative connotation, sometimes described as a failure to homeward migration (Keefer and Caudill, 2014; Lamarins and Buoro, 2023). Besides, the “migration” term can also be found in the literature, yet, as previously detailed, reproduction is not necessarily the ultimate target of migration. Dispersal is highly adaptive, resulting from a cocktail of proximate and ultimate causes, which includes (but not only) phenotypic- and condition-dependence, environmental conditions (*e.g.* habitat quality, external pressures), competition avoidance or kin interactions (Lamarins, 2022). In addition to the terminology, dispersal must be defined with explicit spatial and/or temporal scales (Lamarins and Buoro, 2023). Indeed, according to the study’s objectives, the dispersal rate can be estimated on small- or large-scale areas (Vähä et al., 2007; Bradbury et al., 2014), but also on distinct life stages depending on the specie’s life cycle (*e.g.* larvae, juveniles, adults), and therefore, based on days or years. However, these perspectives are also debatable as studies of movements during the larval or juvenile phase are not typically designed to assess effective dispersal.

Therefore, if we consider dispersal as a movement that leads to potential gene flow, spatial scale is delimited according to the populational level (at least, potentially at a stock level for harvested species), regardless of the distance between two adjacent populations. For example, in the Bay of Biscay, distinct populations are mostly found at a regional scale (roughly tens to hundreds of kilometers) (Perrier et al., 2011b; Almodóvar et al., 2023). According to that definition, it is possible to estimate two additional metrics that are sometimes confused or not clearly

identified: the emigration and immigration rates (Table 1-2). In that context, one population would be considered as the donor population (or the source population) while the population(s) that gain non-natal individuals would be defined as the receiving population (or the sink, or recipient population) (Table 1-2). Both metrics are particularly important to measure from a management perspective because the effect of “losing” or “gaining” non-natal individuals will necessarily depend on the absolute size and dynamic of the studied populations (Keefer and Caudill, 2014). Resulting from the exchange of individuals between discrete and spatially distinct populations, salmon populations are therefore interconnected, by a fluctuating network, forming a metapopulation structure (Schtickzelle and Quinn, 2007).

1.7.2 What is an “healthy” dispersal rate for a metapopulation?

Philopatry and dispersal can be seen as “the opposite sides of the same coin” (Källo, 2023), they act synergistically in a spatio-temporal dynamic. While elevated philopatric behavior favors local-adapted populations, with subsequent fitness benefits for the next generations, dispersal allows colonizing new or restored habitats (Perrier et al., 2014; Willmes et al., 2021; Cordoleani et al., 2024), enhances gene flow between distinct populations (*i.e.* spreading the risk of local extinction), which can ultimately stabilize the portfolio effect (Anderson et al., 2015; Schindler et al., 2015) (Table 1-2). Additionally, dispersal can also result in a demographic, genetic, or evolutionary rescue effect (Carlson et al., 2014; Keefer and Caudill, 2014; Lamarins, 2022). Therefore, migratory flows are essential to maintain viable and stable metapopulations, which in turn, ensure the persistence of a healthy, shifting balance.

Although dispersal is a desirable trait in natural salmonid populations, excessive exchange of individuals can disturb the metapopulation structure, whether the donor and/or the receiving population(s) (Candy and Beacham, 2000; Horreo et al., 2012; Ford et al., 2015; Bett et al., 2017; Jonsson and Jonsson, 2017). Just as dispersion can act as a demographic rescue,

disproportionate movement between populations can also lead to a significant loss of potential spawners for the source population, and may ultimately introduce an Allee effect in small populations (Keefer and Caudill, 2014; Berdahl et al., 2016) (Table 1-2). On the other side, unreasonable gains of individuals might increase competition on spawning grounds for the sink population (Essington et al., 2000). In addition, an elevated level of connectivity has been shown to increase population synchrony, which considerably threatens wild populations by eroding the portfolio effect (Schindler et al., 2015). In metapopulations, the diversity of genetic, phenotypic, and demographic characters along with the asynchronous responses to environmental cues ensure natural biocomplexity (Figure 1-11), which is crucial to maintain stable populations over time and space (Huber et al., 2024). By homogenizing genetic and phenotypic traits, excessive dispersal may considerably jeopardize metapopulation persistence. As described in Des Roches et al., 2021, “the rapid loss of intraspecific variation is a hidden biodiversity crisis”.

To date, scientific literature detailing dispersal rates in salmonid populations is scarce (Birnie-Gauvin et al., 2019), but it is even rarer to find studies that depict the temporal variability of dispersal. Regarding Atlantic salmon, a homing rate that roughly varies between 90 and 95% is generally acknowledged to be “natural” (Keefer and Caudill, 2014), but it is interesting to note that estimated immigration rates are more variable than emigration rates (Lamarins and Buoro, 2023). This observation highlights two key points: (i) as previously detailed, terms and their meanings must be precisely defined to ensure comparable/transferable results and (ii) there is an obvious lack of data concerning the effect of both space and time on dispersal. Yet, a better knowledge of temporal dispersal patterns is fundamental in our contemporary world where numerous and strong environmental pressures consistently occur, across all life stages (see section 1.3). As dispersal is strongly variable, potentially adaptive to environmental stressors (whether biotic or abiotic) that vary with time, it is essential to quantify the temporal variation of migratory flows in order to better appreciate the drivers of dispersal movements.

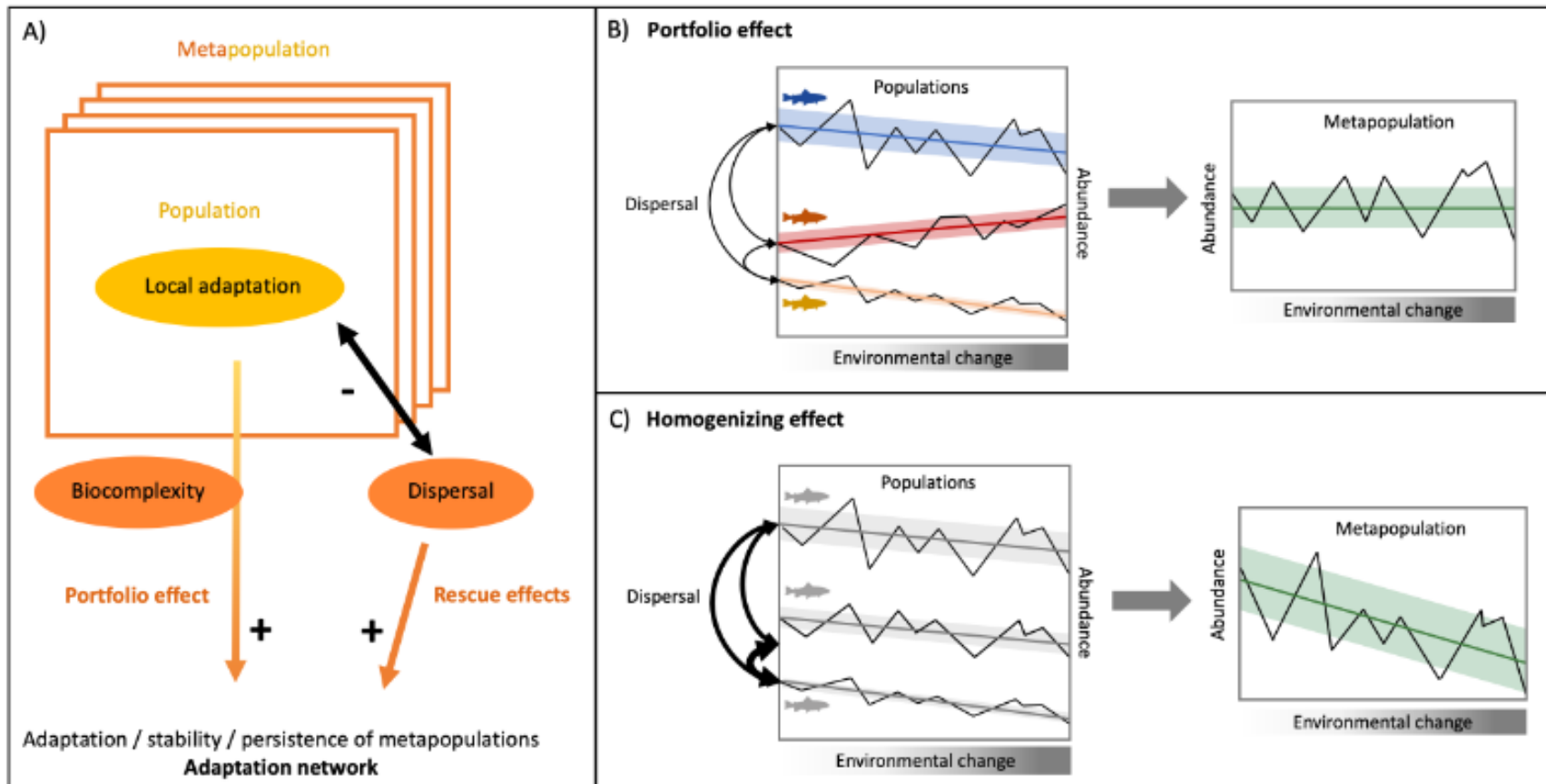


Figure 1-11: A) Conceptual framework of an adaptation network, with biocomplexity emerging from the diversity of local populations dynamics providing portfolio effects and interacting with dispersal and its rescue effects, ultimately fostering the adaptation, stability and persistence of metapopulations. B) Schematic illustration of the portfolio effect: a diversity of populations dynamics and life histories lead to the stability of the metapopulation dynamics. C) Schematic illustration of the homogenizing effect of dispersal, which synchronizes populations dynamics and homogenizes life histories, ultimately reducing the stability of the metapopulation. From Lamarins (2022).

1.7.3 Current knowledge of connectivity levels in the Bay of Biscay

In scientific literature, studies of dispersal mechanisms in the Bay of Biscay are confined almost exclusively to its national limits, focusing on either Spanish or French Atlantic salmon populations. In Spain, a large number of genetic studies have been conducted to examine the “genetic variability, population structure, and response to different management and conservation measures” (Almodóvar et al., 2023). Some of these research works demonstrate the negative effects associated with stocking programs (Horreo et al., 2011a, 2011b; Almodóvar et al., 2020), while others show limited impacts on natural populations (Blanco et al., 2005; Consuegra et al., 2005), but very few studies discuss dispersal levels. For example, Almodóvar et al. (2023) compared the genetic dynamics of Atlantic salmon from eight Spanish rivers before the major decline of the species (in the 1950’s) in the Iberian Peninsula with contemporary data. The authors demonstrate a strong genetic structure, with limited gene flow corresponding to exchanges between nearby rivers (the strongest connectivity rates being estimated for rivers distant from approximately 50 to 80km). In another study, Leunda et al. (2013) used Coded Wire Tag (CWT) – tagged Atlantic salmon, captured in the Bidasoa River from 1996 to 2012, to estimate the homing and immigration rates. The authors point out three key metrics: 1) the homing rate was found to be 86.3%, 2) more than 75% of the immigrants were identified from rivers within a 300km range and 3) only three fish from the Bidasoa River had emigrated, and dispersed in the Urumea river, distant from 17km, indicating very low and proximate emigration patterns.

In France, similar to Spain, most studies that have inferred dispersal movements are based on genetics, and designed to investigate the genetic structures and the effects of hatchery-releases on wild populations. In their study, Perrier et al. (2011) demonstrated a hierarchical genetic structure stratified into five distinct clusters, associated with five different regions (using the genotypes of 975 Atlantic salmon, from the early 2000’s). The authors also suggested that

geological substrates, along with river length, were reliable factors to explain potential gene flow between distinct populations or sub-populations. Resultingly, connectivity levels seem to be limited to regional populations or sub-populations, with a weak inter-regional exchange, although here too, stocking practices have strongly and differentially (*i.e.* at a populational level) affected natural dynamics (Perrier et al., 2011b, 2013a, 2013b).

Overall, studies carried out on the populations of the Bay of Biscay show (i) a hierarchical genetic structure, with limited exchanges of individuals between distinct watersheds, (ii) the gene flows occur between adjacent populations, most often a few dozen kilometers apart, and (iii) stocking practices have strongly affected the natural genetic structure of salmon populations. However, we clearly lack information on potential inter-basin migratory flows, and on the possible temporal variation of these exchanges (Figure 1-12).

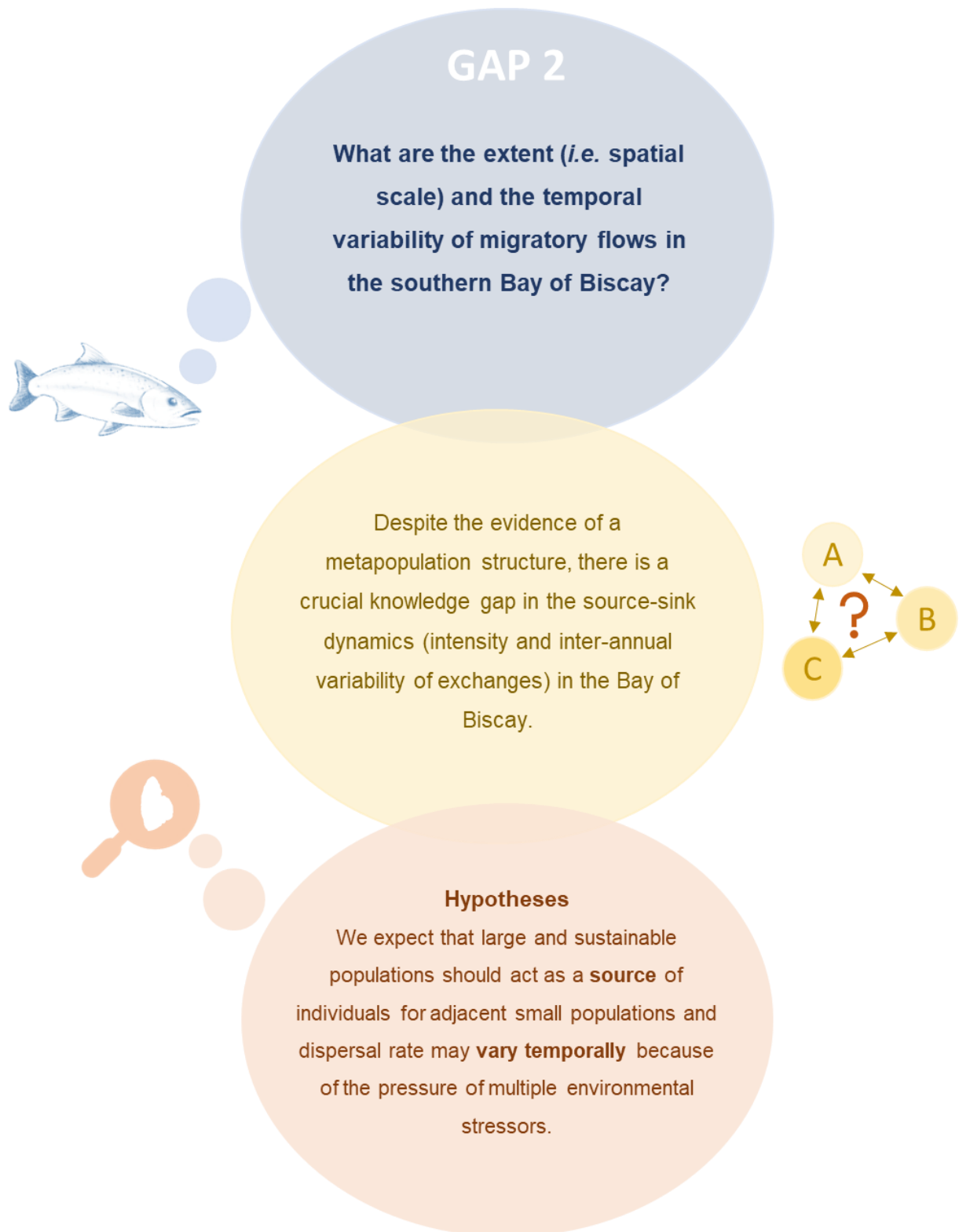


Figure 1-12: Second knowledge gap identified in the thesis, with the associated hypotheses of research work.

FACTORS AFFECTING COEXISTING POPULATIONS STABILITY

1.8 Influence of stocking programs on the (meta)population dynamic

Because of the high prevalence of philopatry, management strategies have most commonly focused on the populational level (Thorstad et al., 2021), and as a result, the connectivity between populations has clearly been overlooked to date (Birnie-Gauvin et al., 2019). However, there is an apparent antagonism between the metapopulation structure of salmon and the local management guidelines, including restoration and stocking programs. As previously detailed, heavy stocking programs have been carried out to mitigate the rapid collapse of natural populations (Sturrock et al., 2019; Almodóvar et al., 2020; Huber et al., 2024) but various unintentional negative effects of hatchery rearing and release have been pointed out in the literature, as recently reviewed by McMillan et al. (2023) (Figure 1-13).

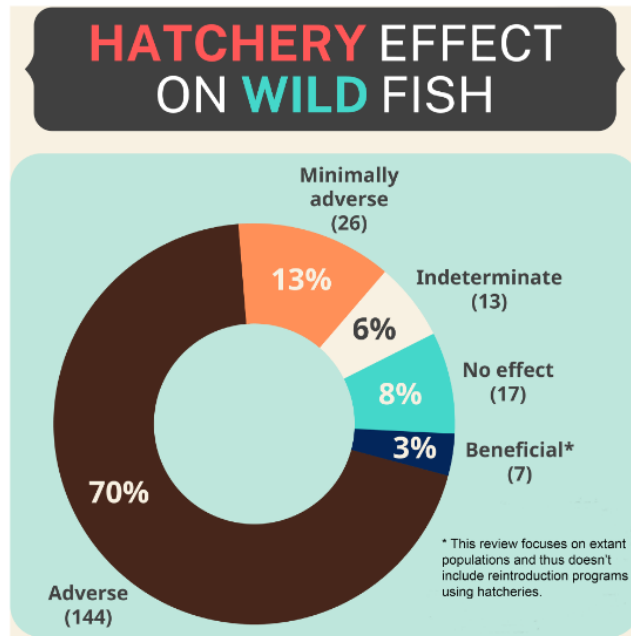


Figure 1-13: Donut plot displaying proportion (and number, in parentheses) of publications by the effect of hatchery salmonids on wild salmonids, including adverse, minimally adverse, indeterminate, no effect, and beneficial, from McMillan et al. (2023).

In the beginning of stocking programs, many organizations used foreign hatchery strains to cope with the urgent decline of wild populations. In the Bay of Biscay for example, both French and Spanish populations would then be supplemented by fish originating from Northern Europe (Perrier et al., 2013b; Almodóvar et al., 2020; Vandeputte et al., 2021). However, because habitat heterogeneity has led to local adaptation through eco-evolutionary mechanisms, the introgression of non-natal individuals may strongly affect the genetic make-up (e.g. domestication, hybridization, lower fitness) of the managed, endangered population (McMillan et al., 2023). As an alternative, captive breeding programs were then proposed to avoid or minimize genetic impacts (Fraser, 2008) and to enhance individual survival. Although it is difficult to isolate the effect of local hatchery-rearing alone (vs. wild) on general fitness (James et al., 2023), while they appear to perform better than the foreign strains, fish from captive breeding programs also express lower fitness than their wild counterparts (Araki et al., 2008). Indirect carry-over effects from the rearing environment have been suggested in the literature to explain this lower fitness (Thériault et al., 2010; Cogliati et al., 2019; ICES, 2024). While direct effects such as individual survival and abundance are relatively easily observed, it is important to consider that, ultimately, these genetic changes may alter population characteristics (e.g. age structure, habitat use, the timing of seaward and upstream migrations), which can in turn considerably reduce biocomplexity and threaten population stability and persistence (Zaporozhets and Zaporozhets, 2012; Milot et al., 2013; Huber et al., 2024). Therefore, it is crucial to consider the stability of intraspecific diversity in stocking programs and management actions (Figure 1-14) from a conservation perspective.

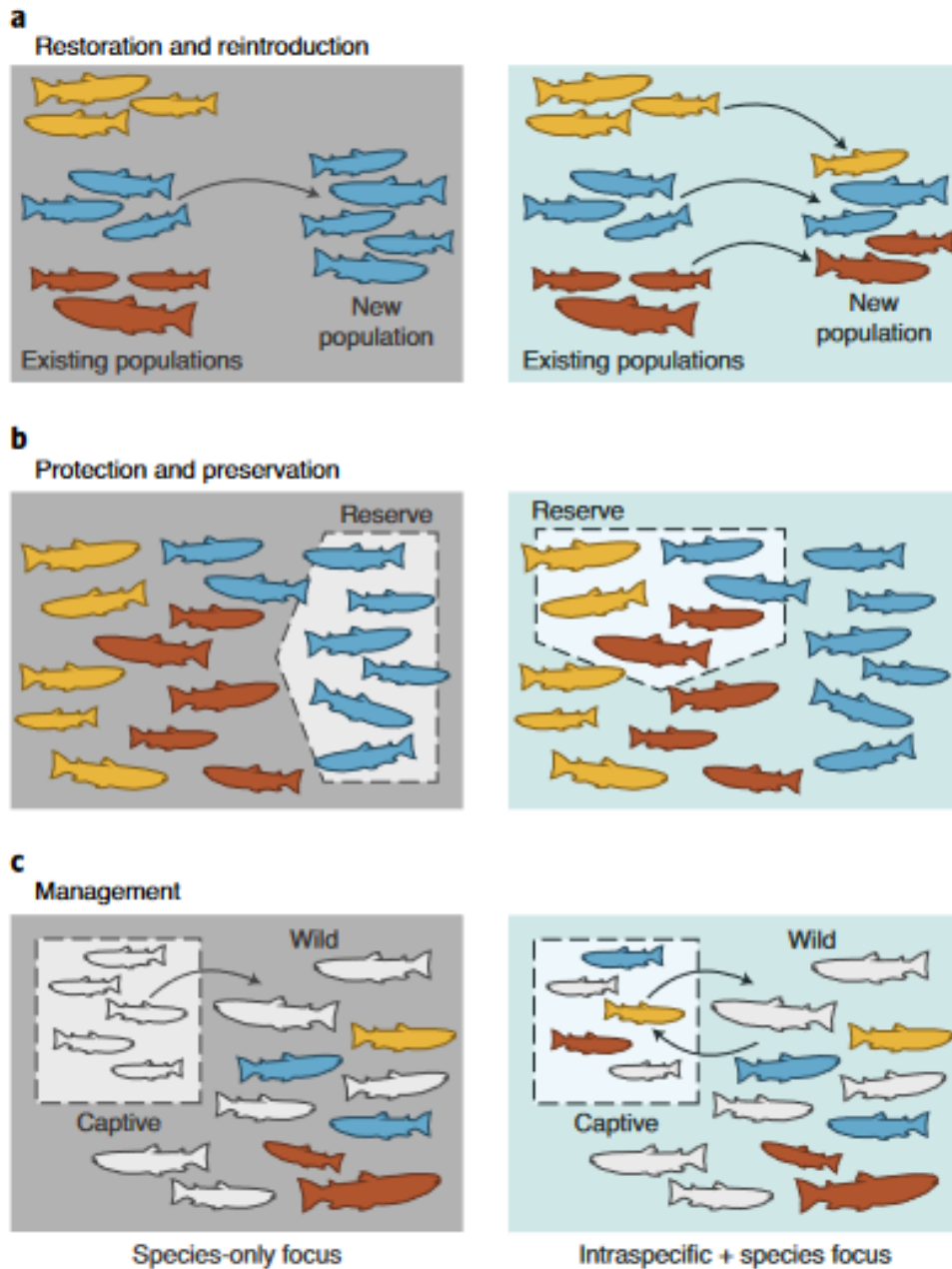


Figure 1-14: Opposite extremes of conservation strategies that ignore intraspecific variation, only focusing on species (left panel in grey) versus those that explicitly focus on preserving intraspecific variation (right panel in teal). a–c, to help protect NCP, successful conservation methods can use restoration (a), preservation (b), and management strategies that consider intraspecific diversity rather than just number of individuals (and species) (c). These tactics will help maintain the stability and persistence of species, and therefore the continuance of their contributions, into the future. From Des Roches et al. (2021).

In addition to long-term genetic effects on historical populations, hatchery practices have also indirect effects on wild populations, by reinforcing density-dependence mechanisms for example (Weber and Fausch, 2003; Laffaille, 2011). Although the direct increase in population size is desirable from a short-term fishery perspective (for a harvested population or one that supports recreational fishery), competition between wild and hatchery-fish for natural resources, mostly habitats, and food, can lead to an overall decline in wild population productivity in a conservation prospect (McMillan et al., 2023). Another issue identified with rearing programs is the exacerbated dispersal rate of stocked-fish (Jonsson et al., 2003; Brenner et al., 2012; Bett et al., 2017), which can false the real dynamic of the managed, often coexisting population. In their study, Johnson et al. (2012) clearly demonstrate that fish from hatcheries have masked a demographic sink of the natural population, with more than 90% of the potential spawners being identified as hatchery-produced fish, which poses a particularly complex management challenge. Because of the net difference in the diversity of life-history traits between wild and hatchery fish (Huber et al., 2024), an excessive proportion of hatchery salmon may increase population synchrony (Satterthwaite and Carlson, 2015) and decrease natural population portfolios (Sturrock et al., 2019) by “replacing” wild individuals. Therefore, a better understanding of source/sink dynamics between targeted and untargeted populations, with knowledge of natal fish origins (wild vs. hatchery) is highly recommended to inform correctly managers and policymakers (Carbonneau et al., 2024).

In the Bay of Biscay, we have seen that (i) the majority of salmon populations are supplemented with stocked fish, (ii) management actions are governed regionally (see section 1.5) and (iii) they vary in time, both in term of intensity of production and time-at-release. However, little is known about the effect of rearing strategies (biomass and stage-at-release) on juvenile-to-adult survival, and their subsequent effects on population sustainability (Figure 1-15).



Figure 1-15: Third knowledge gap identified in the thesis, with the associated hypotheses of research work.

1.9 Influence of life strategies

Life-history events (*i.e.* phenology) play a key role in the propensity of adult return rates, successful homing, and reproductive success. Indeed, in addition to the wide range of stressors that diadromous salmonids must face to complete their life cycle (see section 1.3), a solid corpus of studies has now demonstrated how life-histories traits influence individual survival and ultimately, population stability (Simmons et al., 2022; Crozier and Siegel, 2023; Gillis et al., 2023; Källo et al., 2023; Wilson et al., 2023). Such inter-dependent mechanisms are called carry-over effects (Harrison et al., 2011; Teichert et al., 2023) and may result from single or multiple event(s), possibly acting in concert (Smialek et al., 2021; Bull et al., 2022).

For example, Källo et al. (2022) recently demonstrated that pre-smolt and smolt of brown trout (*Salmo trutta*) had a higher likelihood to disperse than parr. In addition, individuals who have spent more time at sea had a greater homing rate, which contradicts the theory that the odor bouquet is “forgotten” with a long sea journey. In a complementary study, the same authors showed that outmigration phenology of brown trout has an effect on the likelihood of adult returns (Källo et al., 2023) and varies spatially, at a river scale. Regarding salmon species, Westley et al. (2013) identified a greater homing rate for Chinook salmon that have spent at least one year in freshwater compared to their conspecifics that migrated during their first year of life, suggesting an effect of juvenile imprinting on homeward migration. Still, on the Pacific side of the globe, Sturrock et al. (2015) have described that the relative proportion of Chinook salmon phenotypes (fry, parr, and smolt in this study) in adult returns would vary inter-annually, partly because of the hydrological regime experienced as a juvenile. More particularly, while sea-departure as parr always contributed the most to the adult population, the fry contribution was greater in wetter years and the smolt contribution was higher in drier years (Sturrock et al., 2015). Altogether, these

studies on several Salmonid species suggest a potential carry-over effect of the phenology at sea departure, but also of marine strategies on adult return rates.

In Atlantic salmon, the condition of smolt migration has been suggested as one of the most important drivers of subsequent marine survival (Russell et al., 2012; Harvey et al., 2020; Lilly et al., 2023), with a “bigger-is-better” hypothesis (Gregory et al., 2019; Simmons et al., 2022), although an asymptotic relationship is plausible, especially for stocked fish (James et al., 2023). Along with the post-smolt stage (Friedland et al., 2017; Long et al., 2023), smolts are particularly vulnerable to environmental factors encountered during their downstream migration (Thorstad et al., 2012), potentially leading to mismatch conditions in unfavorable ecosystems (Teichert et al., 2020). Therefore, an increased body length (and other indicators of good condition) is considered a fair predictor of survival because bigger individuals are usually greater competitors for food and habitat resources, less subjected to predation (Gregory et al., 2019; Falkegård et al., 2023) and they may exhibit higher survival rate to adverse environmental conditions, whether biotic or abiotic (Chaput et al., 2019). It is also well-established that, in coexisting populations, wild smolts have a higher return rate than their stocked conspecifics (Saloniemi et al., 2004; van Rijssel et al., 2024), although reared smolts are often bigger than wild individuals (Armstrong et al., 2018), which probably demonstrates their lower fitness because of potential carry-over effects from hatchery-rearing (Araki et al., 2008). Yet, in recent years, an earlier timing of smolt emigration has been described in the literature (Kennedy and Crozier, 2010), presumably related to global warming effects (Otero et al., 2014). This earlier entrance at sea is hypothesized to be one factor explaining the global decline in salmon population abundance (Russell et al., 2012; Otero et al., 2014) as the match/mismatch dynamics would severely bend over the second option (Chittenden et al., 2010; Satterthwaite et al., 2014). Again, and in relation to the previous sections, this is where we see the value of considering portfolio effects from a conservation perspective, as the diversity of life histories will promote an overall population resilience to climate change (Figure

1-16). Additionally, besides the "biotic side" of management strategies, a corpus of recent studies also highlights the importance of their abiotic counterparts, demonstrating the importance of habitats complexity for long-term salmon persistence (Phillis et al., 2018; Cordoleani et al., 2021; Coleman et al., 2022; Cordoleani et al., 2024).

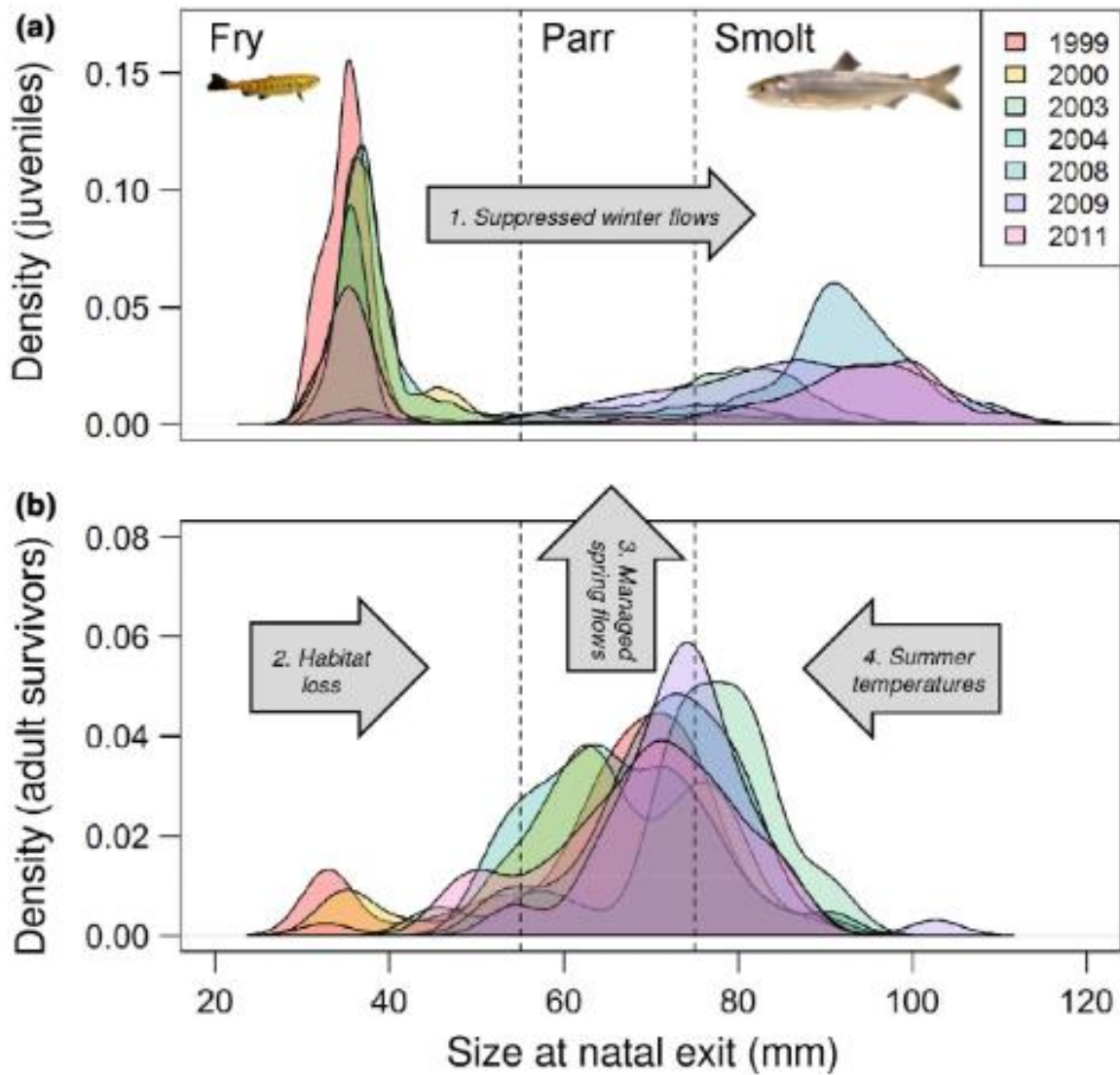


Figure 1-16: Selection against phenological extremes in a modified riverscape. Natal exit size distributions of (a) juvenile salmon sampled by rotary screw traps, versus (b) surviving adults from the same cohort (reconstructed using otolith strontium isotopes), from Sturrock et al. (2020).

Cumulative (or synergistically) to condition and timing of outmigration, the marine phase is also known to be a decisive, although more obscure (Thorstad et al., 2021), factor in adult return rates. For example, regarding sea age, Chaput, (2012) demonstrated how, in recent years, the 1SW/MSW ratio has increased, probably because of a marked decline in MSW abundance compared to 1SW salmon. This results were further supported by Gregory et al. (2019) who showed that MSW individuals had a substantially higher mortality rate compared to 1SW fish, although the authors warn between the mortality and maturation confusion (*i.e.* is a low return rate of MSW salmon due to an elevated mortality during the second year at sea or because of a low proportion of individuals maturing as MSW ?). The fact that Power et al. (2023) showed probable carry-over effects from the first to the second summer of feeding may strengthen the hypothesis of a differential mortality between 1SW and MSW fish. However, contrasted results are also found in the literature with, for example, a population that has shifted from primarily 1SW to 2SW salmon (Harvey et al., 2022) in Norway. In addition to sea age, other phenological traits such as condition (length, mass) and timing of adult returns are also known to vary in response to global change. In France, Bal et al. (2017) showed evidence of a general decline in length, mass, and a delayed spawning migration timing for Atlantic salmon from several populations (Normandie, Bretagne, and Aquitaine). However, while such observations were similar in the three regions, phenological shifts were more pronounced for 1SW individuals than for MSW fish. In another study, identical “tactics” (*i.e.* earlier return to breeding grounds) have been demonstrated in salmon populations from Ireland (de Eyto et al., 2022), and more generally, the evidence of the marked decline in salmon condition when entering freshwater areas to spawn from long time-series studies is unequivocal (Legrand et al., 2021; Vollset et al., 2022) (Figure 1-17).

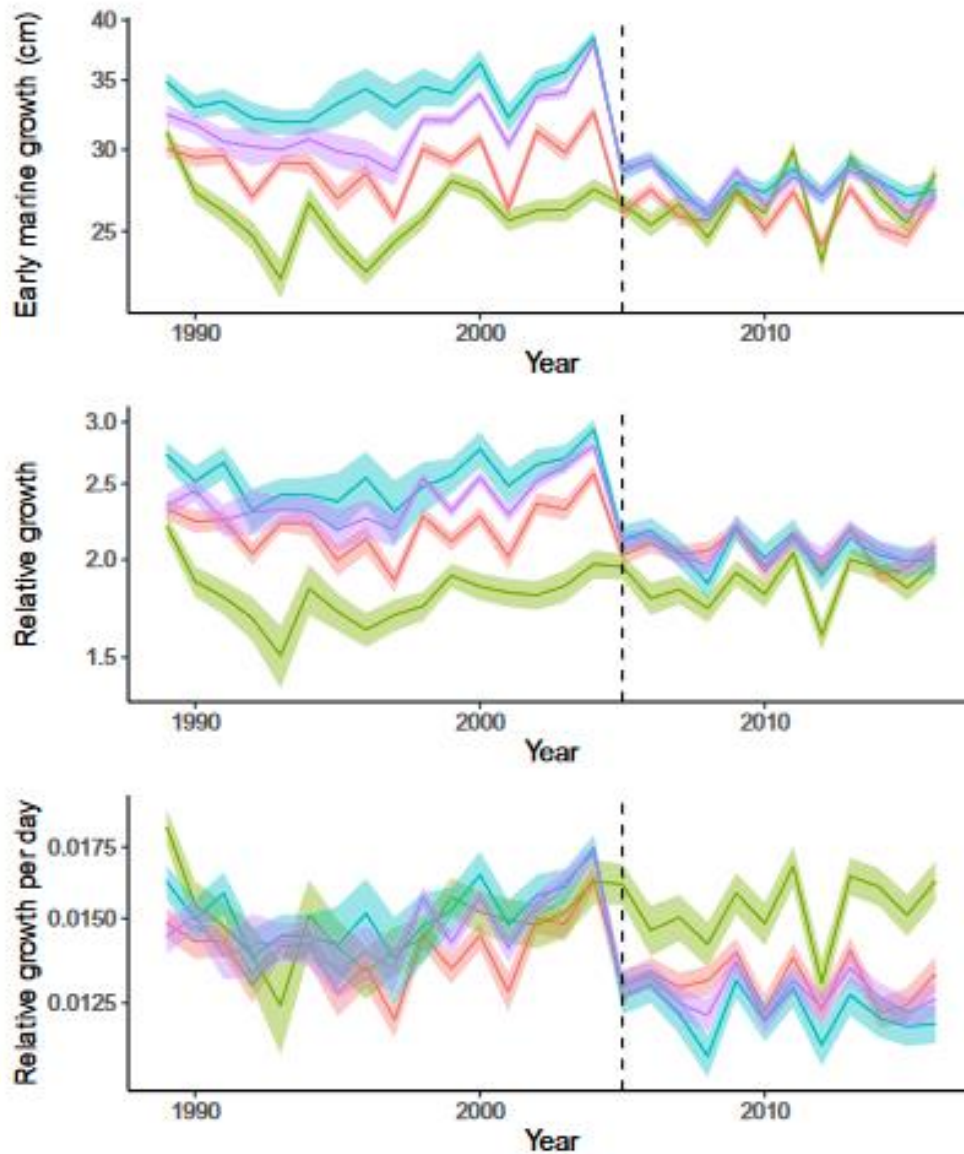


Figure 1-17: Comparison of three growth measurements on adult Atlantic salmon from Norway. Error envelopes are 95% confidence intervals from a model for each region, where year is a fixed effect and river ($N = 180$) is a random effect. Color code indicates regional divisions into south-eastern (purple), south-western (cyan), middle (red), and north (green). Relative growth is defined as early marine growth divided by the smolt size, while relative growth per day is relative growth divided by estimated days spent at sea until October 31. From Vollset et al. (2022).

Although we demonstrated strong evidence of freshwater and marine phenological shifts, studies that investigate (i) both freshwater (*i.e.* age and size at sea departure) and marine strategies (*i.e.* sea age) in (ii) coexisting populations on adult returns are scarcer. Yet, contrasted results are found in scientific literature and stress the need to better understand life history diversity in managed populations (Stich et al., 2015a). For example, Teichert et al. (2020) highlighted that natal origin had “a small influence compared with the local environmental conditions” on smolt emigration timing in a Belgian population. Similarly, in Norway, Urke et al. (2013) demonstrated that hatchery fish had a similar migratory behavior compared to wild salmon. In opposition, results are more ambivalent on the other side of the Atlantic, with studies showing a net difference in migratory patterns between wild and hatchery smolts (Frechette et al., 2023), or similar behaviors with asymmetric survival in favor of wild individuals (Hawkes et al., 2017), or contrarily, dissimilar behavior with no significant effect on survival rate (Stich et al., 2015b). Regarding the marine phase, Erkinaro et al. (2019) showed an inverse relationship between the river age and the sea age, which may emphasize the importance of the freshwater phase. Inversely, Freshwater et al., (2023) described that “age classes sharing the same years of ocean growth had more similar patterns of variation than those sharing a common brood year, suggesting a dominant role of marine life history”. Finally, in addition to temporal considerations, spatial scale is also on the table as both synchronous (Olmos et al., 2020) and potential asynchronous responses to marine changes have been discussed in the literature, even at relatively low spatial scale (Feeney et al., 2022).

Obviously, disentangling the role of specific phenological characteristics that contribute to adult returns is very challenging (Thorstad et al., 2021). For example, environmental stressors such as water discharge or temperature can directly affect juvenile phenology via a cascade of effects (Sturrock et al., 2020; Bjerck et al., 2021). Yet, a better understanding of the role of

“individual tactics” in coexisting populations would be highly valuable from a conservation perspective (Stich et al., 2015a; Gregory et al., 2019). This is particularly true for populations in the Bay of Biscay, which occupy the southern limit of the species' range, and are probably even more at risk from global change events (Valiente et al., 2010) (Figure 1-18).



Figure 1-18: Fourth knowledge gap identified in the thesis, with the associated hypotheses of research work.

THESIS OBJECTIVES AND MANUSCRIPT STRUCTURE

Throughout the previous sections, I highlighted four knowledge gaps about the spatial and temporal variation in the metapopulation structure of Atlantic salmon populations in the Bay of Biscay. For the first and second knowledge gaps, the inter-annual quantification of migratory flows, and therefore the level of connectivity between populations of the Bay of Biscay is unknown, although we have shown that management and population dynamics vary greatly from one region to another. Third, as most localities are independently using stocking programs to preserve natural populations, the role of distinct management strategies in adult returns has yet not been studied. Finally, the influence of carried-over effects from specific phenological traits is not well understood in coexisting populations. Therefore, in the following sections, this thesis aims to enhance our understanding and propose insights into the gaps identified.

- Firstly, chapter 2 presents the methodological, analytical, and statistical tools used in this research work.
- Secondly, chapter 3 addresses gaps 1 and 2 by providing the quantitative estimation of immigration and emigration rates in the southern Bay of Biscay over a 10-year period.
- Then, chapter 5 investigates gap 3 by examining the role of hatchery-reared fish releases in returning adults from the Gironde and the Adour areas.
- Once migratory flows between populations are quantitatively examined, and the role of stocking practices in the persistence of mixed populations is estimated, chapter 6 will provide suggestions into the effect of life-history traits in the dynamic of southern populations from the Bay of Biscay.

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2 TOOLS TO RECONSTRUCT FISH LIFE HISTORIES

2.1 Overview of the current methods frequently used

In order to study fish movements and population dynamics, a multitude of tools have been developed both in the field and the laboratory to accurately reconstruct individual life history. The main methods used include CMR, video-counting stations, natural (e.g. otolith chemistry, stable isotopes analyses, and parasite loading) and artificial (e.g. pop-up satellite archival tag and data storage tags) markers, acoustic and satellite telemetry or genetic studies (Sturrock et al., 2012; Cooke et al., 2022). Undoubtedly, from all these methods, genetics and telemetry (the term used hereafter refers to all methods that include tagging or telemetry) are predominantly employed over the world (Birnie-Gauvin et al., 2019; Lamarins and Buoro, 2023).

Telemetry has been more and more used in recent years, thanks to technological development (Chaput et al., 2019; Källo et al., 2022; Nilsen et al., 2023). Tagging methods are particularly useful for studying fish behavior with accurate spatial and/or temporal resolution (Drenner et al., 2012), especially in a climate-change context where there is an urgent need to understand the “animal-environment interactions” (Lennox et al., 2024). Although telemetry should be applied more largely than it currently is according to the same authors (Lennox et al., 2024), tracking fish life histories with tagging methods present two main constraints: (i) their application with small-size fish is limited because of potential damages and (ii) it is cost-effective, which implies restrictions in the spatial and/or the temporal scale of study. Genetic studies have also been largely performed around the globe to address scientific questions about the effect of hatchery-fish releases (*i.e.* estimations of return rates and level of introgression with natural populations) (Horreo et al., 2008; Ford et al., 2015; Glover et al., 2017; Dedrick and Baskett, 2018), the spatio-temporal variation in the genetic structure (Borrell et al., 2008; Palstra and

Ruzzante, 2010; Gudmundsson et al., 2013), the identification of genetic stocks (Griffiths et al., 2010; Carbonneau et al., 2024), or the drivers of genetic landscape (Bradbury et al., 2014; Nicola et al., 2018). Although genetic studies have proven very useful in examining effective dispersal, it is sometimes limited because it needs a considerable effort to record a representative sample of the parent's genotype. Additionally, specifically to our study system, since the Gironde population was supplemented by strains from the Adour and the Allier until 1988 (see section 1.5.1), the genetic tool may not be suitable for assessing exchange of individuals, due to high levels of admixture (Perrier et al., 2013). Therefore, telemetry or genetics alone may not be ideal to investigate the knowledge gaps identified in this thesis, but as any method, proved to be useful in complement with other tools.

Regarding salmon populations in the Bay of Biscay, two strategies are essentially deployed to study individual movements and/or fish origin: video-counting stations and genetics. Video-counting stations (mainly used in the Adour) are primarily intended to follow stocks evolution, partially characterize the population, examine egg's deposition, and assess the potential benefits of restoration programs. On the other hand, genetic studies (mainly used in the Gironde) allow tracking fish maternal origin to determine the ratio of wild and hatchery individuals from a management perspective (*i.e.* examine the success of stocking programs) (Vandeputte et al., 2021) and investigate the successful life strategies with returning adults (Valiente et al., 2010; Horreo et al., 2011; Perrier et al., 2014). Although very informative, both of these methods are not destined to ultimately reconstruct life histories from a perspective of metapopulation structure. More specifically, we clearly lack spatial and temporal resolution on the level of connectivity between salmon populations from the Bay of Biscay, a scientific issue also encountered in other parts of the globe (Sturrock et al., 2015; Maguffee et al., 2019). To overcome this gap in fisheries science, otolith chemistry has emerged as a reliable, complementary tool to reconstruct life histories for 25 years (Campana, 1999) and is particularly useful when studying diadromous fish

species (Tabouret et al., 2010; Walther et al., 2011; Sturrock et al., 2019). Successful use of otolith chemistry has been demonstrated in the southern part of France (Martin et al., 2013), yet, again, the spatio-temporal dynamic is limited to capture the “big picture”.

2.2 Otolith: a gem of migration story

2.2.1 Roles and properties

Otoliths or “ear bones” are paired calcified structures located in the inner part of teleost fish (Appendix 7), playing a key role in vestibular function and hearing (Popper et al., 2005). Three pairs of otoliths, *i.e. sagitta, lapillus, and astericus*, are found in three otolith sacs, *i.e. saccule, utricle, and lagena*, respectively (Panfili et al., 2002). These distinct chambers are interconnected by semicircular canals and filled with endolymph (Figure 2 1). The *macula*, a sensory epithelium that connects each pair of otoliths to the semicircular canals, detects linear acceleration and sound, enabling fish to maintain their balance (Panfili et al., 2002; Hüsey et al., 2020). As the *sagitta* is the largest otolith in most fish species, it is also the most widely used in fisheries and for this reason, the term "otolith" will refer to the *sagitta* pair throughout the rest of the manuscript.

Otoliths are acellular mineralized structures (Schulz-Mirbach et al., 2019), that develop during early ontogeny and grow by accumulating incrementally concentric calcium and protein layers (Campana and Thorrold, 2001) in three dimensions from the central nucleus, the *primordium*. They are 98% calcium carbonate (CaCO_3), with the remaining 2% defined as the organic matrix of otoliths (Hüsey et al., 2020). Crystals of CaCO_3 can be arranged in three different structures: aragonite, vaterite, or calcite (Campana, 1999). Although aragonite is the most widespread structure (Payan et al., 2004), vaterite is regularly found in fish (symmetrically or asymmetrically, slightly or strongly pronounced), and particularly in hatchery-reared salmonids (Austad et al., 2021). Since otoliths consist of successive layers, which are superimposed on one

another on a daily basis (Pannella, 1971) for most teleost fish, they are natural, archival timekeepers. As a result, three main temporal levels of resolution are observable: daily, seasonal, and annual (Panfili et al., 2002). The latter gave it its fame in fisheries sciences, since otoliths have been and still are used to estimate fish age by reading the number of annual marks, *i.e.* *annuli*, making it possible to monitor the evolution of age structures and the population dynamics of exploited species. Further, for more than 30 years now and the first international otolith symposium (IOS) in 1993 (Wang et al., 2019), otolith chemistry has emerged as a new, promising research area (Campana, 1999) based on four important otolith's properties: i) they are present from birth, ii) they have a continuous growth throughout the fish's life, iii) they can incorporate elements from their environment and iv) they are metabolically inert (*i.e.* no resorption during physiological events such as starvation, reproduction, metamorphosis).

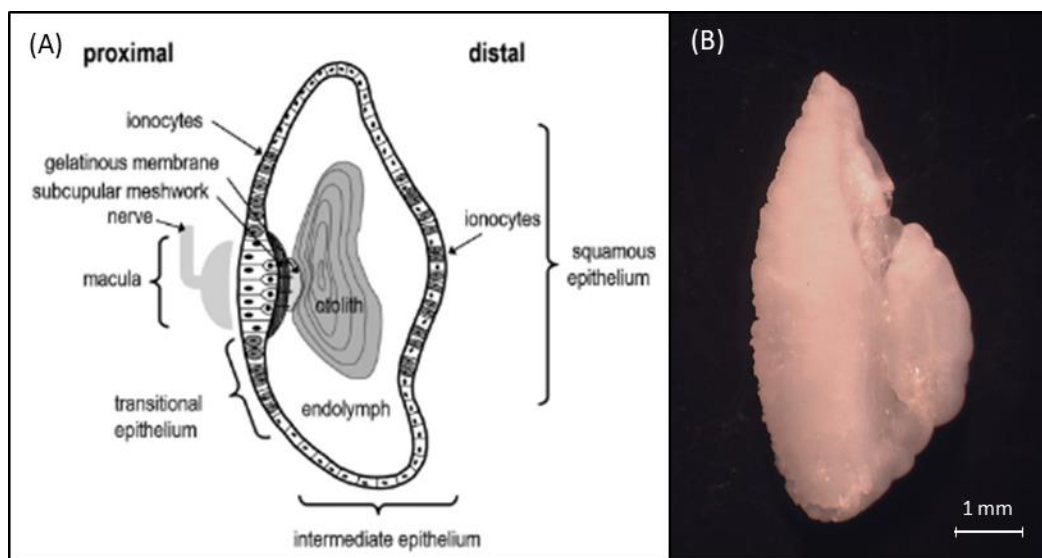


Figure 2-1: (A) Schematic model of a cross section across otolith and endolymphatic epithelium, representing different cell types and their spatial distribution patterns within the epithelium, from Hüsey et al. (2020). (B) Picture of Atlantic salmon right otolith from the thesis dataset (ID: AD818).

2.2.2 Bases of otolith chemistry applications

During the biomineralization process, various elements and their isotopes (to date, 50 elements have been measured in otoliths) can be incorporated into the crystal lattice, bounded to the organic matrix or included in interstitial spaces of the otolith, from water and/or diet sources (Hüssy et al., 2020). There are three mechanisms for an element to be incorporated into a daily layer: (i) the element is randomly trapped in the matrix, (ii) because of a similar ionic radius to calcium (Ca), an element can substitute on the surface of crystallization and (iii) an element can be bounded to a matrix compound (Thomas and Swearer, 2019). However, as the otoliths are not in direct contact with surrounding water, elements must pass, actively and/or passively depending on the considered element and its form, two successive natural barriers to be incorporated into the otolith's surface (Figure 2-2). Resultingly, because of these interfaces, otolith elemental concentrations do not necessarily reflect the environmental concentrations encountered by the fish (Campana and Thorrold, 2001; Elsdon and Gillanders, 2003), as a consequence of physiological regulations.

In this thesis, we focus on using otolith biogeochemistry to investigate geographical and natal (*i.e.* wild or hatchery) origins during the freshwater stage of a diadromous species, the Atlantic salmon. Nevertheless, this is just one application of this tool among many, which has been recently reviewed in Reis-Santos et al. (2022). Regarding the reconstruction of fish life histories, scientists have focused on elements that reflect surrounding waters (Walther and Limburg, 2012). To successfully examine the freshwater geographical origin based on otolith chemistry, four assumptions are established: (i) elements used to reconstruct fish habitats are primarily reflecting the ambient environment, (ii) whatever the spatial scale resolution, environmental chemical concentrations between distinct locations (*e.g.* from a river to another) must be significantly different, (iii) the habitats experienced during a fish's life are reliably recorded

in the otoliths and (iv) the physiological influence on elemental uptake processes are negligible. Numerous studies have been carried out to test reliable elements that will meet the first assumption and from the 50 candidates, two of them are widely used in migration or dispersion studies, the strontium (Sr) plus its isotopes (^{86}Sr and ^{87}Sr) and the barium (Ba) (Elsdon and Gillanders, 2003; Brown and Severin, 2009; Walther and Limburg, 2012). The second assumption is important because, if we want to be able to investigate fish origins, individuals must have inhabited environments with chemical signatures that are sufficiently discriminated between them to be observable in the otolith. Additionally, that specific presumption reminds us of the importance of clearly defining the spatial scale of the study depending on the methods employed (see sections 1.6 and 1.7). Thirdly, several studies have shown the importance of considering the possible delay between "exposure" to a natural environment and the incorporation of this chemical information into the otolith. In particular, individual metabolism (Grønkjær, 2016; Vignon et al., 2023) and extreme climatic events such as flash floods (Bareille et al., 2024) play a major role in elemental uptake. Here too, this variability of response highlights the need to define both spatial and temporal scales. Finally, the fourth assumption, while generally acknowledged for most study cases, is subjected to caution (Izzo et al., 2018). A substantial amount of research has demonstrated that, especially for fully marine fish, the physiological influence can significantly influence the otolith concentrations of elements that supposedly primarily reflect environmental conditions (Walther et al., 2010; Sturrock et al., 2012, 2014). However, this also apply for freshwater fish, especially for the widely used Sr/Ca and Ba/Ca ratios, as recently demonstrated by Bareille et al. (2024). Therefore, although otolith chemistry is a reliable, complementary method to study fish origin and dispersal patterns, it is important to keep in mind all these possible limits when interpreting the results.

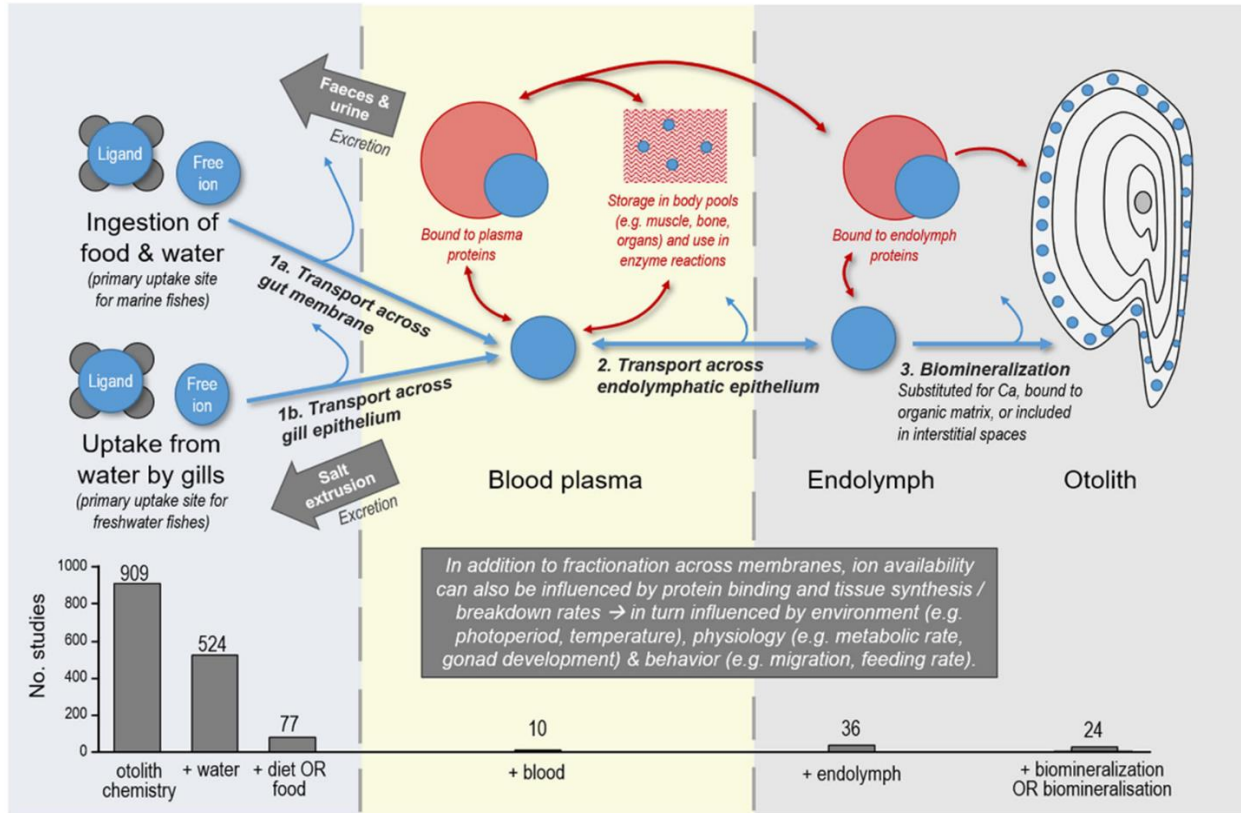


Figure 2-2: Schematic representation of the main ion pathways into an otolith, primarily involving uptake across gill and gut membranes into the blood plasma, transport across the endolymphatic epithelium into the endolymph, then incorporation into the growing crystal lattice of the otolith. Adapted from Hüseyin et al. (2020).

2.3 Analytical and methodological strategies

In order to fulfill the thesis objectives as previously defined, a succession of methodological, analytical, and statistical choices is necessary to obtain four key pieces of information on collected Atlantic salmon: the geographical origin, the natal origin, the age to access the cohort, and the estimated parr and smolt sizes. Therefore, in the following sections, I present the reasoning and methods followed to access these four levels of information.

2.3.1 Which element or combination of elements should be used?

Geographical and natal origins

To characterize fish origin and migration patterns between distinct areas, several elements and their isotopes are commonly employed, especially in the case of diadromous fish species. Traditionally, three proxies are almost routinely used now to reconstruct life histories: Sr, Ba (both elements are always expressed as the molar ratio to Ca, *i.e.* Sr/Ca and Ba/Ca, in mmol·mol⁻¹), and the ratio of ⁸⁷Sr/⁸⁶Sr (Walther and Limburg, 2012). Briefly, Sr and Ba are both very useful to distinguish riverine from marine habitats as the concentration of Sr is usually higher in the open ocean than in freshwater, while an inverse relationship is described for Ba, making them ideal markers of salinity gradients (Brown and Severin, 2009; Walther and Limburg, 2012). Although the marine concentrations of Sr and Ba are relatively stable over time and space, particularly for Sr, their freshwater concentrations are more variable as they rely on bedrock geological composition and weathering of terrigenous structures for Sr and Ba, respectively (Walther and Limburg, 2012). Additionally, as both elements express an opposite pattern with salinity gradients, the Sr/Ba ratio has also been employed in the scientific literature (Limburg et al., 2011; Walther et al., 2011). Finally, primarily because no fractionation occurs from external sources (either water or diet) to internal handling and ultimate otolith incorporation, the use of ⁸⁷Sr/⁸⁶Sr has become an optimal tracer of natal environments (Barnett-Johnson et al., 2008; Walther and Thorrold, 2009; Brennan et al., 2015).

Although the use of these four variables (*i.e.* Sr/Ca, Ba/Ca, Sr/Ba and ⁸⁷Sr/⁸⁶Sr) occurs almost obvious from the literature, it is impossible to know whether adding one or more other variable(s), or subtracting one or more, would provide better discriminating power without testing it (Mercier et al., 2011). Here, the combination of variables employed results from a nested

analysis that has been conducted prior to the start of the thesis, using otolith chemistry collected from Atlantic salmon, ensuring the right choice (Figure 2-3).

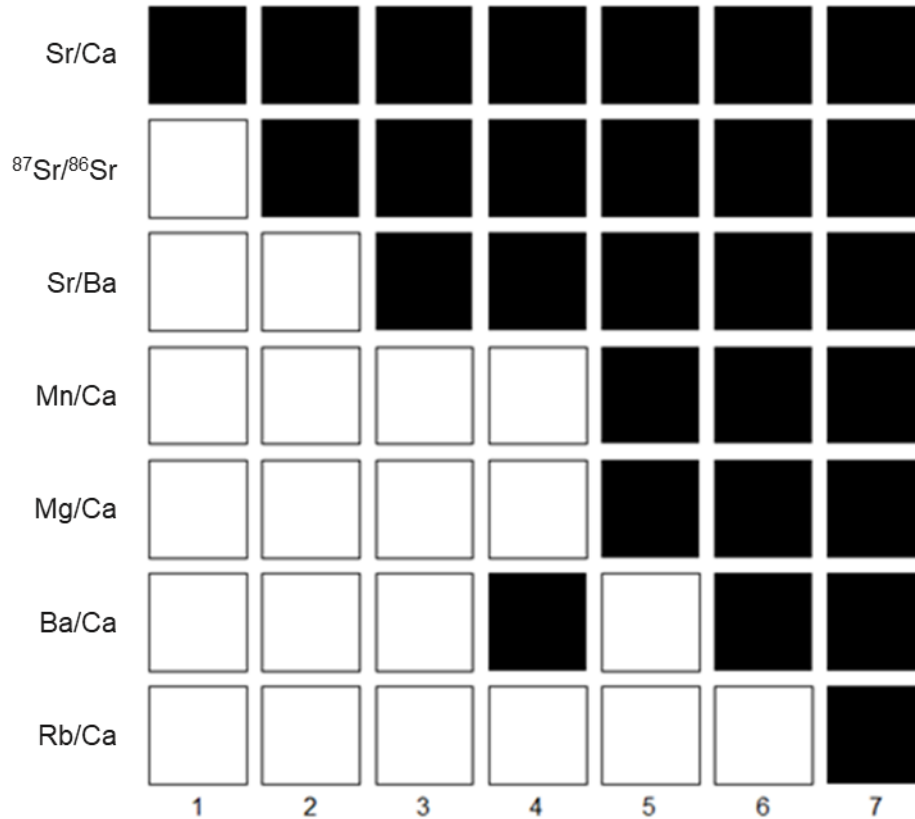


Figure 2-3: Nested analysis showing the best combination of variables (from $n = 1$ to $n = 7$ possibilities) to discriminate 16 rivers from the Atlantic coast.

Age estimation

To estimate the total age of every sampled fish, we combined two distinct methodologies to assess (i) the river age and (ii) the sea age. Since the method to predict the river age has been the subject of a scientific publication (Fontaine et al., 2024), which is presented in Chapter 4 of this thesis, I only discuss the approaches to determine the sea age in this chapter. And, because we did not use otolith chemistry to evaluate the marine age, the processes are presented in a further section (see section 2.3.5).

2.3.2 How do we measure otolith elemental and isotopic concentrations?

Depending on the final application (e.g. paleoclimatology, stock assessment, ecophysiology, seafood provenance) various methods have been employed in otolith chemistry to quantify elemental and/or isotopic concentrations including probe-based techniques (e.g. laser ablation – inductively coupled plasma mass spectrometry (LA-ICPMS), secondary ion mass spectrometry (SIMS)), methods based on sample dissolution (e.g. solution-based ICPMS, isotope ratio mass spectrometry (IRMS)) or 2D mapping using LA-ICPMS, particle induced x-ray emission (PIXE), scanning X-ray fluorescence microscopy (see Reis-Santos et al. (2022) and references therein). In this thesis, elemental otolith concentrations were performed using an inductively-coupled plasma mass spectrometer (ICPMS DRC II, Perkin Elmer) coupled to a high-repetition-rate infrared femtosecond laser ablation (fs-LA Alfamet-Novalase, France) system. The Sr isotopic ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) was obtained on the same otolith using a multi-collector inductively-coupled plasma mass spectrometer (Nu-Plasma MC-ICPMS) coupled to the same laser. All the elemental and isotopic analyses were performed at the *Plateforme d'Analyse des Métaux Traces par Ablation Laser* (PAMAL), expertise center of the Inorganic Isotopic Imaging (I3) CNRS Platform (UPPA, Pau).

Briefly, the principle of LA-ICPMS is based on the ability to extract matter, in aerosol form, using a large quantity of light energy focused on the otolith's surface. As this technique enables direct analysis of otolith without the need for prior dissolving, it limits the contamination possibility in addition to provide a very good spatial resolution of the distribution of elements (Arai et al., 2007; Tabouret, 2009). However, its main disadvantage is the lack of matrix-matched standards. The use of a femtosecond laser considerably reduces thermal effects, which greatly preserves the sampled structure, and results in a “cold ablation” with greater analytical accuracy and, potentially, greater sensitivity (Pécheyrans et al., 2007). Once the laser hits the otolith's surface,

the product of ablation is then transferred by argon (Ar) and/or helium (He) to the ICPMS and introduced as an aerosol into the system via a nebulizer. An argon plasma atomizes and ionizes the sample and the produced ions are then directed towards the mass spectrometer via an interface formed by two successive cones. Ion lenses focus the diverging ions beam before it enters the mass filter (quadrupole) and then, ions are selected according to their mass/charge ratio (M/Z) and detected by an electron multiplier (Figure 2-4). Altogether, the combination of fs-LA with ICPMS offers a robust spatial and temporal resolution, as recently demonstrated by Vignon et al. (2023). In their study, the authors have modeled the elemental composition within the ablation cell and the mass spectrometry to estimate an artefactual time-lag which was about 20 μm , corresponding to a mean of 6.4 days in their study case (using otoliths from *Salmo trutta*). Details of the main analytical parameters used in this thesis were as follow: ablation strategy: 2D scan in a ventral-dorsal axis; transect width: 30 μm ; ablation depth: 10 μm ; transect length: from 200 μm before the nucleus to the dorsal edge; platine speed: 5 $\mu\text{m}\cdot\text{s}^{-1}$. Calibration was performed using three NIST standards (610, 612, and 614; NIST, USA) and accuracy was verified with two certified referenced materials (CRM), the NIES 22 (NIES, Japan) and the FEBS 1 (NRCC, Canada), both obtained from the otoliths of marine fish (*Lutjanus sebae* and *Lutjanus campechanus*, respectively).

Once the otolith was analyzed for elemental concentrations, we measured the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio using a Nu Plasma MC-ICP-MS. The MC-ICP-MS is the only ICP-MS that truly allows simultaneous measurement of several isotopes, unlike other instruments such as quadrupole, high resolution, or time of flight (TOF) ICP-MS. This compensates for signal variations due to plasma instabilities, ion extraction, or sample introduction systems and provides a separate and simultaneous measurement of ions of different masses formed at the same time in the plasma (Martin, 2013). Shortly, the ions beam is conveyed to the electrostatic sector (ESA) which consists of two charged plates between which a constant electrostatic field acts as a kinetic energy filter.

Then, the electromagnet acts as a mass filter, separating ions according to their M/Z ratio. The magnetic sector allows mass dispersion at the magnet outlet (essential for simultaneous measurement), meaning that each ion beam must be focused on its own detector, which remains fixed (Figure 2-4). As we aimed at measuring the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in this thesis, the laser width was adapted (min: 50 μm ; max: 180 μm) to the previously quantified Sr otolith concentration, (i) to ensure a minimal voltage of 2V (for the measurement of the exact isotopic ratio) and (ii) to avoid any saturation issue when reaching the marine part of the otolith. In addition to accuracy verifications with both CRM, the reliability of our analyses was checked by ensuring a stable $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in the external part of the otolith, corresponding to the marine phase. Every analysis was conducted by scanning a laser beam parallel and juxtaposed to the transect previously established by the elemental analysis.

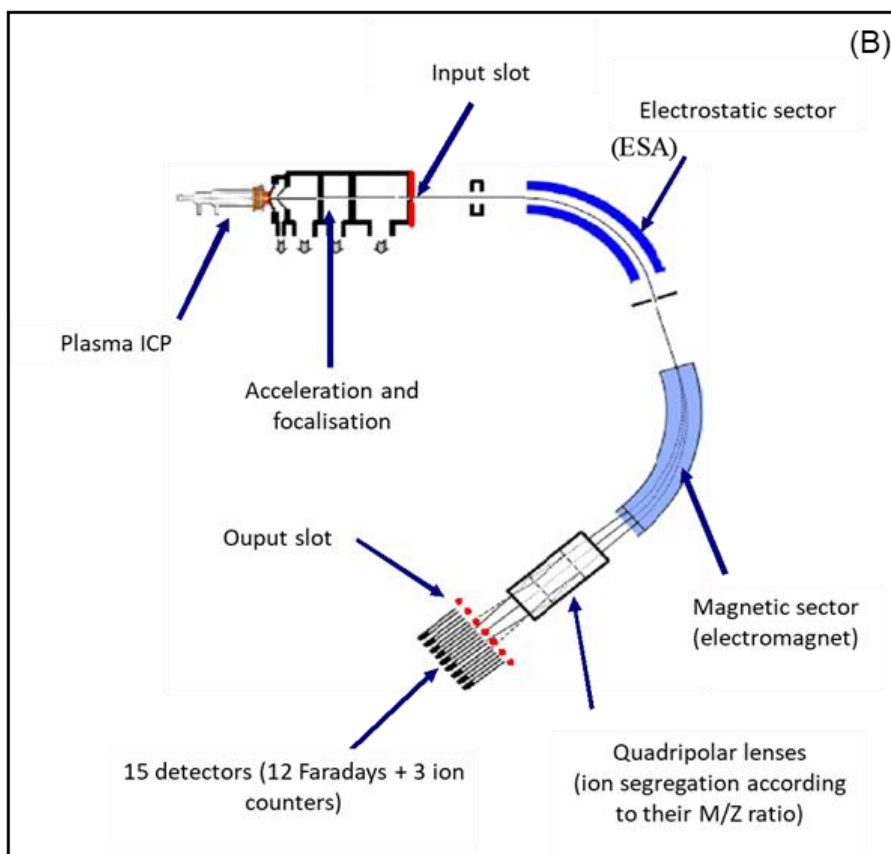
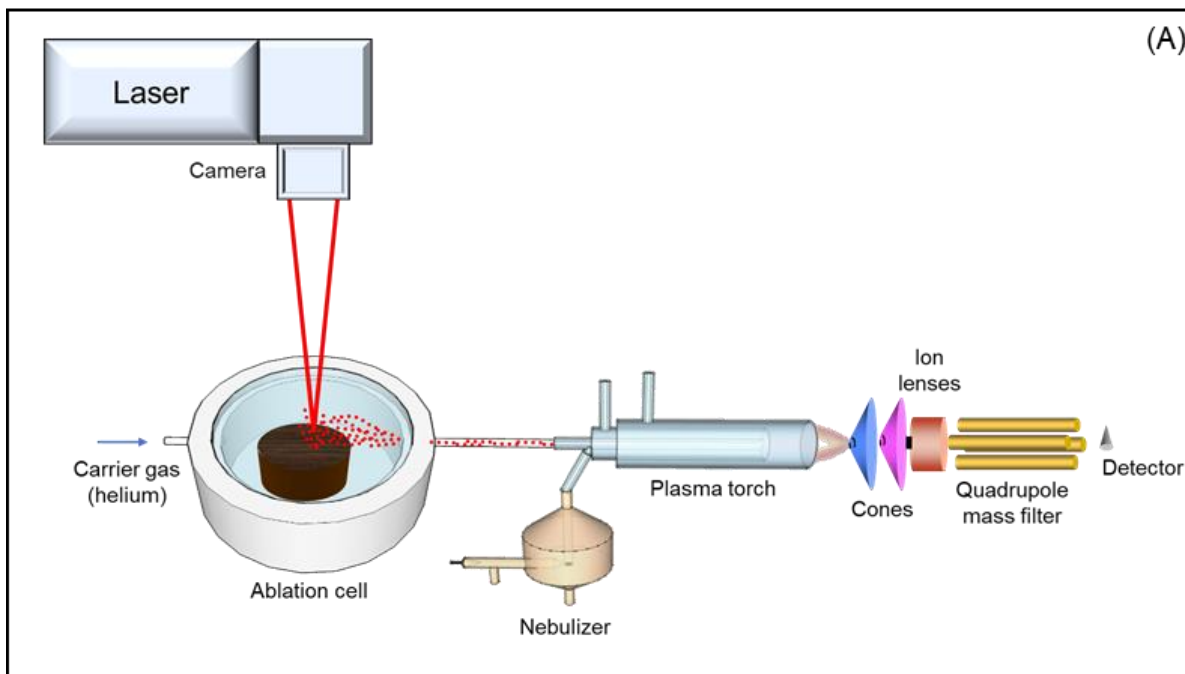


Figure 2-4: Schematic overview of (A) a LA-ICPMS and (B) a Nu Plasma MC-ICPMS, adapted from Martin (2013).

2.3.3 Prediction of geographical origin

Just like the optimal combination of variables to be used, the choice of a statistical model is also important to accurately track fish life histories and has been globally overlooked. During the early expansion of the “otolith geochemistry area” (approximately the 2000’s), discriminant analyses such as Linear Discriminant Analysis (LDA) or Quadratic Discriminant Analysis (QDA) were predominantly performed in the literature. Yet, they “fail to model the complex and nonlinear relationships observed in such large multivariate data sets” (Mercier et al., 2011). Therefore, to cope with the complexity generally produced with otolith chemistry datasets, machine learning classification methods such as Random Forest (RF) are suitable candidates, as they allow to use untransformed data, with no need to respect multi-normality parameters, to build models (Mercier et al., 2011; Jones et al., 2017; Morissette et al., 2021) (Figure 2-5). Resultingly, the use of RF has recently gained in popularity in otolith chemistry studies (Maguffee et al., 2019; Bassi et al., 2023; Kállo et al., 2023; Pan et al., 2023). Succinctly, RF is an ensemble learning method that constructs multiple decision trees during training and merges their outputs to improve accuracy and reduce overfitting. Each tree is built using a random subset of the data and features, ensuring diversity among the models. During prediction, the RF aggregates the results of individual trees and as more trees are included, the generalization error tends to stabilize (Breiman, 2001). Therefore, this approach leverages the power of multiple decision trees to create a robust predictive model. To produce reliable predictions, the model is fed with elemental and isotopic profiles from individuals whose origins are certified. The objective being to determine the geographical origin of unknown origin salmon, we therefore selected the portions of the otolith profiles corresponding to the juvenile stage of the individuals, *i.e.* freshwater residency. To this end, we considered the average value of every variable of interest (Sr/Ca, Ba/Ca, Sr/Ba, and $^{87}\text{Sr}/^{86}\text{Sr}$) from this portion. This is further detailed in the Figure 3-2, which describes our complete methodology.

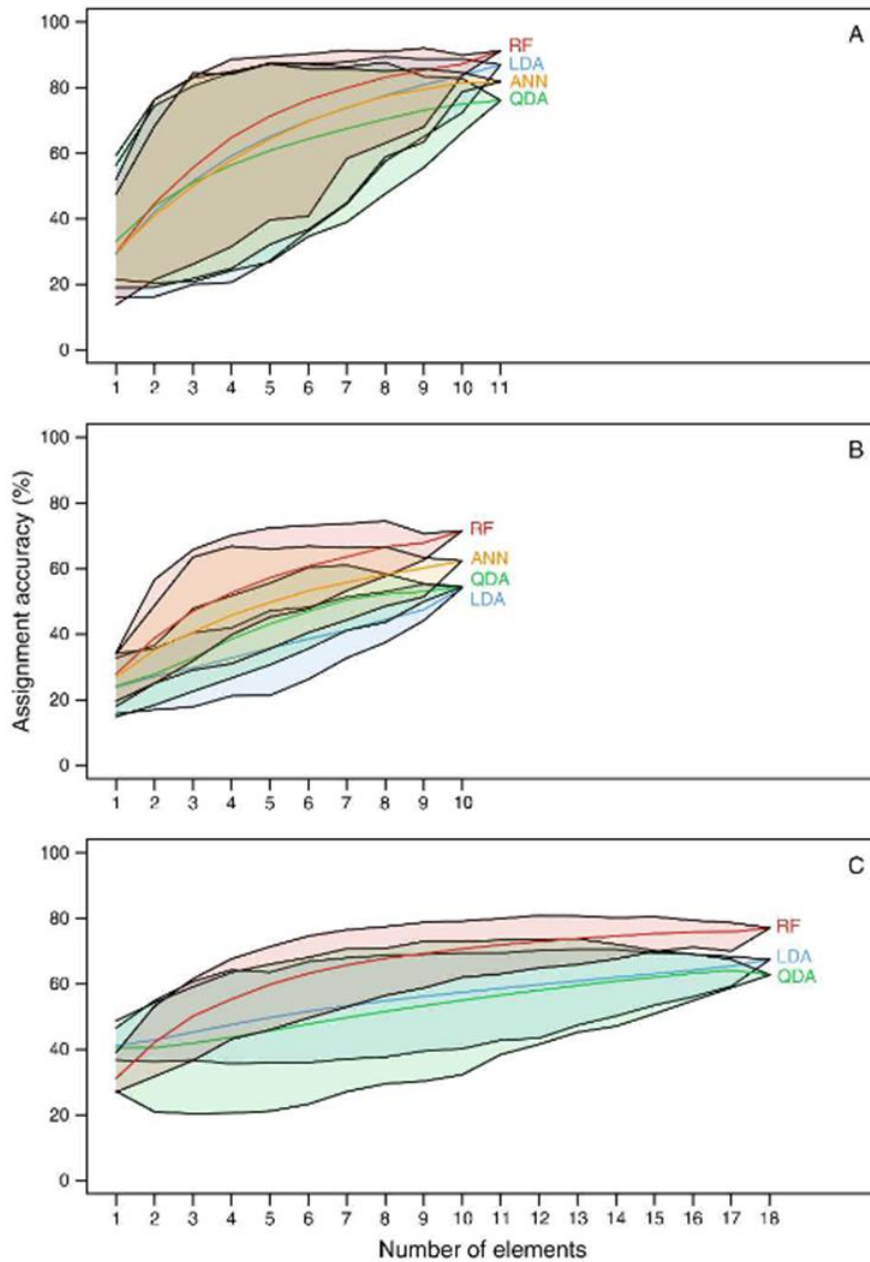


Figure 2-5: Accuracy in assigning fish origins by otolith microchemistry obtained according to element combination size (combinations with 1, 2, ..., N elements) for Random Forest (RF; in red), Artificial Neural Networks (ANN; in orange), Linear Discriminant Analysis (LDA; in blue), and Quadratic Discriminant Analysis (QDA; in green) in the three data sets tested: (A) French lagoons, (B) Portuguese estuaries, and (C) U.S. coastal nurseries. In each case, the shaded area depicts the difference between maximum and minimum accuracies for a given method, and calculated mean accuracy is shown by the bold colored line. From Mercier et al. (2011).

Depending on the level of spatial resolution we are aiming for to predict an origin for unknown individuals, several models can be performed. In this thesis work, a two-step approach was followed to estimate the geographical origin of returning adults at (i) a regional (or basin) scale and (ii) a river scale according to the predictions from the first model. In both spatial approaches, the model itself is identical, the only difference being the input sources (*i.e.* chemical signatures from regional areas for the “basin-scale” or within one specific watershed for the “river-scale”) and therefore, the prediction output. An example of the proximity or dissimilarity of otolith geochemical signatures on a regional scale is shown in the following figure (Figure 2-6).

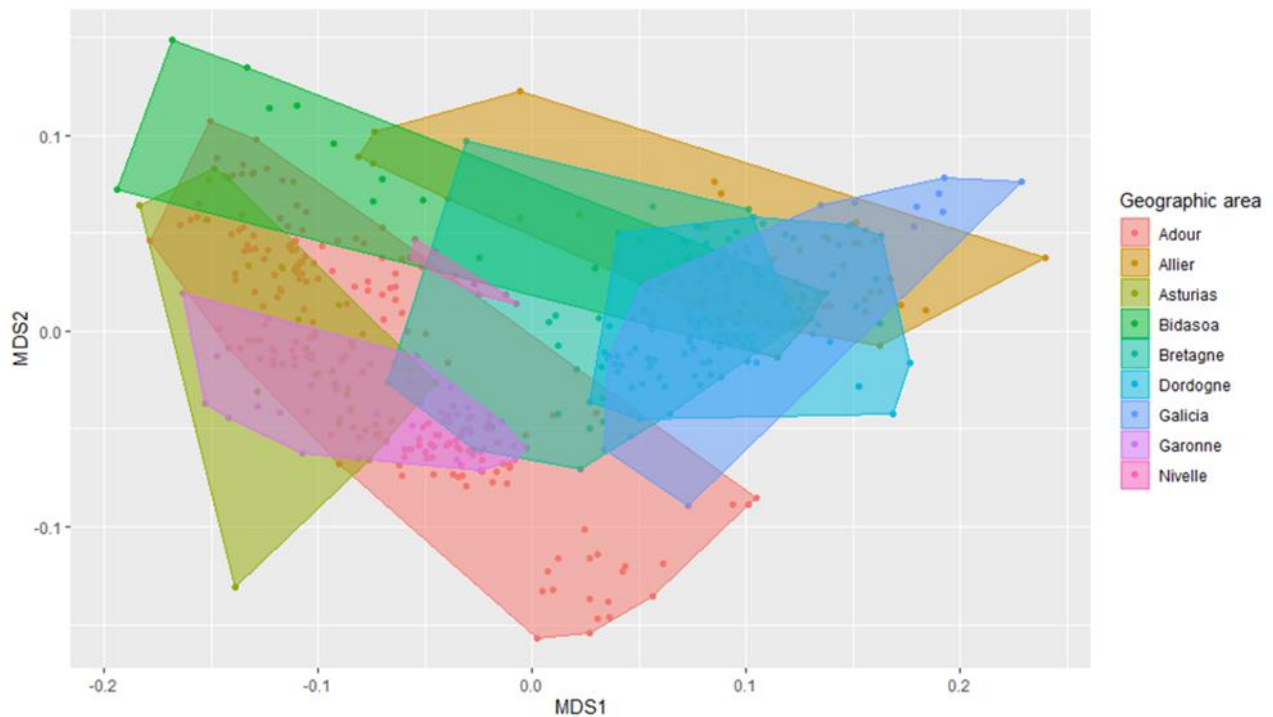


Figure 2-6: Representation of the chemical landscape by geographical area of interest using a Multidimensional Scaling (MDS). The MDS was performed using raw data of otolith elemental (Sr/Ca, Ba/Ca and Sr/Ba) and isotopic ($^{87}\text{Sr}/^{86}\text{Sr}$) signatures available for the thesis work. One convex polygon per locality. Stress: 1%.

2.3.4 Prediction of natal origin (wild vs. hatchery)

In the general introduction of this thesis, we have seen that numerous release strategies are employed in the southern Bay of Biscay. Resultingly, this will translate into a large heterogeneity in the profile sections that correspond to the hatchery residence, varying from a couple of days (eggs or early fry) to several months (parr 0⁺ and smolts). Similarly, the measured elemental and isotopic ratios differ substantially as the rearing site can have a very distinct geochemical signature compared to the site of release. Therefore, to distinguish between the wide temporal (*i.e.* growing period) and spatial (*i.e.* hatchery site) range of possible “rearing signatures”, we used a naïve univariate functional clustering method. The approach is based on an “expectation-maximization” (EM) algorithm (Bouveyron and Jacques, 2011) and allows clustering functional data according to their similarities (Figure 2-7), which is exactly the case with otolith elemental and isotopic profiles. Broadly, it can be used to distinguish targeted hatcheries on the basis of their typical geochemical signatures, e.g. minimum or maximum values along the profile or curve amplitudes.

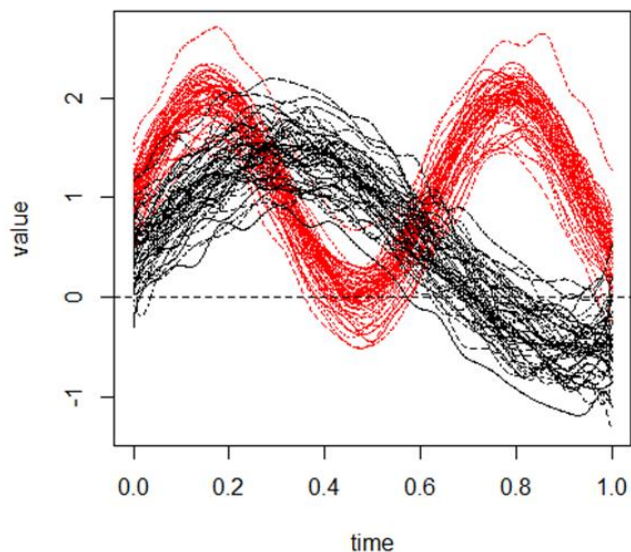


Figure 2-7: An example of univariate functional clustering using the R package *funHDDC* with the “trigo” dataset. Source: https://rpubs.com/stat17_hb/functional_data_clustering.

2.3.5 Age estimation

As previously mentioned, the method to assign a river age is presented in the Chapter 4. Besides, to determine the marine age of every sampled fish, we used two distinct methods. First, when available (50.1% of the total sampling), scale-reading was performed by MIGRADOIR employees by counting scale *annuli* (by two independent readers) to provide a sea age. Scalimetry has been routinely used for several decades (Baglinière et al., 1985) and provides robust estimates as the reading is facilitated in the marine phase with larger *annuli* (Figure 2-8). However, since the scales were not always available (or most of them could not be read during the thesis due to lack of time), we used the mass-to-age or the fork length (FL)-to-age relationships as a secondary approach. To make sure that both methods provided similar and comparable results, we compared sea age estimations between all the individuals for whom we had the three estimates (*i.e.* scalimetry, mass-to-age estimation, and fork length-to-age estimation) and found a 94.9% correspondence. Nevertheless, it should be noted that for every fish without scales, in most cases, we used the mass-to-age relationship as length data were scarcer (length: 311 observations; mass: 1043 observations). A visual assessment of both mass-to-age and fork length-to-age is further presented (see Figure S 5-1).

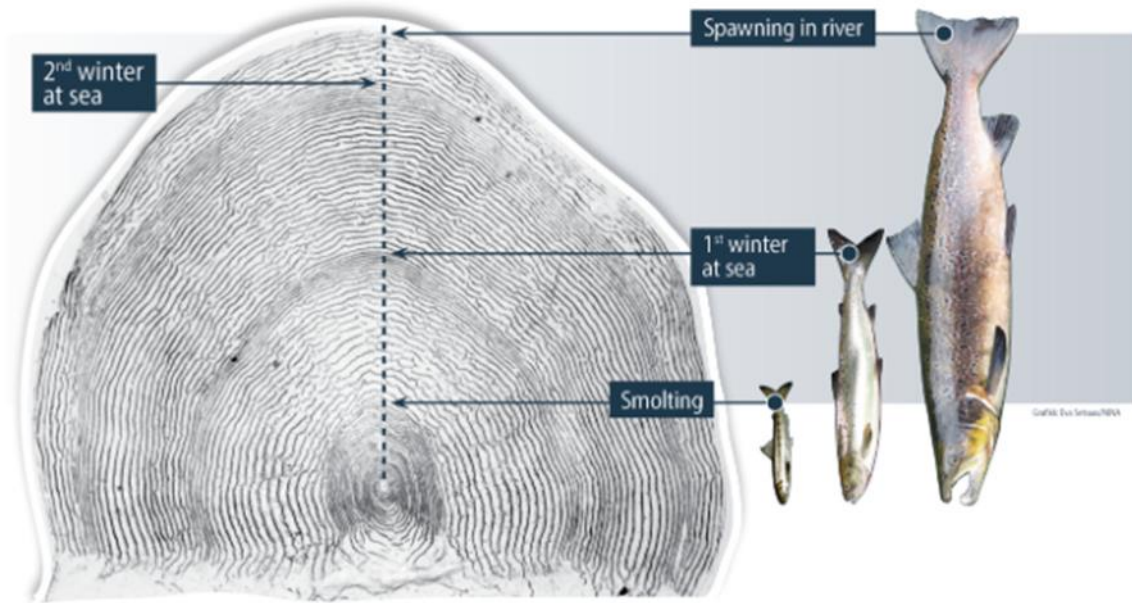


Figure 2-8: Atlantic salmon scale showing patterns of freshwater and marine growth, from Burton et al. (2024).

2.3.6 Reconstruction of parr and smolt sizes

To back-calculate the parr (*i.e.* size-at-first winter) and smolt (*i.e.* size-at-outmigration) lengths, we used the relationship between the fork length of juveniles and the size of the otolith radius on the dorsal axis (Sturrock et al., 2015) (see Figure S 6-1). This relationship was first calibrated using juveniles collected in twelve rivers from the Adour watershed (Figure 1-6) and the “otolith distance” was obtained on an axis at 90° to the rostrum/post-rostrum axis. Specifically, to back-calculate the parr size, we measured the otolith distance from the nucleus to the point where a sharp decline in the Zn/Ca ratio was observed, reflecting the winter season (Fontaine et al., 2024). For the size-at-outmigration, we measured the otolith distance from the nucleus to the inflection point marked by a simultaneous sharp increase in the Sr/Ca ratio and a pronounced decrease in the Ba/Ca ratio, corresponding to ocean entry (Walther and Limburg, 2012).

2.4 References Chapter 2

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3 INTER-ANNUAL DISPERSAL STABILITY WITHIN THE ATLANTIC SALMON METAPOPOPULATION FROM THE BAY OF BISCAY

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3.1 Abstract

Natural biocomplexity, characterized by genetic and phenotypic diversity, enhances the resilience of metapopulations by buffering against environmental fluctuations and stochastic events. This diversity acts as a natural hedge, where different populations may thrive under varying conditions, ensuring the overall stability and survival of the species. Regarding migratory Salmonid species, the portfolio effect is particularly important due to their complex life cycles and reliance on diverse and interconnected habitats along their ontogenic migration. To date, little is known about the temporal variability of dispersal movements, both in terms of intensity and direction. Yet, dispersal behavior is expected to vary over the next decades, in response to the overwhelming stressors (biotic and abiotic, from natural and anthropogenic sources) that Salmonid are facing. In this study, we investigated Atlantic salmon dispersal patterns on a regional scale in western Europe, *i.e.* the Bay of Biscay, using otolith chemistry. Our results display significant connectivity between salmon subpopulations, particularly that of the Adour, which appears to be both a source and a sink for related populations. Although changes in Atlantic salmon dispersal could be expected with the acceleration and intensification of global change effects, our study shows very stable philopatric and dispersal rates over the last decade. Combined with genetic studies, our observations suggest that the metapopulation structure may help in the stability of the system, probably via a demographic but also perhaps genetic rescue effect.

Keywords: *Salmo salar*, homing, straying, temporality, life history

3.2 Introduction

Philopatry or the “homing” to natal spawning areas is recognized to be a fundamental behavior for the maintenance of many migratory species. This unique and ubiquitous trait is found in many taxa, from marine mammals (Baker et al., 2013) to reptiles (Lee et al., 2007), insects (Buehlmann et al., 2013) and birds (Cava et al., 2016). Returning mature adults that migrate to natal sites favor match occurrence between locally-adapted mates in spawning areas, therefore strengthening fitness benefits for the next generations (Dittman and Quinn, 1996; Clutton-Brock and Lukas, 2011). Alternatively, dispersal or “straying” is also a key component in the dynamic of wild populations, highly adaptative to proximate and ultimate environmental cues (Coulson, 2016; Lamarins, 2022), which can foster natural resilience (Perrier et al., 2010). Thus, populations that occupy spatially distinct environments are, to an extent, interconnected through the exchange of individuals, resulting in a metapopulation structure (Hobson et al., 2004; Schtickzelle and Quinn, 2007). From an evolutionary perspective, this dynamic network prevents natural populations from synchronous responses to environmental changes, which may ultimately threaten their overall stability (Anderson et al., 2015), while still promoting the adaptation of distinct populations to a given ecosystem. Additionally, dispersal may allow individuals to colonize new or restored habitats (Willmes et al., 2021), decrease the risk of genetic isolation (Källo et al., 2022b) and potentially provide demographic and/or genetic and/or evolutionary rescue effects (Lamarins, 2022).

Along the freshwater-sea continuum, many salmonid populations exhibit a metapopulations structure (Schtickzelle and Quinn, 2007), although other strategies (e.g. freshwater residence or precocious maturation) are observed *in natura* (Birnie-Gauvin et al., 2019). While natural populations generally express an elevated homing rate (Lamarins and Buoro, 2024), studies have shown that salmonid species can exhibit a wide variety of life histories

(Erkinaro et al., 2019), and that globally, the role of dispersal has been overlooked (Birnie-Gauvin et al., 2019; Källo et al., 2022a). Yet, the sustainability of this wide and complex diversity (*i.e.* biocomplexity) in life histories is crucial to prevent from population synchrony and destabilizing the portfolio effect (Greene et al., 2010; Schindler et al., 2010; Satterthwaite and Carlson, 2015; Sturrock et al., 2015), especially in a global change context (Anderson et al., 2015; Herbold et al., 2018; Crozier and Siegel, 2023). However, although dispersal is a desirable trait in a healthy metapopulation (Dittman and Quinn, 1996), excessive dispersion can be detrimental for both the donor population, mainly via the loss of potential mature adults, and the receiver population with competition on spawning grounds and the loss of local genetic adaptations (Keefer and Caudill, 2014). Unfortunately, with the unprecedented increase in anthropogenic pressures (*e.g.* habitat alterations, pollution) and environmental stressors (*e.g.* extreme climatic events such as floods or droughts) on aquatic ecosystems, dispersal rate of salmonid species is expected to vary in the next years (Crozier et al., 2008; Sturrock et al., 2019), potentially jeopardizing healthy populations.

The Atlantic salmon (*Salmo salar*, Linnaeus 1758) is perhaps the most emblematic and iconic salmonid because of its important cultural, economic, and recreational role in our contemporary world (Thorstad et al., 2021). In response to the collapse of wild European and North-American populations in the late 1980s' and the beginning of the 1990's (Chaput, 2012; ICES, 2019), stocking programs have been encouraged in many rivers and watersheds where Atlantic salmon breed or used to breed (ICES, 2021). As a consequence, many systems are now "hatchery-dominated" and the exacerbated dispersal rate of individuals from artificial reproduction (Candy and Beacham, 2000) threatens wild populations with behavioral (Brenner et al., 2012; Zaporozhets and Zaporozhets, 2012; Nilsen et al., 2023) and genetic (Quinn, 1993; Perrier et al., 2013b; Ford et al., 2015) effects observed in salmon species. From a management perspective, as a metapopulation gathers source and sink populations by definition, one of the main tasks would therefore be to identify populations that "provide" or "receive" individuals. Considering the

natural biocomplexity of wild populations and the massive effects of hatchery-releases on metapopulation, effective quantification and understanding of “source-sink dynamics” are crucial to preserve and maintain salmon populations (Johnson et al., 2012; Willmes et al., 2021) in this very complex mosaic. Ultimately, since population structure occurs in relatively small systems (Gudmundsson et al., 2013), it emphasizes the need to address dispersal rate at multiple regional scales, not to also mention the temporality as the direction of gene flow varies with environmental conditions (Palstra et al., 2007).

In the North-East Atlantic Ocean, the Bay of Biscay represents the southern range of European Atlantic salmon populations, with individuals from the Galicia region (northern Spain) being at the edge of the species distribution (Hatfield, 2020). From the Bretagne region (north-west France) to the Galicia, seven regional populations are identified: Bretagne, Allier, Gironde, Adour-Nivelle, Bidasoa (as part of the Gipuzkoa region), Asturias and Galicia (Figure 3-1) (Blanco et al., 2005; Saura et al., 2006; Perrier et al., 2013b); and they all exhibit very different characteristics in term of size (annual number of returning adults), composition (proportion of one sea winter (1SW) and multi-sea winter (MSW)), habitat structure (patchy riverine ecosystems and/or large rivers) and sustainability (proportion of wild and hatchery-fish). Interestingly, over the 2010-2020 decade, most populations continued to decline or remained stable at low levels of abundance (Almodóvar et al., 2023; Lebot and Rivot, In press), except for the Gironde and the Adour, both of which recorded a global increase in the number of returning adults, which is unrivaled in the Bay of Biscay. Among the hypotheses that can be drawn to explain these observations, increased dispersal from the surrounding populations would be a plausible assumption in the context of the ongoing climate change and the intensive stocking programs in adjacent basins (Perrier et al., 2011a, 2013b; Almodóvar et al., 2023). To date, a limited number of studies have examined the level of dispersal in the Bay of Biscay for Atlantic salmon and most of these results rely on genetics (Valiente et al., 2010; Perrier et al., 2011b, 2013b), tagging

(Leunda et al., 2013) or the combination of genetics and tagging (Consuegra and García de Leániz, 2007; Kuparinen et al., 2010). However, tagging programs often rely on stocked individuals only and genetics generally provide information on effective dispersal (gene flow), yet, an increase in dispersal does not necessarily translate into successful breeding of migrants. Besides these two methods, otolith chemistry has been demonstrated to be a robust and reliable tool, complementary to genetics and telemetry, to quantitatively assess the emigration and immigration rates.

Otoliths or “ear bones” are calcified structures located in the inner ear of teleost fish (Panfili et al., 2002) that grow incrementally, at a daily rate, making them natural tags of fish movements in contrasted environments (Campana, 1999; Campana and Thorrold, 2001; Elsdon and Gillanders, 2003). Based on the geochemical differences among estuarine and freshwater habitats, otolith chemistry has been successfully used for more than 20 years to track the life histories and investigate the metapopulation structures of migratory fish species (Tabouret et al., 2010; Martin et al., 2013b; Randon et al., 2018; Nachón et al., 2020; Teichert et al., 2022). Among the multiple elements that can be measured in otoliths, strontium (Sr), barium (Ba), and the isotopic ratio of Sr ($^{87}\text{Sr}/^{86}\text{Sr}$) are the most employed to reconstruct life histories as they primarily reflect past environmental conditions, encompassing from the “physiological noise” (Hüssy et al., 2020; Bareille et al., 2024). Regarding salmon, Pacific salmon species have received more attention in otolith studies (Barnett-Johnson et al., 2008; Hamann and Kennedy, 2012; Brennan et al., 2015; Sturrock et al., 2015; Willmes et al., 2021) compared to Atlantic salmon, especially in western Europe. Yet, Atlantic salmon populations from the Bay of Biscay are essential to study as populations at the edge of the species distribution are more vulnerable to global change (Lassalle et al., 2009b; Valiente et al., 2010; Nicola et al., 2018). In the Adour system, a previous study has demonstrated the potential of otolith chemistry to distinguish Atlantic salmon origins on a fine spatial scale (*i.e.* intra-basin, Martin et al., 2013a), hence providing first insights into

dispersal rates in relatively small areas (Martin et al., 2013b). However, one limitation of this study is the lack of perspectives considering the exchange of individuals in the Bay of Biscay on a larger spatial scale, particularly in a global change context where dispersal is expected to increase with extreme climate events. Specifically, in our contemporary world, where environmental and anthropogenic pressures are constantly increasing, both on continents and seas (e.g. chemical and light pollution, overfishing, global warming, match-mismatch dynamics), we could expect a shift in migratory flows, in terms of quantity but also of connectivity (*i.e.* direction and intensity). This study examines Atlantic salmon dispersal patterns and metapopulation dynamics among the large rivers draining the southern Bay of Biscay (North-East Atlantic Ocean): the Gironde, Adour, and Nivelle locations. Using otolith chemistry to determine fish origin, with chemical signatures representing every main population from the Bay of Biscay, we address two main objectives: (i) to investigate the spatial philopatry and dispersal rates within each so-called population in the southern Bay of Biscay and (ii) to assess the temporal variation in the exchange of individuals using a ten-year collection of otoliths from the Gironde and Adour systems.

3.3 Materials and methods

3.3.1 Sampling sites and population characteristics

The southern Bay of Biscay

Three distinct areas are home to Atlantic salmon in the southern Bay of Biscay, namely the Gironde to the north and the Adour and Nivelle to the south. The Gironde system gathers two large-river sub-basins, *i.e.* the Dordogne and Garonne, that join together at the Bec d'Ambés to form the estuary of Gironde (Carry et al., 2023). The sub-population of the Dordogne is about 3-times larger than the Garonne's sub-population (Table 3-1), and they are both largely set on fish from hatchery releases (<https://www.migado.fr>). In the last decade, the number of mature salmon returning to the Dordogne sub-basin was found to gently increase whereas it stagnated in the Garonne sub-basin. Since geochemical signatures strongly differ between the Garonne which drains substrates from the Pyrenean mountains and the Dordogne which flows over rocks from the Massif Central mountains (Willmes et al., 2018), and considering the significant difference in sub-population dynamics, these two geographical areas have been examined independently. About 230 km to the south (Figure 3-1), the Adour system represents a medium-size basin (Table 3-1) which can be separated into three sub-basins: Nives, Oloron, and Pau. The Adour basin hosts the largest population in the southern part of France (Table 3-1) and returning mature adults can be found in thirteen rivers (Figure 3-1). Nevertheless, the population is not equally distributed across sub-basins as approximately 70% of the mature salmon that have escaped the fisheries would ascend to the Oloron sub-basin, 20% to Pau, and only 10% to the Nives (<https://www.migradour.com/>). Additionally, native and self-sustaining sub-populations are found in the Oloron and the Nives meanwhile the Pau sub-population is still being restored with monitoring programs. Finally, a few kilometers southwest of the Adour estuary, the Nivelle represents a small coastal river (Figure 3-1) and carries the smallest, native and self-sustaining

French Atlantic salmon population (Table 3-1). Initially clustered with the Adour (Perrier et al., 2013b), a further study, with a larger sample size, has shown that the genetic structure of the Nivelle population was significantly different from the Adour (Perrier et al., 2014). Hence, combined with the distinct watershed system and population characteristics from those of the Adour, the Nivelle has been investigated independently.

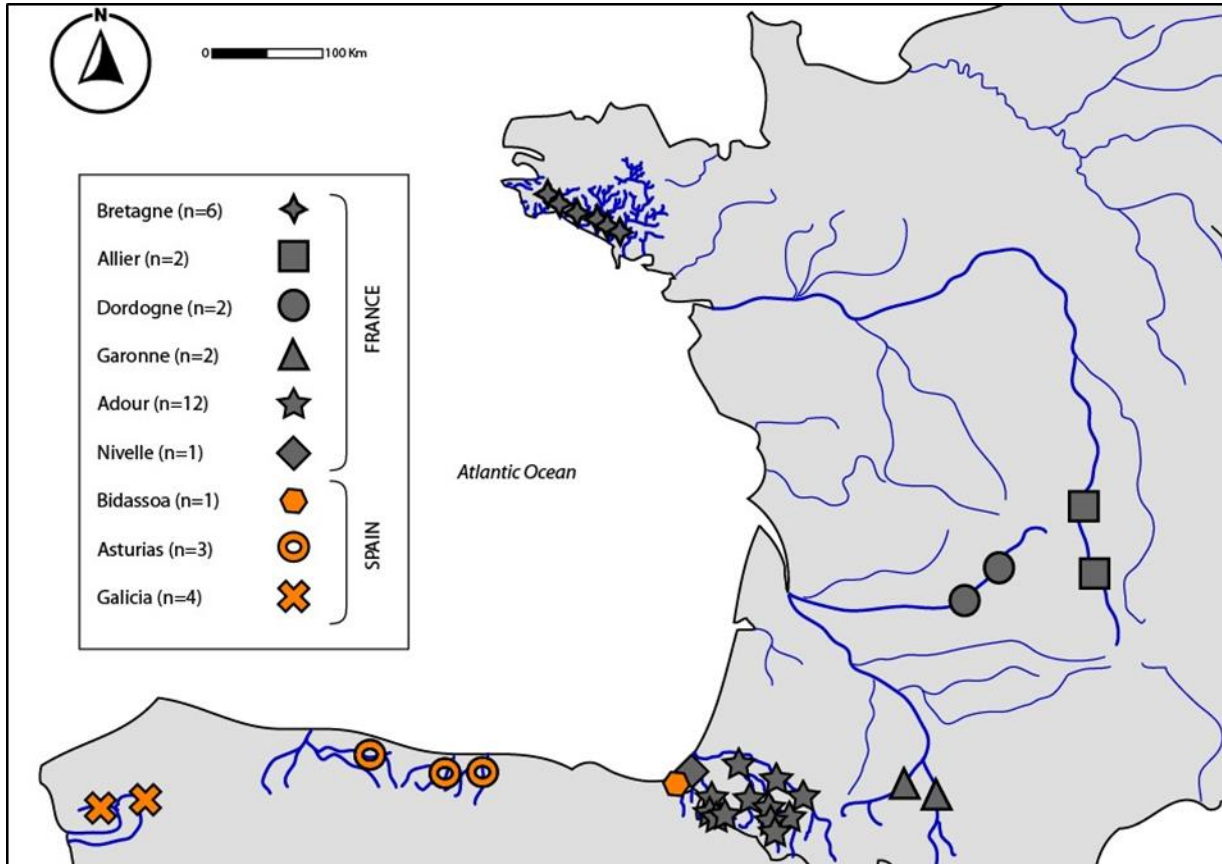


Figure 3-1: Map of the sampling sites (regional scale, $n = 9$; river scale, $n = 33$) used in this study, from North to South: Bretagne, Allier, Dordogne, Garonne, Adour, Nivelle, Bidassoa, Asturias and Galicia. The number of rivers available from each watershed is specified in brackets.

Table 3-1: Geographical and ecological characteristics of the locations used in this study. Population sizes range from 2011-2020 to ensure comparable information between sites, as estimations were not available for some locations prior to 2011. Stocking actions are classified into three categories (*i.e.* null, moderate, and intense) according to the importance of management actions in each location.

Geographic area	Sub-basin	Substrate type	Maximum length (km)	Distance to the Adour estuary (km)	Distance to the Gironde estuary (km)	Atlantic salmon population size	Stocking actions
Bretagne		Mainly crystalline	149	~550	~300	11100 ± 1600 ¹	Null
Allier		Crystalline/volcanic	1,006	~440	~210	660 ± 260 ²	Intense
Gironde	Dordogne	Mixed sedimentary/crystalline	483	~230		380 ± 160 ³	Intense
	Garonne	Mixed crystalline/sedimentary	525	~230		130 ± 50 ³	Intense
Adour		Mixed sedimentary/crystalline	308		~230	5200 ± 1200 ⁴	Moderate
Nivelle		Sedimentary	39	~19	~250	100 ± 25 ⁴	Null
Bidasoa		Sedimentary	66	~27	~240	475 ± 130 ⁵	Intense
Asturias		Sedimentary	145	~330	~560	3100 ± 620 ⁶	Intense
Galicia		Mainly crystalline	340	~700	~930	420 ± 320 ⁷	Intense

Notes: Distances between each geographic area was estimated along the coast line. Data of Atlantic salmon population sizes are from ¹Lebot and Rivot (In press);

²<https://www.logrami.fr>; ³<https://www.migado.fr>; ⁴<https://www.migradour.com>; ⁵Navarre government; ⁶NASCO (2020); ⁷Courtesy of the Galicia government.

Additional sampling sites in the Bay of Biscay

The other salmon collected in this study have been chosen to cover most of the populations potentially connected to those of the Garonne, Dordogne, Adour, and Nivelle. Southwards from the main salmon stocks under study, along the Bay of Biscay, we included samples from the Bidasoa and two Spanish regions, *i.e.* the Asturias-Cantabria (northern part of Spain) and the Galicia (north-western part of Spain, *i.e.* the southern limit of the Atlantic salmon distribution area) (Figure 3-1). They mainly consist of small coastal rivers (Table 3-1) and stocking programs are, here again, important to conserve and preserve natural populations. Northwards from the main salmon stocks under study along the Bay of Biscay, the Allier basin is defined by large and long rivers intensively fed by fry stocking, in contrast to the Bretagne river system that is shaped by many small coastal rivers and where populations are mostly renewed by natural reproduction (Table 3-1). A summary of watershed characteristics, population sizes, and possible management actions are found in Table 3-1.

3.3.2 Sample collection and analysis

Otolith sampling

The present study takes advantage of a previous dataset available from Martin et al. (2013a), where the authors demonstrate the reliability of otolith chemistry to assign a geographical origin (river-scale) for Atlantic salmon in the Adour system. Here, we merged the data produced in this previous study (exclusively from the Adour basin; assignment database: $n = 168$ parr from twelve rivers, unknown origin database: $n = 180$) with a new dataset (assignment database: $n = 345$; unknown origin database: $n = 1362$) including samples from the nine regions of the Bay of Biscay aforementioned. Additional samples in the assignment database include both juvenile and adult sagittal otoliths (referenced as otolith from hereafter) as juvenile were not available at some

locations (Bretagne, Allier, Gironde, Bidasoa, Asturias, and Galicia). Parrs were only accessible for the Adour, Nivelle, and partially for the Allier basin. Details of the complete otoliths collection (assignment database: $n = 513$; unknown origin database: $n = 1542$) are presented in Table 3-2.

Assignment database

This dataset was exclusively composed to create and train a discriminant model allowing us to further infer the natal origin from an unknown individual. In the Adour basin, new otoliths of salmon juveniles ($n = 38$, from nine rivers) were collected in 2014 and 2017 during the survey of juvenile abundance. Parr otoliths from the Nivelle ($n = 8$, from 2011) were provided by the *Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement* (INRAe) at Saint-Pée-sur-Nivelle (ECP INRAe, 2018). In the Allier basin, otoliths of smolts ($n = 8$) were sampled in 2008 by a rotary screw trap as they emigrated from the Allier river and adults ($n = 41$) were captured in 2013 during their spawning migration (both stages were collected for sustaining programs). The otoliths of adult salmon from other systems (Bretagne, $n = 58$; Gironde, $n = 103$; Bidasoa, $n = 19$; Asturias, $n = 24$ and Galicia, $n = 46$) were recovered from 2007 to 2015 from recreational anglers, institutions that collect broodstocks during their spawning migration for sustaining programs and carcass surveys. In the Bidasoa, otoliths have been collected from nasally tagged (using coded wire tags (CWT)) individuals in this river (information supplied by the Navarre government). Individuals from the Gironde originate from fish farm batches certified by parental genetic analysis, and whose river of discharge is known (Vandeputte et al., 2021). We also verified that the geochemical signatures of otoliths from the Gironde were consistent with those of the waters in which fry had been discharged. Finally, for all remaining locations, *i.e.* Bretagne, Asturias, and Galicia, only otoliths from adults for which the chemical composition of the otolith matched that of the river of capture were selected.

Table 3-2: Number, origin (capture site), and sampling year(s) of Atlantic salmon (*Salmo salar*) used in the assignment database and the unknown origin database in this study.

Sampling site			Assignment database			Unknown origin database		
Geographic area	Sub-basin	River	Number of known origin juveniles	Number of known origin adults	Years of collection	Number of unknown origin adults	Years of collection	
Adour	Nives	Arnéguy	20		2011, 2014, 2017			
		Béhérobie	21		2011, 2014, 2017			
		Laurhibar	9		2011, 2014, 2017			
		Nive	6		2011			
	Oloron	Aspe	14		2009, 2010, 2014, 2017			
		Lourdios	12		2009, 2010	1259	2009-2018	
		Oloron	22		2009, 2010, 2014, 2017			
		Ossau	31		2009, 2010, 2014, 2017			
		Saison	15		2009, 2010, 2014, 2017			
		Verts	10		2009, 2010			
		Pau	Ouzom	16		2006, 2009, 2010, 2014, 2017		
	Pau		30		2006, 2009, 2010, 2014, 2017			
	Gironde	Dordogne	Dordogne		60	2007-2012		
			Vézère		13	2007-2012		
Garonne		Ariège		15	2007-2012	261	2007-2016	
		Garonne-Neste		15	2007-2012			

Nivelle	Nivelle	8		2011	22	1997-2014
Allier	Alagnon-Sioule		8	2009-2013		
	Allier	8	33	2009-2013		
Asturias	Deva-Cares		15	2012, 2013		
	Sella		3	2012, 2013		
	Nansa-Pas-Ason		6	2012, 2013		
Bidasoa	Bidasoa		19	2015		
Bretagne	Aven		2	2015		
	Blavet		2	2015		
	Elle		27	2015		
	Jet		5	2015		
	Odet		12	2015		
	Scorff		10	2015		
Galicia	Lerez		11	2008-2013		
	Minho		4	2008-2013		
	Tambre		12	2008-2013		
	Ulla		19	2008-2013		

Unknown origin database

To investigate the dispersal behavior of Atlantic salmon populations in the southern Bay of Biscay, new otoliths from MSW adults have been collected in the Gironde ($n = 261$, from 2007 to 2016), the Adour ($n = 1079$, from 2011 to 2018) and the Nivelle ($n = 22$, from 1997 to 2014) systems (Table 3-2). In the Adour, we merged the 180 otoliths of adult salmon published by Martin et al. (2013b) with our new otolith collection to reassign every individual ($n = 1259$) identically. Atlantic salmon heads were provided by professional fishermen in the Adour estuary as well as recreational anglers (Bretagne, Adour, and Nivelle), carcass surveys on spawning grounds (Adour and Nivelle) and organisms that harvest salmon during their spawning migration for rearing programs (Allier, Gironde, Bidasoa, Asturias and Galicia).

Otolith preparation and chemical analysis

After being extracted from salmon's head, as it has been reported that the presence of vaterite could lead to significant differences in chemical composition compared to aragonite (Pracheil et al., 2019), every otolith with the occurrence of vaterite during the freshwater stage was disregarded. Otoliths were then prepared following the protocol described by Tabouret et al. (2010). Briefly, otoliths were embedded in resin epoxy (Araldite 2020, Escil) before being grounded to highlight the nucleus. Once prepared, otoliths were analyzed for ^{86}Sr , ^{138}Ba , and ^{43}Ca as it is largely recognized that Sr and Ba otolith concentrations are primarily influenced by environmental concentrations (Walther and Thorrold, 2006; Walther and Limburg, 2012). Elemental concentrations were obtained using an inductively-coupled plasma mass spectrometer (ICP-MS DRC II, Perkin Elmer) coupled to a high-repetition-rate infrared femtosecond laser ablation (fs-LA Alfamet-Novalase, France) system and Sr isotopic ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) was measured on the same otolith using a multicollector inductively-coupled plasma mass spectrometer (Nu-Plasma MC-ICP-MS) coupled to the same laser. The elemental and isotopic analyses were

performed at the *Institut des Sciences Analytiques et de Physico-Chimie pour l'Environnement et les Matériaux* (IPREM), and the analytical parameters were set according to Martin et al. (2013a). During the analyses, the signal of Ca was used as an internal standard and we applied the theoretical concentration of Ca in otolith (0.383 g of Ca per g of otolith (Brown and Severin, 2009)) to standardize the measured elemental concentrations as follows: Ba/Ca and Sr/Ca. Calibration was performed using three NIST standards (610, 612, and 614) and accuracy was checked with two certified referenced materials (CRM), the NIES 22 and the FEBS 1, both obtained from the otoliths of marine fish (*Lutjanus sebae* and *Lutjanus campechanus*, respectively). Standard deviations were $4.9 \pm 3.0\%$ and $7.4 \pm 4.9\%$ for Sr (NIES 22 and FEBS 1 respectively), and $5.1 \pm 5.4\%$ and $5.8 \pm 4.3\%$ for Ba (NIES 22 and FEBS 1 respectively). The detection limits were $0.02 \mu\text{g}\cdot\text{g}^{-1}$ for Ba and $0.06 \mu\text{g}\cdot\text{g}^{-1}$ for Sr. Regarding the quantification of $^{87}\text{Sr}/^{86}\text{Sr}$, the width of the laser spot was set according to the concentration of Sr previously acquired (min: 50 μm ; max: 180 μm) to make sure that the voltage we measured was above the 2V threshold and thus, exploit reliable results.

Ethical statement

Every otolith analyzed in this study were collected from monitoring and carcass surveys or from amateur fishermen. Each salmon was sampled according to animal welfare laws, guidelines and policies as approved by sampling permits or the number of individual tag.

3.3.3 Data analysis

In order to be consistent with previous data treatment, we applied the method presented by Martin et al (2013b) to select the portion of elemental transect that corresponds to juvenile freshwater residency (*i.e.* portion of the profile out of the maternal influence and before the sharp increase of Sr, characterizing sea migration) to investigate geographical natal origin for each individual.

Individual average values of Sr/Ca, Ba/Ca, Sr/Ba, and $^{87}\text{Sr}/^{86}\text{Sr}$ within this portion were used to assess the origin of salmon. Since environmental chemical signatures are known to vary with time (Walther and Thorrold, 2009), we included several years and seasons of sampling in our assignment database to account for temporal variation (Table 3-2). Among statistical methods preferably used to assign geographical origin for fish, a machine-learning algorithm such as Random Forests (RF) was found to be one of the most efficient models to perform natal prediction (Mercier et al., 2011; Jones et al., 2017; Maguffee et al., 2019; Morissette et al., 2021; Bassi et al., 2023; Stewart et al., 2023). Briefly, RF are unsupervised ensemble methods that operate by recursively splitting a dataset based on microchemical data. The final classification relies on aggregating the splits from multiple trees (the random forest), and as more trees are included, the generalization error tends to stabilize (Breiman, 2001). Here, we used the *randomForest* R package (version 4.7-1.1) to investigate the natal origin of returning Atlantic salmon. A schematic illustration of the successive steps and parameters followed in this study is presented in Figure 3-2. We ultimately inferred per locality the natal origin of adult individuals and as in any discriminant analysis, the related confusion matrix was used to quantify the uncertainty in the natal assignment. All statistical analyses were conducted using the R (version 4.2.1) software.

In scientific literature, depending on the methods used to study fish origin and migration (e.g. otolith chemistry, genetics, tagging, telemetry, capture–mark–recapture (CMR)), “homing and straying” patterns are mainly estimated and interpreted in two ways. First, philopatry can be defined using the number of fish reallocated to location A, regardless of the capture site. This method would preferentially investigate the “fidelity” itself and the “donor potential” of every location considered, *i.e.* the emigration rate (*ER*). Second, philopatry can be assessed according to the collection site, exploring every possible origin (A, B, or C) of fish caught in location A for example. Hence, this second approach would examine the “receiving potential” of one specific area, *i.e.* the immigration rate (*IR*). Depending on the chosen approach, it is crucial to precisely

define the objective(s) in light of the results, as the two approaches will not provide the same information. In this study, we have performed the analyses following the two methods, however, our sampling does not allow to robustly study the “complete” fidelity and *ER*, as it ideally requires a homogeneous sampling effort across all geographic areas likely to receive individuals (Table 3-2). Therefore, hereafter we present and discuss our results regarding the investigation of (i) the homing rate (*HR*) and *IR* in the Adour, Garonne, and Dordogne populations, with potential sources of donors from all over the Bay of Biscay, whereas (ii) the fidelity rate (*FR*) and *ER* were focused on exchanges between the Adour, Garonne and Dordogne. This second point is partial by definition, as we cannot estimate *ER* into unsampled systems, and is therefore likely to represent the upper range of fidelity and the lower range of *ER*.

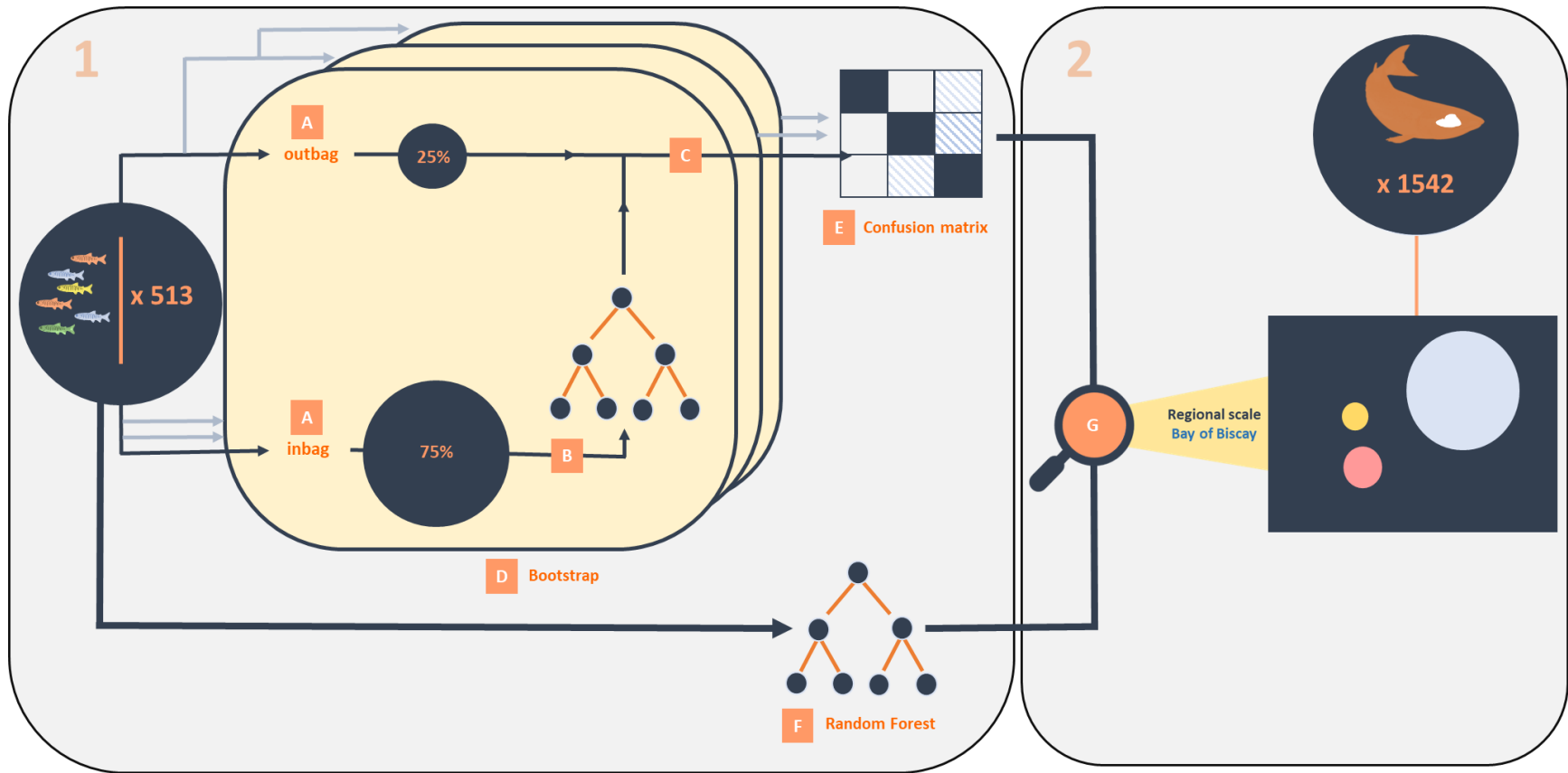


Figure 3-2: Schematic overview of the statistical processes followed in this study to assign a geographical origin for returning Atlantic salmon using a Random Forests (RF) approach. Step 1: A total number of 513 fish, with certified origin, is used to build/train the model and estimate the relative probability of attribution to each geographical area, or each cluster. (A) The dataset is partitioned into an inbag fraction (*i.e.* training set, 75% of the total dataset randomly sampled with replacement, used to build the classification trees) and an outbag fraction (*i.e.* test set, the remaining 25% of the total dataset, used to test the predictions). (B) Classification trees provided by the RF analysis, set to $\beta = 10000$ trees. (C) Predictions of natal origin for each individual from the outbag fraction. (D) For cross-validation purposes, 5000 bootstrapped in/outbag fractions were computed. Then, for more realistic

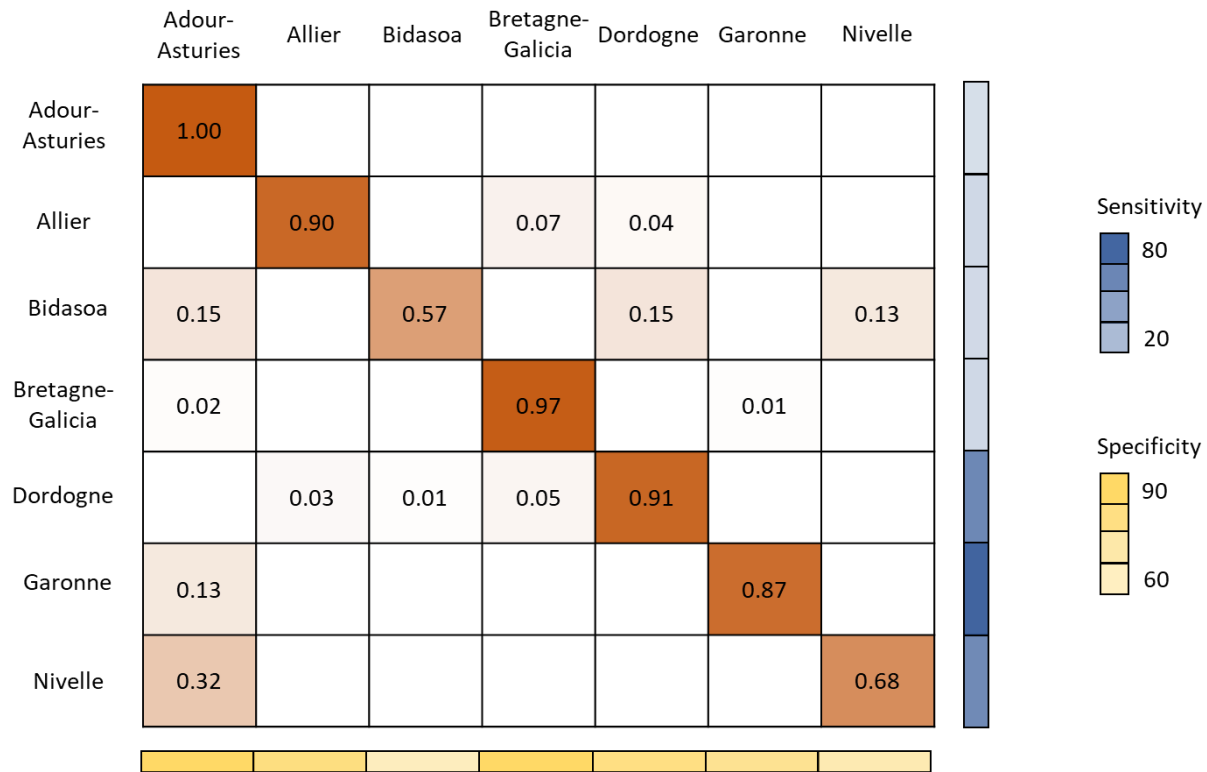
investigations, discriminant performances were evaluated only based on individuals meeting some reassignment criteria (*i.e.* the greatest relative probability of reattribution must be superior or equal to 0.5 and at least two times higher than the second highest probability). Every individual who did not meet this condition was disregarded. (E) A confusion matrix is then produced, by aggregating all bootstraps, to provide a detailed quantification of the models' performances. From the matrix of proximity provided by the RF, a distance matrix is established to form an ascending hierarchical classification in order to visually assess the locations that are preferably discriminated, or, that are conversely disentangled with difficulty. Operations (A) to (E) are then repeated for each possible clustering combinations, from $k = 2$ to the maximum number of possibilities (*i.e.* the number of initial geographical locations, here $k = 9$). (F) The model selected to predict the natal origin of unknown origin salmon is the one that provides the best trade-off between the global error and the number of fishes conserved. Step 2: (G) A total of 1542 adult salmon are used to predict a geographical origin.

3.4 Results

3.4.1 Model performances

The best trade-off between the number of individuals assigned to a geographical origin and the generalization error was a model resulting in seven clusters (Figure S 3-1). Resultingly, the possible clusters or locations of attribution were as follows: Adour-Asturias, Allier, Bidasoa, Bretagne-Galicia, Dordogne, Garonne, and Nivelle. As displayed in Table 3-3, the Bidasoa and the Nivelle present the lowest probabilities of correct reattribution (0.57 and 0.68 respectively) compared to the other clusters. More particularly, individuals from the Bidasoa are in part attributed to the Adour-Asturias (0.15), the Dordogne (0.15), and the Nivelle (0.13) while an important proportion of the individuals from the Nivelle is improperly attributed to the Adour-Asturias cluster (0.32). The performances of correct reattributions ranged from 0.87 to 1 for the other five geographic areas. In total, 1450 salmon were reassigned to a natal origin out of the 1542 individuals (*i.e.* 94.0%), with strong differences between locations (Gironde: 88.9%; Adour: 95.1% and Nivelle: 63.6%). Hereafter, we only present and interpret the data according to the individuals that were successfully attributed to one location. To facilitate the results' understanding, every fish assigned to the Adour-Asturias cluster was interpreted as originating from the Adour in the following sections. Although we could misinterpret some individuals, we are confident that this assumption is negligible considering the amount of salmon collected in the Adour and the minor amount of fish that would disperse from the Asturias to the Adour as highlighted by genetic (Blanco et al., 2005; Borrell et al., 2008) and tagging studies (Leunda et al., 2013).

Table 3-3: Confusion matrix presenting the probabilities of reattribution for each cluster or location. The certified origin is provided in line while the origin predicted by the model is shown in columns. The specificity and the sensitivity of the model are provided in heatbars. Empty boxes represent values inferior to 0.01.



3.4.2 Spatial philopatry and dispersal rates throughout the southern Bay of Biscay

The proportion of individuals with their geographical origin according to their capture site is presented in Figure 3-3 and Table 3-4. In the Gironde system, even if the majority of returning adults were assigned to the Dordogne or the Garonne (*HR*: $76.6 \pm 13.6\%$ and $78.1 \pm 13.9\%$ respectively), a significant number of fish was attributed to the Adour-Asturias cluster (*IR*: $13.1 \pm 13.4\%$). Our results suggest that almost all immigrants would originate from one of the most proximate locations (Adour) as salmon assigned to the Allier, the Bidasoa, and the Bretagne-Galicia clusters are much less represented (*IR*: $1.6 \pm 2.7\%$) and we have not identified any fish

from the Nivelle. Considering the Dordogne and Garonne separately (Table 3-4), most of the immigrants from the Allier and Bidasoa mainly dispersed into the Dordogne while those from Bretagne-Galicia were equally found in both sub-basins. Nevertheless, the number of individuals attributed to the Allier, the Bidasoa, and the Bretagne-Galicia cluster tend to be underestimated while the number of fish from the Dordogne and Garonne appears to be moderately overestimated (Figure 3-3A). Regarding fish collected in the Adour (Figure 3-3B), results are unequivocal with an estimated homing rate of 95.1%, even if the possible associated errors would indicate a trend to minimize the proportion of fish originating from any potential donor population. In opposition to the Gironde, our results indicate that immigrants would come from all over the Bay of Biscay, regardless of the distance between geographic areas, although the proximate locations would contribute slightly more (1.5 ± 0.9 and $1.1 \pm 1.0\%$ for the Bidasoa and the Garonne respectively) than the others ($<1\%$). Surprisingly, in the Nivelle (Figure 3-3C, Table 3-4), most of the sampled fish were attributed to the Adour-Asturias cluster (71.4%), with only 2 individuals out of 14 assigned (14.3%) being attributed to the Nivelle. However, considering the very low sample number in this area in addition to the high percentage of possible misattribution to the Adour (32%), results must be interpreted with caution. This is also the reason why the Nivelle was not included in the inter-annual analyses performed in the following sections.

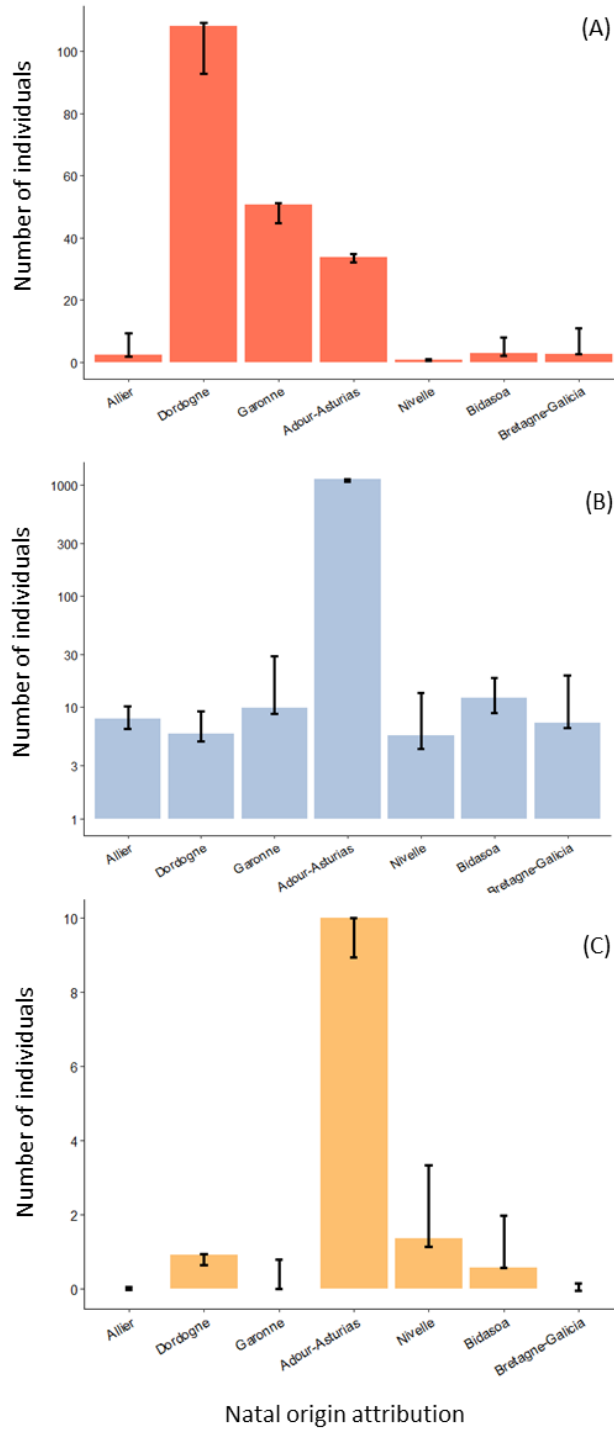


Figure 3-3: Number of individuals reattributed to each possible cluster according to their capture site: (A) Gironde, (B) Adour, and (C) Nivelle. The confidence intervals have been determined using the specificity and the sensitivity provided by the model for each cluster. Note that the y-axis is in the log-scale for (B), whereas a linear scale is provided for (A) and (C).

Table 3-4: Summary of homing and immigration rates (mean \pm standard deviation, in %) for each receiving population considered. Estimations are provided for the 2009-2018 period in the Adour, the 2007-2016 period in the Gironde, Dordogne, and Garonne, and the 1997-2014 period for the Nivelle.

		Sources of donors							
		N	AD	ALL	BID	BRE-GAL	GIR		NVL
							DOR	GAR	
Receiving populations	AD	1197	95.1 \pm 4.3	0.8 \pm 2.5	1.5 \pm 0.9	0.5 \pm 0.8	0.5 \pm 0.7	1.1 \pm 1.0	0.6 \pm 0.9
	GIR	232	15.1 \pm 11.3	1.3 \pm 3.0	2.1 \pm 2.9	1.4 \pm 2.5	80.1 \pm 12.4		0
	DOR	156	17.3 \pm 15.1	1.6 \pm 3.8	2.5 \pm 3.5	1.0 \pm 2.1	76.6 \pm 13.6	1.0 \pm 2.0	0
	GAR	76	14.6 \pm 13.3	0	0.7 \pm 2.3	1.1 \pm 3.5	5.5 \pm 8.5	78.1 \pm 13.9	0
	NVL	14	71.4	0	7.1	0	7.1	0	14.3

Note: No standard deviation can be presented for the Nivelle, as the number of individuals was too weak for inter-annual comparisons. Abbreviations: AD, Adour; ALL, Allier; BID, Bidasoa; BRE-GAL, Bretagne-Galicia; DOR, Dordogne; GAR, Garonne; GIR, Gironde; N, number of individuals assigned; NVL, Nivelle.

Estimations for the fidelity rate and the emigration rate over the 2009-2016 period between the populations of the Adour, Dordogne, and Garonne rivers are displayed in Figure 3-4. The Adour and Dordogne populations both recorded relatively high fidelity rates (98.7 ± 0.9 and $92.4 \pm 7.6\%$ respectively), while the Garonne population exhibited a much lower rate ($71.0 \pm 24.9\%$). Although individuals from the Adour represent the largest part of emigrants identified in the Gironde, it only suggests a direct emigration rate of 0.9 ± 0.6 and $0.3 \pm 0.4\%$ (for the Dordogne and Garonne respectively), in relation to its population size (Table 3-1). Inversely, while we identified a low immigration rate in the Adour from the Garonne and Dordogne, based on population sizes, it represents a direct emigration rate of 26.6 ± 25.7 and $4.8 \pm 7.0\%$ for the Garonne and Dordogne respectively. Finally, lower migratory flows are observed between the two Gironde sub-populations ($ER \sim 2.5\%$).

3.4.3 Temporal variation in the exchange of individuals in the Gironde and Adour systems.

Inter-annual variation of homing and immigration rates in the Gironde and the Adour basins with their associated errors are displayed in Figure 3-5. In the Gironde, an elevated immigration rate (from 25.0 to 39.7%) is estimated in the first years of sampling (from 2007 to 2009) and tends to stabilize around 13% in the following years ($13.4 \pm 6.0\%$, from 2010 to 2016). As anticipated in the previous section, the homing rate is definitely higher in the Adour compared to the Gironde, and that is for every year. In the Adour, with the exception of 2011 (83.2%), the homing rate remains remarkably stable over the 10-year period of study, being always greater than 94%. With regards to both geographic areas, even if the overall trend in homing and immigration rates is stable, the inter-annual variation is much higher in the Gironde system than in the Adour.

To better identify the contribution of each location to the inter-annual variation of immigration rate in the Gironde and the Adour, the proportion of fish allocated to each cluster according to their geographical origin is presented in Figure 3-5C and D. In the Gironde, a decreasing proportion of fish is attributed to the Garonne over the years meanwhile an inverse relationship is observed for the Dordogne, which is likely due to the sampling effort (Table 3-2). Immigrants from the Allier are observed in two independent years (2013 and 2015), individuals from the Bretagne-Galicia cluster in three independent years (2009, 2014, and 2016) while fish from the Bidasoa are found in four years of sampling. Besides, salmon from the Adour-Asturias cluster are identified in every investigated year. As previously described, the proportion of fish from the Adour-Asturias is quite massive in the first years of sampling (from 25.0 to 34.8% between 2007 and 2009) and stabilizes in the 2010-2016 period ($9.7 \pm 5.7\%$). Interestingly, the relative proportion of fish captured in the Gironde and assigned to the Adour-Asturias cluster mirrors the global curve of homing rate observed in Figure 3-4A. In the Adour, a significant proportion of immigrants from the Allier is detected in 2011, corroborating the one exception observed in Figure 3-4B. Surprisingly, no fish from this region were observed in any other years of the study, making it an isolated case. In contrast, the proportion of fish captured in the Adour and assigned to the Bidasoa, the Bretagne-Galicia, and the Garonne is more equally distributed over the studied period. Fish determined as immigrants from the Dordogne and the Nivelle are observed in similar years (2011 and 2016-2018).

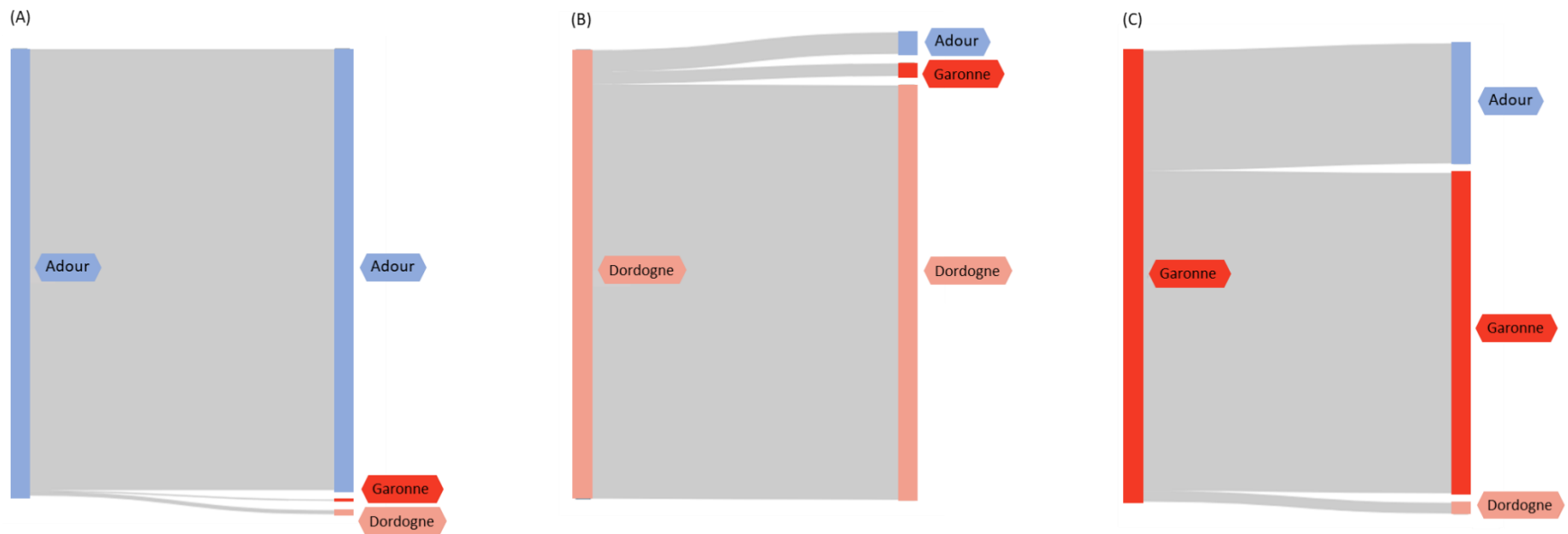


Figure 3-4: Fidelity and emigration rates, based on population sizes, examined for the Adour (A), the Dordogne (B), and the Garonne (C) populations. Estimations are provided for the 2009-2016 period as it combines a substantial sampling effort in every investigated system.

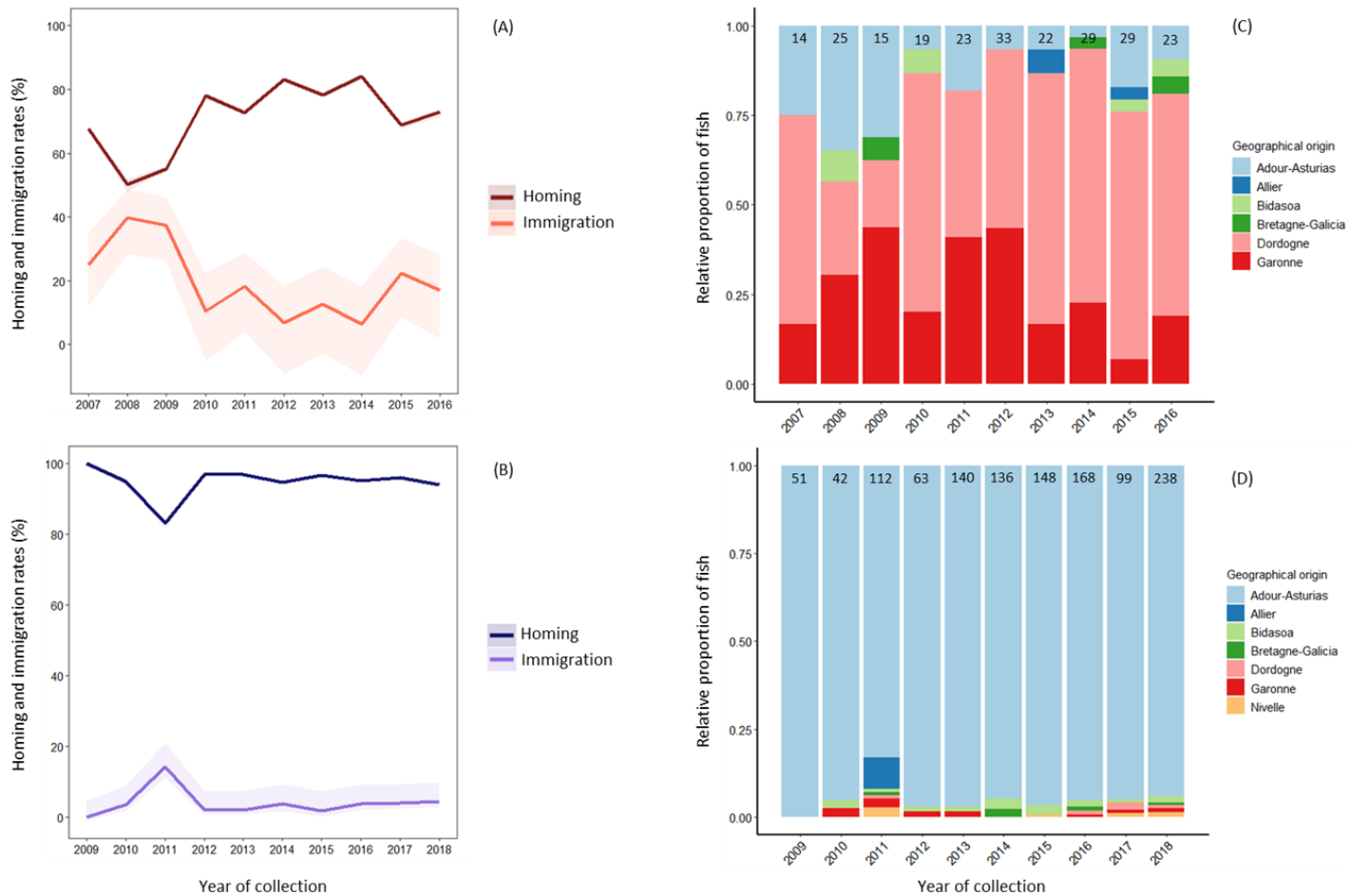


Figure 3-5: Homing and immigration rates (%) determined in the Gironde (A) and the Adour (B) in addition to the relative proportion of individuals collected in the Gironde (C) and the Adour (D) according to their natal origin, over the periods of study (2007-2016 and 2009-2018, respectively). The associated error in (A) and (B) was determined using the sensitivity and specificity of the model performed in this study and the sample size for each year in both locations is displayed at the top of each bar in (C) and (D).

3.5 Discussion

The effective estimation of philopatric and dispersal rates in salmonid metapopulations remains an important methodological and analytical challenge in fisheries science (Keefer and Caudill, 2014; Chat et al., 2022; Lamarins and Buoro, 2024). In the Bay of Biscay, to the best of the author's knowledge and based on a recent literature review conducted by Lamarins and Buoro (2023), where the authors examined studies that effectively estimate dispersal rates in wild salmonid species including Atlantic salmon, except a few investigations using genetics (Consuegra et al., 2005; Valiente et al., 2010; Perrier et al., 2011b) or a combination of tagging and modeling (Kuparinen et al., 2010), no studies have been carried out to quantitatively estimate dispersal rates of Atlantic salmon over a regional scale. Yet, such information would be highly valuable in complement to genetics as it would provide a quantitative estimation of the reproductive success (*i.e.* effective dispersal) over time.

3.5.1 Metapopulation structure in the southern Bay of Biscay

In the Gironde system, our results indicate an unexpected high proportion of immigrants ($19.9 \pm 12.4\%$). Although some studies have estimated immigration rates ranging from 25 to 30% in Atlantic salmon populations (Fraser et al., 2007; Palstra and Ruzzante, 2010; Jonsson and Jonsson, 2017), and even over 50% (Lamarins and Buoro, 2024), this value more likely represents the upper range of what is found in the literature (Lamarins and Buoro, 2024). Several hypotheses can be drawn to explain this elevated immigration rate. First, as detailed in Keefer and Caudill (2014), it is crucial to consider the "absolute number of strays". In our case, most of the immigrants would originate from the Adour population, which is about 10-times larger than the Gironde population (Table 3-1). Hence, although the number of fish attributed to the Adour ($n = 33$) represents 15.1% of the fish captured in the Gironde system over the 10-year period, it only

suggests a direct emigration rate of 1.3% from the Adour, based on population sizes. This observation corroborates previous studies demonstrating a substantial proportion of dispersal from large to small salmon populations (Brenner et al., 2012; Johnson et al., 2012; Bett et al., 2017). Additionally, the immigration distance separating the Adour and the Gironde estuaries (Table 3-1, ~ 230km) is within the range of common observations for anadromous salmonids (between 100 and 300km) (Leunda et al., 2013; Lamarins and Buoro, 2024), which supports our investigation. Second, the Gironde population is largely hatchery-dominated (Vandeputte et al., 2021) and relies on stocking programs that have taken place since the 1980s, after the population completely disappeared in the late 1800s (Thibault, 1994). A solid corpus of research has now demonstrated that salmon from hatcheries disperse more than their wild counterparts (Jonsson et al., 2003; Johnson et al., 2012; Jonsson and Jonsson, 2017; Sturrock et al., 2019; Nilsen et al., 2023), which could explain the modest estimated homing rate in this location. Hence, a moderate homing rate combined with a large adjacent population that “provides” a realistic proportion of individuals would strengthen our observations. Third, several studies have suggested that rather than environmental variation, geological and ecological riverine characteristics would be the primary determinant of dispersal in Atlantic salmon (Perrier et al., 2011b; Bowlby et al., 2016; Almodóvar et al., 2023). On one hand, according to this assumption and considering the similar geochemical signatures of the Garonne sub-basin and the Adour, both originating from the Pyrénées, the exchange of individuals between these two locations could therefore be favored. On the other hand, because the use of otolith chemistry is based on river geochemical signatures, this hypothesis can also be interpreted as a source of potential mixing between location, which is moderately the case in our study (13% of individuals originating from the Garonne may be incorrectly assigned to the Adour, see Table 3-3).

In the Adour basin, we determined a strong homing rate (95.1%) compared to the Gironde system. This result was expected as previous studies based on genetics have suggested that a

large proportion of fish caught in the upstream parts of the system had parents originating from downstream sites (Perrier et al., 2014), which supports the hypothesis of a population composed mainly by wild, local fish. Our results also confirm previous estimations of homing rates for wild Atlantic salmon populations (Jonsson et al., 2003; Palstra and Ruzzante, 2010), reinforcing the higher philopatric behavior in wild populations. Surprisingly, immigrants identified in the Adour emigrate from adjacent but also far-distant systems, in similar proportions, and although the immigration rate is estimated to be 4.9%, the absolute number of fish attributed to other locations is non-negligible considering the population sizes, particularly for the Nivelle and the Bidasoa to the south, and the Gironde and the Allier to the north. These migratory patterns mirror previous research demonstrating that large populations could also receive individuals from smaller, adjacent populations (Consuegra et al., 2005; Almodóvar et al., 2023). Combined with the donor potential we previously described from the Adour population to the Gironde, this attractive aspect would strengthen the buffering role of a large population for adjacent populations that are smaller, and highly stocked, both in terms of source and sink dynamics.

In the Nivelle river, our results showed an unprecedented immigration rate, with 71.4% of the fish collected being attributed to the Adour and 7.1% to both the Bidasoa and the Dordogne. Nevertheless, these observations must be interpreted with caution due to the limited sample size of the Nivelle. Hence, any misattribution could drastically change the aforementioned results, especially considering the substantial possible error between the Nivelle and the Adour (32% of individuals originating from the Nivelle may be incorrectly assigned to the Adour, see Table 3-3). Yet, even if we consider the more optimistic scenario from our model, the Nivelle population would still largely rely on fish emigrating from the Adour system. A previous study from Valiente et al. (2010) has established that 12 to 23% of returning salmon in the Nivelle are emigrating from the Bidasoa. In Perrier et al. (2014), the authors also suggest a possible gene flow from the Adour to the Nivelle, as they found a lower census population size (*i.e.* total number of returning adults)

than the effective population size (*i.e.* total number of spawners). In this study, our results would indicate an emigration rate of 1.4% of the Adour population into the Nivelle, but the reproductive success of the emigrants is unknown. This is where we see the value of combining several tools such as genetics and otolith chemistry, as our observations support the hypotheses of Perrier et al. (2014), which ultimately suggest an effective dispersal from the Adour to the Nivelle. Additionally, although barely detected, the concurrent low homing rate and high immigration rate observed in the Nivelle could suggest a demographic Allee effect (Stephens and Sutherland, 1999; Stephens et al., 1999; Rougier et al., 2012), where lower population density leads to decreased rates of population growth.

Consequently, in the three systems that compose the southern Bay of Biscay, the connectivity between populations appears relatively important, and stable, both in terms of intensity and direction. The observed biocomplexity of the metapopulation might help in the sustainability of each population, particularly for the Nivelle and the Gironde, potentially via demographic and genetic rescue effects. Indeed, combined with genetic studies, our observations suggest a key role of immigration from the Adour to maintain a sustainable, viable population in the Nivelle. Additionally, the Spanish populations appear to contribute only minimally to the observed exchanges, likely due to their low abundance levels, in addition to the distance separating them from the main rivers in the study area. Similarly, the populations from the northern Bay of Biscay provide few (Adour) or almost no (Gironde and Nivelle) individuals, which would confirm the lower connectivity between populations that are significantly distant (Chat et al., 2022).

3.5.2 Inter-annual variability of philopatry and dispersal

If the study of salmonid dispersal is recognized to be overlooked in the scientific literature (Källo, 2023; Lamarins and Buoro, 2024), finding information about the temporal variations in dispersal

is considerably more challenging. In our study, we do not identify such patterns over the 10-year periods. Although we could notice a greater inter-annual variability in the Gironde system than in the Adour basin, the overall philopatric and dispersal rates remain stable over the years.

Gironde

Over the 2009-2016 period, both the homing (from 60 to 96.6%) and the fidelity approach (from 65.7 to 100%) provided relatively similar results to estimate the philopatry. What most characterizes the temporal evolution of philopatry in this location is the great variability from one year to another. One potential explanation can be advanced to explain our results. As previously hypothesized, the Garonne sub-basin could be more attractive to salmon from the Adour compared to the Dordogne as they both originate from the Pyrénées, hence displaying similarities in physical and chemical water properties, which in turn, can favor dispersal (Perrier et al., 2011b; Keefer and Caudill, 2014; Almodóvar et al., 2023). Therefore, in sampling years when the proportion of individuals caught in the Garonne (relative to the total number of individuals caught in the Gironde) is greater, we could observe an associated higher proportion of immigrants from the Adour. Overall, regarding the Gironde system, although the population is rather small and largely depends on hatchery releases, we do not observe any pattern of decreasing philopatric behavior. Additionally, we suggest that salmon from the Adour play a key role in the Gironde population, even if we cannot rule on a potential gene flow as it is impossible to know if these immigrants will succeed to breed. In fact, Perrier et al. (2013) have demonstrated that the Gironde population is genetically distinct from the Adour population, which suggests that effective dispersal is unlikely, or extremely scarce. Nevertheless, they also indicate a higher genetic admixture in their recent cohorts (in the beginning of the 2000's) compared to their historical cohorts (between the 1960's and the 1980's), which could reveal an increasing gene flow in the last decades.

Adour

In the Adour system, our results indicate a remarkable stability of philopatry and dispersal over the years. Although it has been suggested that homing behavior could be negatively affected because of climate change and hatchery releases (Bett et al., 2017), our research corroborates previous studies which highlighted that, for populations composed of wild individuals, or a large majority of them, homing rates are stable over time (Jonsson et al., 2003; Palstra et al., 2007). From an eco-evolutive perspective, such stability may indicate a portfolio effect, which favors the persistence of the whole population via the diversity of inter-individual life histories. According to this theory, the potential role of connectivity is difficult to appreciate, as it would require a better knowledge of the reproductive success of immigrants. Nevertheless, as we identified an important portion of salmon from the Adour into the Gironde, the temporal stability of this large population may help buffering demographic and/or genetic variability of adjacent populations, therefore reinforcing the biocomplexity of the system as a whole, *i.e.* the metapopulation structure, over time. Contrarily to the Gironde, immigrants identified in the Adour come from every location we sampled across the Bay of Biscay, which contrasts with previous scientific literature detailing a preferential neighboring dispersal (Hamann and Kennedy, 2012; Chat et al., 2022). Particularly, individuals from the Allier were only observed in one year (2011), and in relatively large proportions (8.0%). In 2011, the rivers in the Allier basin witnessed historically low water levels in its rivers because of a severe drought, rendering conditions extremely unfavorable for adult migration to breeding grounds (Keefer and Caudill, 2014; Bett et al., 2017). Thus, episodic dispersal into what appears to be the most attractive basin, in response to these unfavorable environmental conditions, would be a plausible hypothesis to explain this result. Albeit the immigration rate is fairly low in the Adour system (4.9%), the relative importance for regular donor populations (namely the Gironde to the north and the Nivelle and the Bidasoa to the south) is not negligible. Indeed, most of these donor populations are small in size, and although we do not

have sufficient data to robustly infer the emigration rates from the Nivelle and Bidasoa to the Adour, we can reasonably assume that these rates are substantial, as identified for the Gironde (13.8%). Such estimations would be consistent with what is observed in the literature (Lamarins and Buoro, 2024). Therefore, our results would suggest a stable, considerable asymmetric dispersal, from the smallest (Gironde, Nivelle, and Bidasoa) to the largest (Adour) populations. To the best of the author's knowledge, only a couple of studies have evaluated the temporal stability of effective dispersal (*i.e.* gene flow) in salmon populations (Fraser et al., 2007; Palstra et al., 2007; Palstra and Ruzzante, 2010). Here, we demonstrate an inverse relationship between the relative importance of emigration rate (*i.e.* 1.3% from the Adour into the Gironde and 13.8% from the Gironde into the Adour) and the immigration rate (*i.e.* 18% from the Adour in the Gironde and 1.6% from the Gironde in the Adour).

Hence, our study reinforces the importance of (i) considering the absolute number and the relative proportion of migrants, especially when investigating the connectivity between small and large populations, (ii) considering temporal variation in dispersal (for example in the Adour, we only detected salmon from the Allier in one sampling year but individuals from the Bidasoa and the Gironde were much more frequent) and (iii) assess dispersal mechanisms on a regional scale (*e.g.* "freshwater ecoregion", Gillis et al., 2023) as dispersal may be primarily influenced by environmental stochasticity (Palstra et al., 2007). Finally, the initial hypothesis that dispersal may be responsible for the positive dynamics observed in the Dordogne and the Adour systems between 2010 and 2020 has not been verified considering the temporal stability of homing and immigration rates highlighted in this study. Other explanations, such as improved (1) efficiency of rearing programs and/or (2) access to spawning grounds, or (3) environmental conditions more resilient to climate change, should be examined in the future.

3.5.3 Limitations and perspectives

The authors acknowledge that several factors can limit our interpretations. First of all, otolith chemistry could be coupled with other tools such as genetics or tagging methods, as recently demonstrated by Källo et al. (2023), to strengthen our interpretations. Another limitation lies in the sample design itself. It is nearly impossible to properly sample exhaustively every possible river or tributary where fish may access or stem from (Källo et al., 2022b). In addition, Atlantic salmon have a relatively wide period of upstream migration (roughly from February to September) making it very difficult to collect a representative sample from all potential spawners. Here, because fishing is mostly warranted in the latest period of upstream migration, where almost all 1SW are migrating, we mainly captured MSW salmon. Yet, previous studies have shown that considering the age structure is essential when investigating patterns of dispersal (Palstra and Ruzzante, 2010), as it could explain short-term genetic variation between cohorts. Therefore, it would be relevant to account for the “age effect”, especially considering the diversity of systems within the Bay of Biscay with salmon populations mainly composed of MSW (e.g. Allier, Gironde), or 1SW (e.g. Bretagne), while others are more proportionately distributed (e.g. Adour).

Besides these methodological limits, we identify three main perspectives in our study. First, several authors have pointed out the importance of spatial-scale definitions in dispersal investigations. Here, we assessed philopatric and dispersal rates at a regional scale. However, in their study, Perrier et al. (2014) have demonstrated a clear genetical structure within the Adour basin. Even if this result suggests a limited gene flow between sub-basins, which is in accordance with Lamarins and Buoro (2024), it would be relevant to study the movement behaviors at both large (*i.e.* regional) and small (*i.e.* sub-basins) spatial scales. In this study, our sample size across sub-basins is not suitable for such investigation (see Figure S 3-2). Second, because we used otolith chemistry to investigate dispersal, we cannot infer on potential demographic or genetic

effects as we do not know if the observed dispersal is effective, with subsequent gene flow (Masson et al., 2018). Again, coupling otolith chemistry with other tools would be desirable to access such information. For example, Nilsen et al. (2023) have recently shown that fish from hatcheries displayed aberrant reversal movements, which can be interpreted as temporary dispersal (Keefer et al., 2008; Peterson et al., 2016; Bett et al., 2017). Finally, in parallel to this last point, it would be essential to depict the proportion of wild from hatchery-fish in dispersal, as numerous studies have detailed a higher dispersal rate for hatchery-originated salmon compared to their wild counterparts (Jonsson et al., 2003; Brenner et al., 2012; Johnson et al., 2012; Keefer and Caudill, 2014; Bett et al., 2017). Therefore, the investigation of the role of hatcheries in Atlantic salmon populations from the southern Bay of Biscay would be the next step.

3.5.4 Management implications

In their review, Keefer and Caudill (2014) suggested that “the emphasis should perhaps be reversed, as many of the most pressing management and ecological questions related to straying are from the perspective of the receiving population”. Here, our study highlighted a clear metapopulation structure for Atlantic salmon in the Bay of Biscay, and more particularly the main populations. Our estimations would indicate a key role of the Adour population to the Gironde population, both in terms of donors and receivers. Hence, it emphasizes the need to jointly conserve and protect large and small populations, and consider management implications with the exchange of individuals between locations, especially considering the temporal stability we observed in dispersal. Although one genetic study has demonstrated a low admixture rate between the Gironde and the Adour populations (Perrier et al., 2013b), suggesting an ineffective dispersal, indirect effects could still be observed via competition behaviors for habitats and feeding or resources of sexual mating for example (Essington et al., 2000).

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3.7 Author contributions

AF: Formal analysis, Methodology, Validation, Investigation, Writing – Original Draft, Writing – Review & Editing, Visualization; **MV:** Methodology, Validation, Writing – Review & Editing, Visualization; **HT:** Formal analysis, Investigation, Writing – Review & Editing; **AH:** Resources, Investigation; **G.Barranco:** Resources; **SB:** Resources, Writing – Review & Editing; **IC:** Resources; **DN:** Resources, Writing – Review & Editing; **JE:** Resources, Writing – Review & Editing; **PC:** Resources, Writing – Review & Editing; **CP:** Resources; **G.Bareille:** Conceptualization, Validation, Writing – Review & Editing, Supervision, Project administration, Funding acquisition.

3.8 Supplementary figures

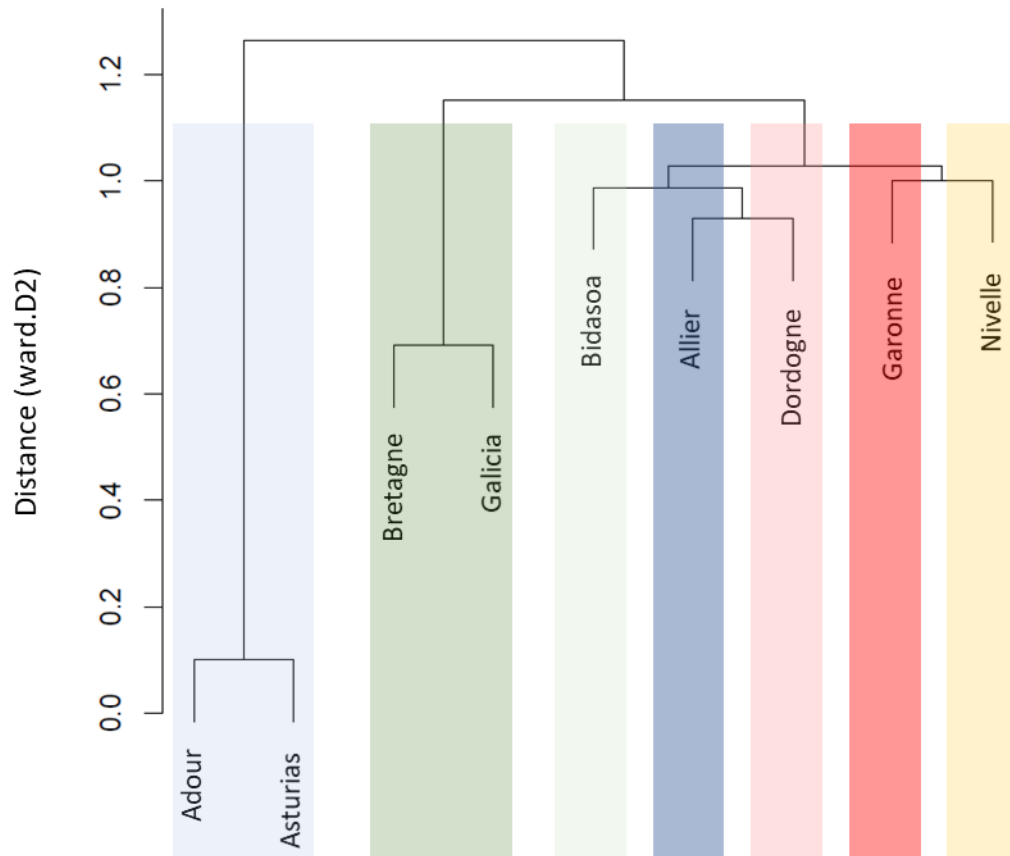


Figure S 3-1: Agglomerative hierarchical clustering of the geographic areas under study. The proximity matrix arising as a byproduct of the RF was converted into a distance matrix to visually investigate the locations with the highest discriminant performances.

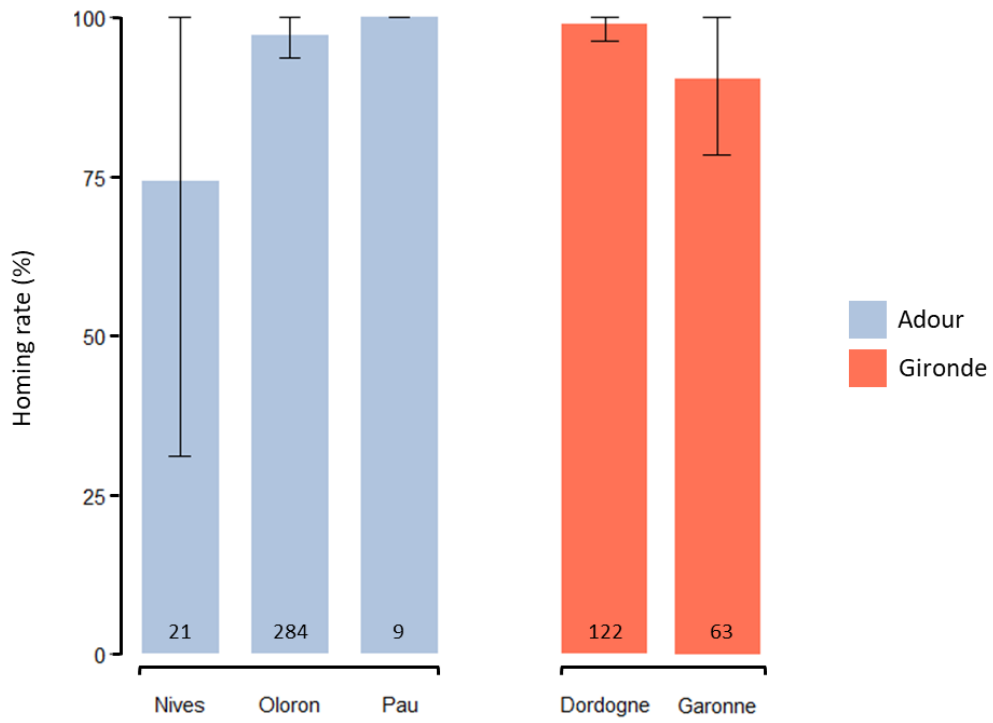


Figure S 3-2: Estimated homing rates at a sub-basin scale for the Adour and the Gironde populations. The sample size for each sub-basin is indicated at the bottom of each corresponding bar.

3.9 References Chapter 3

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TAKE-HOME MESSAGES

- Atlantic salmon populations from the southern Bay of Biscay display a complex metapopulation structure
- Migratory flows and connectivity levels are stable over a 10-year period
- Relative to population size, we determined an asymmetric dispersal between the largest (Adour) and smaller, proximate, and heavily supplemented populations (Garonne, Dordogne, Nivelle)

Future need:

Investigate dispersal patterns with combined spatial scales

Future need:

Coupling otolith chemistry with genetics to assess effective dispersal



IN THE NEXT CHAPTERS

- Since numerous studies have demonstrated that hatchery-fish disperse more than their wild conspecifics, stocking programs may play an important role in the metapopulation dynamic
- To efficiently study the role of stocking practices in a set of local Atlantic salmon populations, we need to access the cohort of every individual
- Therefore, in Chapter 4, I present the method to estimate the river age of returning salmon before investigating the effects of hatchery practices in Chapter 5

4 UNSUPERVISED ESTIMATION OF THE AGE AT SEA DEPARTURE OF ATLANTIC SALMON USING MAGNESIUM, MANGANESE, AND ZINC OTOLITH CHEMISTRY

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4.1 Abstract

Investigating the age at sea departure of returning Atlantic salmon is critical to better understand the role of emigration timing in survival. Among the methods available, the use of otolith chemistry can be challenging in anadromous fish, as the elements frequently used (i.e., magnesium, manganese, and zinc) can jointly reflect individual metabolism and environmental conditions. Here, we present a new unsupervised and robust method for successfully estimating the outmigration age of Atlantic salmon in the Bay of Biscay, based on otolith zinc concentrations.

Keywords: chemical calendar-clock, functional clustering, migration, *Salmo salar*

4.2 Introduction

Age determination from scale and otolith annuli observations has been applied for more than 120 years in fisheries science, as it is crucial information to manage stock structure and understand population dynamics (Campana & Thorrold, 2001). In recent years, researchers have tried to combine chemical profiles from otolith analyses with traditional visual reading to estimate fish age, especially for taxa that do not allow for clear determination of annuli (Heimbrand et al., 2020) or with long-lived species. As some elements such as magnesium (Mg), manganese (Mn), phosphorus (P), or zinc (Zn) are essential for fish and may vary with individual metabolism (Hüssy, Limburg, et al., 2021), their otolith concentrations are likely to be related to physiological mechanisms such as ontogeny, growth, reproduction, metamorphosis, or even diet (Sturrock et al., 2012), thus reflecting seasonal patterns that match with annual opaque and translucent zones in otoliths (Heimbrand et al., 2020; Hüssy et al., 2016).

To date, contrasted results have been pointed out in the literature concerning the cause(s) of Mg, Mn, and Zn variations in otoliths (Hüssy, Limburg, et al., 2021). First applied to track pollution exposure, the use of Zn otolith concentration has more recently emerged as a potential tool to estimate fish age with marine (Heimbrand et al., 2020; Limburg & Elfman, 2010; Sturrock, Hunter, et al., 2015) and migratory species (Brûlé, 2022; Mainguy et al., 2023), as its accumulation would mainly come from diet (Hüssy, Limburg, et al., 2021). Previous studies have also demonstrated that Zn incorporation into the crystal lattice is phylogenetically related, as important and consistent differences in Zn otolith patterns were found between taxonomic groups (Chang & Geffen, 2013; Limburg & Elfman, 2010), suggesting that its use may be particularly relevant in Salmonids (Halden et al., 2000; Lill et al., 2014; Limburg et al., 2001; Limburg & Elfman, 2010). Scientific literature exploring the uptake mechanisms of Mg and Mn in otoliths is also very limited. Magnesium incorporation is reported to be mostly related to individual growth rate and is therefore

possibly associated with foraging strategies and metabolic activity (Hüssy, Limburg, et al., 2021; Limburg et al., 2018). Hypotheses about the main sources of Mn in the otolith are even more inconsistent because some studies have demonstrated a positive effect of growth (Martin & Thorrold, 2005), whereas others did not report any effect (Sturrock, Hunter, et al., 2015). Nevertheless, for both Mn and Mg, a significant effect of diet does not appear to be a valid assumption, in contrast to Zn sources (Hüssy, Limburg, et al., 2021). Finally, a decrease in elemental concentrations over time seems to apply commonly for Mg, Mn, and Zn in otoliths based on ontogenic changes in somatic growth patterns. From the literature, reported as “chemical age-tracers,” Mg, Mn, and Zn otolith concentrations appear to be species-dependent tracers that are expected to vary seasonally, with peaks occasionally observed for all these elements in the spring–summer period (i.e., otolith opaque zone) reflecting high metabolic activity and minima in the winter period (i.e., otolith translucent zone), when foraging and growth are very low (Hüssy et al., 2016; Mainguy et al., 2023; Martin & Thorrold, 2005).

To the best of the authors’ knowledge, every recent study that explored Mg, Mn, and Zn as tracers to estimate fish age has combined its chemical results with optical aging to corroborate the occurrence of elemental variation in otolith zones (opaque and translucent). However, this work is time-consuming and requires expertise to adequately prepare and read the otoliths (Hüssy et al., 2016). In this study, we used a functional clustering method to test the usefulness of Mg, Mn, and Zn variation to assess in an unsupervised manner the age at sea departure (most likely hypothesized to be 1+ or 2+ in our study sites, based on previous studies and reports from regional management associations) for mature returning Atlantic salmon (*Salmo salar*). Combined with life-history reconstruction, also inferred from otolith chemistry, automatic and joint acquisition of age without the need for the traditional reading approach can save time and greatly improve our knowledge about time-dependent migratory patterns, yearly river-spawning

contribution, and efficiency of stocking programmes for salmon populations (Martin et al., 2013; Sturrock, Wikert, et al., 2015).

4.3 Materials and methods

4.3.1 Study area and sample collection

As the incorporation of Mg, Mn, and Zn in the otolith matrix seems to be simultaneously influenced by intrinsic and extrinsic factors (Hüssy, Limburg, et al., 2021), their chemical profiles should theoretically vary between distinct populations that experience contrasted habitat (e.g., river length, temperature and discharge, food availability, density dependence). To account for this natural variability, we selected otoliths from adult Atlantic salmon from three French localities (Adour, Gironde, and Bretagne), whose age was previously estimated by traditional scale-reading method (double-blind, unpublished data). In these regions, smolts commonly migrate to marine waters either after 1 year (defined as “1+” hereafter) or two successive years (expressed as “2+” hereafter) in fresh water, although the proportion of 1+ and 2+ is also expected to vary spatially and temporally between locations. In total, 378 returning adults collected in 2015 in Bretagne (1+ $n = 11$, 2+ $n = 12$) and from 2010 to 2016 in Gironde (1+ $n = 67$, 2+ $n = 16$) and Adour (1+ $n = 232$, 2+ $n = 40$) were used in this paper (Table S 4-1).

4.3.2 Ethics statement

All the otoliths analysed in this study were sampled from monitoring and carcass surveys or from amateur fishermen. Each individual was collected according to animal welfare laws, guidelines, and policies as approved by sampling permits or the number of individual tags.

4.3.3 Otolith preparation and chemical analyses

Detailed otolith preparation and parameters of chemical analyses can be found in Martin et al., 2013. Briefly, sagittal otoliths were extracted from salmon heads, gently cleaned, and embedded in epoxy resin (Araldite 2020, Escil) before being ground with distilled water and sandpaper

(Martin et al., 2013). Prepared otoliths in resin blocks were then analysed for ^{24}Mg , ^{55}Mn , and ^{65}Zn concentrations concurrently with strontium (^{86}Sr) and barium (^{138}Ba) using a femtosecond-laser ablation system (fs-LA, 1030 nm, Alfamet-Novalase, France) coupled to an inductively coupled plasma mass spectrometer (Agilent 8900 triple quadrupole ICP-MS, USA). Calcium (^{43}Ca) was used as an internal standard, and concentrations of measured elements were determined using three-point calibration curves based on certified glass standards NIST 610, 612, and 614 (NIST, USA). Accuracy was checked using otolith reference materials FEBS 1 (NRCC, Canada) and NIES 22 (NIES, Japan). Ultimately, Mg, Mn, and Zn concentrations are expressed as a ratio of Ca concentration (Mg/Ca, Mn/Ca, and Zn/Ca, respectively, in $\mu\text{g}\cdot\text{g}^{-1}$), based on the concentration of Ca in otolith (0.383 g of Ca per gram of otolith).

4.3.4 Modeling

Profiles of elemental ratios were individually investigated to identify the part of the transect that corresponds to the freshwater residence, from fish birth (i.e., primordia, visible with a manganese peak [Ruttenberg et al., 2005] and systematically located 200 μm after the ablation starting point) to the departure at sea (i.e., outmigration, based on the significant increase in Sr/Ca and concurrent decrease in Ba/Ca ratios along the otolith transect). To compare all individuals, we standardized the distance obtained from each of them between the nucleus and the outmigration by calibrating every profile between 0 and 1. As our method requires an identical number of values per individual along transects, we used a generalized additive model (GAM) to resample 150 equally spaced values per profile (i.e., the mean average number of data points in our transects). The GAM was performed using the *mgcv* package (version 1.8-40, in R version 4.2.1) with an equal number of splines per individual ($k = 10$), and we used the GCV criterion as the method for estimating the smoothing parameters. We then used a univariate functional clustering approach based on an expectation–maximization (EM) algorithm following Bouveyron and Jacques (2011)

(Table 4-1). Multivariate approaches were also tested but did not outperform the results obtained via univariate analyses (Table 4-1). The method is an adaptation from the traditional high dimensional data clustering (HDDC) method to functional data that was achieved using the *funHDDC* package (version 2.3.1). We used this unsupervised (naïve) approach to cluster each profile within two groups (most likely hypothesized to be 1+ or 2+ in our study sites, based on the data from the Centre national d'interprétation des captures de salmonidés migrateurs [CNICS], <https://professionnels.ofb.fr/>). We arbitrarily fixed the number of groups equal to two as long-term surveys of salmon in our localities have revealed that a dominant proportion of individuals remain either 1 or 2 years in fresh water before migrating. For robustness purposes we also tested for three groups, but the likelihood did not vary between the two and three-cluster approaches (Table S 4-2). The posterior probability for each profile allowed classifying them into two groups (assumed to be either 1+ or 2+), with the maximum probability of attribution always higher than 0.9, and, given that this naïve classification was performed on individuals of known age, we used the percentage of correctly classified individuals as a performance index of the approach. Finally, we performed a cross-validation approach using out-of-bag (OOB) sampling (training set: 75%, test set: 25%, number of iterations: 1000) to evaluate the performance of the naïve approach for each metal.

Table 4-1: Proportions of correct reattribution and model convergence for each element under study (Mg, Mn, and Zn), obtained from the functional clustering analysis with univariate and multivariate approaches.

Element(s)	Certified origin	Average proportion of fish correctly assigned \pm SD (%)	Proportion of model convergence (%)
<i>Univariate</i>			
Mg	1+	94.2 \pm 4.0	43.2
	2+	3.6 \pm 5.2	
Mn	1+	78.9 \pm 7.2	89.3
	2+	5.3 \pm 6.5	
Zn	1+	83.1 \pm 5.2	99.8
	2+	91.0 \pm 6.4	
<i>Multivariate</i>			
Mg-Mn	1+	79.2 \pm 6.9	89.8
	2+	5.3 \pm 6.2	
Mg-Zn	1+	83.0 \pm 5.0	99.9
	2+	91.0 \pm 6.4	
Mn-Zn	1+	82.6 \pm 5.4	100
	2+	91.3 \pm 6.3	
Mg-Mn-Zn	1+	82.8 \pm 5.3	99.9
	2+	91.5 \pm 6.3	

Note: The results originate from the cross-validation analyses (randomly selected in-bag fraction: 0.75, number of iterations: 1000) we conducted on each metal and each possible combination from the initial sampling ($n = 309$ for 1+ fish, $n = 68$ for 2+ individuals, $n = 377$ for total sample number). The parameters used to perform the analyses were set as follows: $N = 150$, $k = 10$, $n^{basis} = 5$, $n^{order} = 4$, $itermax = 10000$ and $eps = 10^{-5}$ with N being the number of datapoints per profile, k the number of basis to form a spline, n^{basis} the number of β splines used, n^{order} define a polynomial of degree 4, $itermax$ the maximal number of iteration in the *funHDDC* algorithm and eps the threshold of the convergence criterion. Abbreviations: Mg, Magnesium; Mn, Manganese; SD, Standard Deviation; Zn, Zinc

4.4 Results and discussion

Although Mg and Mn have been successfully used in a few studies to reconstruct the “metabolically active” (Hüssy, Krüger-Johnsen, et al., 2021; Limburg et al., 2018) period of fish, our results do not indicate similar trends (Figure 4-1). Considering the wide range of observed raw values, which can be 100 to 500 times higher between salmon, especially for Mn, the biggest challenge is to depict the expected patterns (1+ and 2+) of Mg and Mn profiles from the very massive inter-individual variability. Clearly, in our study, the model does not distinguish between 1+ and 2+ fish as almost all individuals are clustered in the 1+ group (Table 4-1). In both Mg and Mn profiles, elevated concentrations (Figure 4-1) are clearly identified in the core region, which is consistent with previous studies (Ruttenberg et al., 2005; Thomas et al., 2017). Yet, combined with a steady decrease in Mg and Mn otolith concentration with fish growth (Hüssy, Limburg, et al., 2021), the annual fluctuation of both elements is probably masked in the broad spectrum of inter-individual variability. Additionally, as Mg otolith concentration significantly differed between high and low body conditions in cods (Limburg & Casini, 2018), it may reinforce the observed variability within our sampling if such diversity is also occurring in anadromous species. Our results diverge from previous studies on marine (Limburg et al., 2018) fish species for both metals, but also on northern Canadian populations of Atlantic salmon for Mg (Brûlé, 2022). Presumably, it emphasizes the importance of environmental conditions, and more specifically the effect of contrasted seasons in the Arctic area compared to our temperate zones, on elemental availability (because of a decline in food availability) and reduced metabolic activity. Indeed, given that environmental conditions have a direct influence on both individual growth and metabolism that in turn can change the proteomic composition of the otolith matrix on which Mg presumably bounds (Thomas et al., 2019; Thomas & Swearer, 2019), it could explain the observed dissimilarities. In addition, a confounding effect between localities would be a plausible hypothesis to explain the failure to use Mg and Mn profiles. The mixing of three different geographic areas

could mask a potential site- specific signal, preventing the detection of a distinct pattern between 1+ and 2+ fish. It could also explain why the multivariate analysis does not improve, even slightly, the performance obtained with the univariate method. However, analyses computed separately for each locality lead to the same inconclusive results.

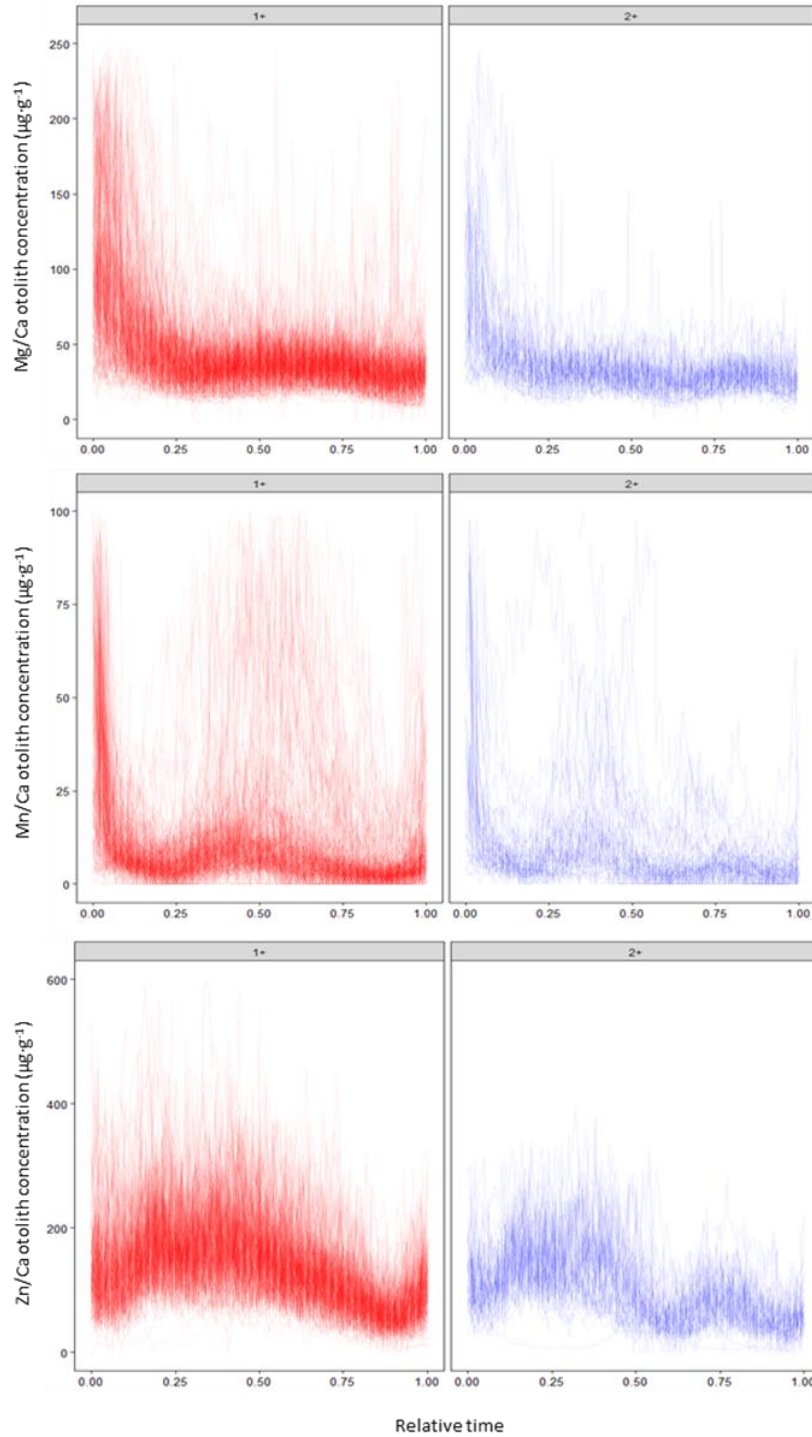


Figure 4-1: Raw data distribution of Mg/Ca, Mn/Ca, and Zn/Ca profiles from Atlantic salmon (*Salmo salar*) sagittal otoliths. The left boxes display chemical profiles that were classified as 1+ river-aged individuals while 2+ are shown in the right boxes. The standardized distance [0-1] was obtained using the otolith length between the core and the departure for marine migration.

In contrast, when looking at Zn variations, the visual pattern for 1+ and 2+ fish is much more apparent than for Mg and Mn, although the signal varies by an order of magnitude 10 (from 50–60 $\mu\text{g}\cdot\text{g}^{-1}$ up to almost 600 $\mu\text{g}\cdot\text{g}^{-1}$; Figure 4-1). This is also in line with the literature as Zn otolith concentration has been reported to highly vary among Baltic cod *Gadus morhua* populations (Hüssy et al., 2016). Significant differences were also observed between males and females of European plaice *Pleuronectes platessa* L. (Sturrock, Hunter, et al., 2015), demonstrating the importance of individual physiological processes in the uptake mechanism, through the identification of some key metalloproteins involved in otolith biomineralization, as highlighted in Thomas & Swearer, 2019. Here, from the raw Zn data (Figure 4-1), our model successfully reclassified 1+ and 2+ fish with a performance of 83.1% and 91.0%, respectively (Table 4-1). Thus, the functional clustering method produced fairly reliable results for this metal as we collected fish from various environments, with particular sharp differences in water temperature, annual discharge, and food availability. In the Adour and Gironde systems, juveniles inhabit rivers under strong influences of snow, with drastic changes between spring (high river flow due to snowmelt and heavy rain associated with cold temperatures) and summer periods (low flow combined with high temperatures). In the Bretagne region, seasonal changes are much less severe. Therefore, in theory, the timing and the intensity of Zn incorporation in the otolith would differ among locations, because the synchrony of biotic and abiotic conditions is a prerequisite to the use of a chemical age-tracer (Hüssy et al., 2016). Nevertheless, the good performance from the functional clustering highlights the robustness of natural Zn signals (1+ vs. 2+) across spatial and temporal scales in the Bay of Biscay. Our results mirror previous patterns highlighted in studies on pelagic (Heimbrand et al., 2020; Hüssy et al., 2016) and coastal (Sturrock, Hunter, et al., 2015) marine fish, in addition to diadromous (Brûlé, 2022; Mainguy et al., 2023) and freshwater fish species.

4.5 Conclusion

In our study and in light of current knowledge, the use of Zn to assess fish age appears to be the most reliable tool across distinct environments (i.e., marine, estuarine, and freshwater systems), although we recognize that it may remain location-dependent and its broad use through disparate taxonomic groups may be elusive (Chang & Geffen, 2013). Our results may be particularly helpful for diadromous fish species in general that live in both fresh water and sea water, and especially useful for Salmonidæ in which our results strengthen the capability of Zn otolith chemistry to investigate fish age. Our observations indeed corroborate previous studies focusing on this family such as Arctic charr (Halden et al., 2000), anadromous brown trout (Limburg et al., 2001), Atlantic salmon (Limburg & Elfman, 2010), and European whitefish (Lill et al., 2014; Limburg & Elfman, 2010). Although the reliability of Mg and Mn has been demonstrated in other studies on marine fish species (Hüssy, Krüger-Johnsen, et al., 2021; Limburg & Casini, 2018), we did not identify such trends with Atlantic salmon from the Bay of Biscay. Their complex life cycle and the associated multiple shifts in their foraging strategies and diet may be responsible for the lack of an annual elemental pattern in this study, in addition to the mix of three spatially separate populations. The fact that Zn is strongly linked to various binding proteins that are found in elevated abundance in the otolith (Thomas & Swearer, 2019) might also explain the highest performance of Zn as a chemical age-tracer. Future research could examine the variability of P in the otolith as it has been proposed as a promising element to estimate fish age (Hüssy, Limburg, et al., 2021).

4.6 Author contributions

Anthony Fontaine: Formal analysis, methodology, validation, investigation, writing—original draft, writing—review and editing, visualization. Matthias Vignon: methodology, validation, writing—review and editing, visualization. H  l  ne Tabouret: formal analysis, investigation, writing—review and editing. Christophe P  cheyran: resources. Gilles Bareille: conceptualization, validation, writing—review and editing, supervision, project administration, funding acquisition.

4.7 Acknowledgments

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Data availability statement

The data are available in the following directory: <https://doi.org/10.57745/LVQDTP>.

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Supporting information

Additional supporting information can be found online in the Supporting Information section at the end of this article.

4.8 Supplementary tables

Table S 4-1: Detailed sampling information for 1+ and 2+ individuals by year of capture in the three localities under study: Adour, Bretagne, and Gironde.

Year of collection	Number of individuals captured in the Adour		Number of individuals captured in the Bretagne		Number of individuals captured in the Gironde		Total
	1+	2+	1+	2+	1+	2+	
2010					2		2
2011					7		7
2012	19	5			14	6	44
2013	70	7			9	4	90
2014	75	11			15	3	108
2015	60	11			12	3	81
2016	8	6	11	12	8		45
Total	232	40	11	12	67	16	

Table S 4-2: Loglikelihood and proportion of convergence for each possible model tested in this study.

Element(s)	Number of groups (k)	Loglikelihood \pm SD ($\times 10^3$)	Proportion of model convergence (%)
<i>Univariate</i>			
Mg	2	-32.7 \pm 1.5	43.2
	3	-33.1 \pm 2.8	2.8
Mn	2	-26.1 \pm 1.6	89.3
	3	-25.3 \pm 2.5	3.7
Zn	2	-40.5 \pm 3.2	99.8
	3	-41.4 \pm 8.2	38.4
<i>Multivariate</i>			
Mg-Mn	2	-26.1 \pm 1.6	89.8
	3	-24.8 \pm 2.0	4.3
Mg-Zn	2	-40.4 \pm 3.1	99.9
	3	-42.0 \pm 8.3	35.9
Mn-Zn	2	-40.5 \pm 3.1	100
	3	-42.2 \pm 8.8	34.5
Mg-Mn-Zn	2	-40.5 \pm 3.0	99.9
	3	-41.8 \pm 8.1	35.2

4.9 References Chapter 4

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5 MANAGING A NEAR THREATENED MIGRATORY SPECIES IN A VOLATILE WORLD: CASE STUDY OF THE ATLANTIC SALMON IN THE SOUTHERN BAY OF BISCAY

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5.1 Abstract

Conserving endangered species is particularly challenging in a rapidly changing environment, as determining appropriate and feasible actions to effectively manage and preserve threatened species in their natural habitats is highly complex. Diadromous fish species, including Atlantic salmon (*Salmo salar*), have experienced dramatic declines, mainly due to global warming and anthropogenic pressures such as habitat alteration. As a result, stocking programs have been widely implemented to counter population collapses, but these efforts raise concerns such as increased dispersal rates in hatchery fish, which can lead to genetic introgression and altered population dynamics. In the Bay of Biscay (western France and southern Spain), regional management of salmon populations with varying stocking strategies complicates the assessment of their effectiveness, prompting this study to investigate the impact of different rearing practices on the return rates of hatchery-origin salmon. Here, we demonstrated that (i) hatchery-fish would disperse more than their wild counterparts, (ii) releasing a larger biomass does not lead to a greater proportion of returns as we found a fairly stable relationship between the proportion of wild and hatchery-fish returning as spawners, and (iii) stage-at-release probably influenced individual survival based on “bigger is better” hypothesis. Together, our results highlighted the need to promote the metapopulation structure from a management perspective, especially in our study system which encompasses a set of local, most often coexisting populations. It is essential to consider local characteristics such as habitat functionality and carrying capacity with varied management, aiming at the maintenance of natural biocomplexity (*i.e.* portfolios) to help populations navigate increasingly rapid and extreme environmental changes.

Keywords: conservation, *Salmo salar*, coexisting populations, stocking, hatchery

5.2 Introduction

In biodiversity and wildlife conservation, one of the biggest challenges is to depict the appropriate and feasible actions in order to correctly manage and preserve endangered species in their natural ecosystems. The critical yet complex measures implemented most often need to be adapted to spatial and temporal scales, as the responses of threatened species to our contemporary world may rapidly vary (Dawson et al., 2011; Månsson et al., 2023; Willmes et al., 2024). Among these measures, stocking programs (and associated initiatives such as captive breeding or translocations) are commonly used to sustain vulnerable species (Holt et al., 2014). First applied to mitigate population declines and prevent natural extinctions, artificial repopulation also aims to bolster natural populations and restore ecosystems that are no longer frequented (Palmer et al., 2020). However, the long-term sustainability of these populations remains a complex objective, strongly dependent on ecological, genetic, and behavioral factors (Araki et al., 2008). The apparent antagonism between a short-term management strategy (*i.e.* stocking) and the durable aspiration of maintaining self-sufficient populations constitutes a daunting task (Holt et al., 2014), and in many cases, repopulation programs alone cannot guarantee the establishment of viable populations without addressing underlying threats, such as habitat loss or climate change (Lowe et al., 2006; Miller and Reading, 2012; Paxton et al., 2018). For instance, studies have shown modest results *in natura* for intense human interventions and implications (van Rijssel et al., 2024). From this perspective, the most is certainly not necessarily the best.

In the last decades, diadromous fish species have undergone a massive decline throughout their repartition range (Limburg and Waldman, 2009; Tamario et al., 2019; Almeida et al., 2023). The main reasons include global warming effects (*e.g.* increasing temperatures, extreme climatic events such as floods or droughts) and anthropic stressors (*e.g.* habitat alterations, pollution, overfishing) (Chaput, 2012; Forseth et al., 2017; Thorstad et al., 2021;

Dadswell et al., 2022; Crozier and Siegel, 2023). Among these fish species, the Atlantic salmon (*Salmo salar*), native to European and North American basins that flow into the northern Atlantic Ocean, as well as the Barents and Baltic Seas (Thorstad et al., 2010), has heavily decreased in most of its worldwide distribution range, with reported nominal catches reducing from about 12,000t in 1974 to 2,400t in 1997 (ICES, 2021). In response, the North Atlantic Salmon Conservation organization (NASCO), which gathers six countries and the European Union, embraced the precautionary approach to shift international efforts from an exploitation-focused to a conservation-focused strategy (White et al., 2023). As part of this policy, stocking programs were initiated to restore, conserve, and ideally maintain stocks above the conservation limits (CLs) set for each water body hosting the species (Fraser, 2008; Thorstad et al., 2021), although such programs are also employed for harvest purposes (Araki et al., 2008) or to recolonize lost habitats (Perrier et al., 2013b; Willmes et al., 2021). For example, in France, every population identified along the Bay of Biscay, all of which have seen their stock decline (Lebot and Rivot, In press) or even disappear in the Gironde (Vandeputte et al., 2021), is managed independently. This regional management strategy raises two questions. First, salmon populations are known to be interconnected, to some extent (whether spatial and/or temporal), via dispersal, hence displaying a metapopulation structure (Schtickzelle and Quinn, 2007). However, it has been demonstrated that hatchery-origin individuals express a higher dispersal rate than their wild counterparts (Candy and Beacham, 2000; Jonsson et al., 2003). Therefore, an appropriate understanding of such biogeographical architecture is important in a management context as both beneficial and undesirable effects related to artificial propagation (Barnett-Johnson et al., 2007; Johnson et al., 2012) have been observed *in situ*. Positive aspects of dispersal are mostly related to demographic rescue effects for endangered populations, thus possibly maintaining genetic diversity via the reduction of inbreeding depression (Carlson et al., 2014). On the other hand, excessive dispersal of hatchery-reared salmon has the potential to increase genetic introgression (Bett et al., 2017

and references therein), which can in turn severely affect the “eco-evolutionary dynamics of local populations and metapopulations as a whole” (Lamarins, 2022). Ignoring or underestimating dispersal from hatchery fish can also lead to false interpretations of population dynamics in a conservation perspective, as shown by Johnson et al. (2012). Second, as management decisions are decided regionally, we witness a considerable heterogeneity in stocking practices (*i.e.* stage-at-release and intensity of production) among each genetically distinct population. Yet, population dynamics are markedly different in these supplemented areas, and the effect of hatchery-fish releases remains difficult to assess, mostly because of the considerable effort needed to explore the proportion of hatchery individuals that are successfully returning as mature adults.

For instance, a substantial number of genetic studies has been conducted (Perrier et al., 2011, 2013a; Vandeputte et al., 2021) to examine the relative importance of fish from hatcheries in the managed populations. However, while it is essential to properly estimate levels of admixture between populations, it is impossible to capture the proportion of immigrants that do not ultimately participate in reproduction via genetics. Yet, this information is crucial and complementary with gene flows levels as indirect effects such as competition for habitat or feeding resources, or sexual mating, can be observed between local individuals and immigrants (Essington et al., 2000; Laffaille, 2011). Additionally, we clearly lack temporal information regarding the success or not of management strategies on returning adults as genetics or tagging approaches, both methods being commonly employed to study the effectiveness of stocking programs, are difficult to deploy over large temporal and spatial scales.

In fisheries sciences, the use of calcified structures such as otoliths have rapidly increased since the beginning of the 21st century (Reis-Santos et al., 2022). Based on biomineralization properties (Hüssy et al., 2020), researchers have recently used otolith chemistry to reconstruct life histories of freshwater (Amano et al., 2018; Radigan et al., 2019), marine (Coussau et al., 2023; Teichert et al., 2024) and diadromous (Tabouret et al., 2010; Walther et al., 2011; Matetski

et al., 2022) fish species. In addition to assessing migratory behavior and habitat use patterns, otoliths have also proved to be a promising tool for distinguishing hatchery fish from wild individuals, which is particularly useful to help management investigations (Carlson et al., 2017). Such investigations have been possible through the use of otolith strontium (Vaisvil et al., 2023) and sulfur (Johnson et al., 2012; Woodson et al., 2013) isotopes, microstructures (Sweeting et al., 2003; Barnett-Johnson et al., 2007), or thermal marks (Brenner et al., 2012; Sahashi et al., 2015). However, regarding salmon species, while a fair amount of studies has been conducted to examine the effect of hatchery practices on Pacific salmon species (Brenner et al., 2012; Johnson et al., 2012; Sturrock et al., 2019; Willmes et al., 2021), there are no comparable research work for Atlantic salmon, especially in the Bay of Biscay.

In this study, we used otolith chemistry to assess the role of stocking programs in Atlantic salmon population stability in two regions from the southern Bay of Biscay: the Gironde and the Adour. More particularly, we examine (i) the natal origin (hatchery vs. wild) of fish that have dispersed from their natal area, (ii) the inter-annual variability in the proportion of hatchery-origin salmon returning as potential spawners and (iii) the effects of stocking practices on this proportion.

5.3 Materials and methods

5.3.1 Study areas

The Gironde and Adour basins are part of the Bay of Biscay, and more specifically in southwestern France (Figure 5-1). The Gironde is formed by two sub-basins, the Dordogne and the Garonne (Figure 5-1), which both strongly rely on stocking programs since the 1980's (Bosc et al., 2020), to maintain and ultimately restore natural populations. Briefly, eggs from captive broodstocks of local strains are transferred toward three structures (Castels and Fialicie in the Dordogne sub-basin and Pont-Crouzet in the Garonne sub-basin) to grow juveniles before releasing them (Clave et al., 2016). Different stages-at-release are used (e.g. eggs, fry, parr and smolt) and overall, intensive stocking was performed with an annual average of 350,000 and 600,000 fish released in the Garonne and Dordogne respectively over the 2006-2018 period. Overall, the Dordogne salmon population is roughly three times larger than the Garonne population ($n = 326 \pm 165$ and $n = 129 \pm 51$ returning adults in the Dordogne and Garonne basins respectively, over the 2006-2018 period, from <http://www.migado.fr/>). South of the Gironde, the Adour is shaped by three sub-basins, *i.e.* the Nives, Oloron and Pau (Figure 5-1). Stocking programs took place in the early 1970's in the Adour, with about 200,000 fry released every year in the Gave d'Oloron until 2010 as a response to the observed decrease in adult return rates (Picoulet and Marty, 2020). This program really intensified between 2004 and 2010 with the introduction of 500,000 juveniles in the Gave de Pau. Since 2011, only the Pau sub-basin is still supplemented with hatchery-origin fish (about 300,000 fry/parr 0⁺ annually), the Nives and Oloron being considered as self-sustaining. Shortly, in the Adour system, the Cauterets hatchery is used to produce eggs from a captive broodstock of Adour strain. Depending on the targeted stage-at-release, eggs are transferred to three possible structures: Arcizans, Sassis and Médous (Figure 5-1). For both

regions, the inter-annual intensity of fish releases per stage and location is presented concurrently with the number of returning adults in Figure 5-2.

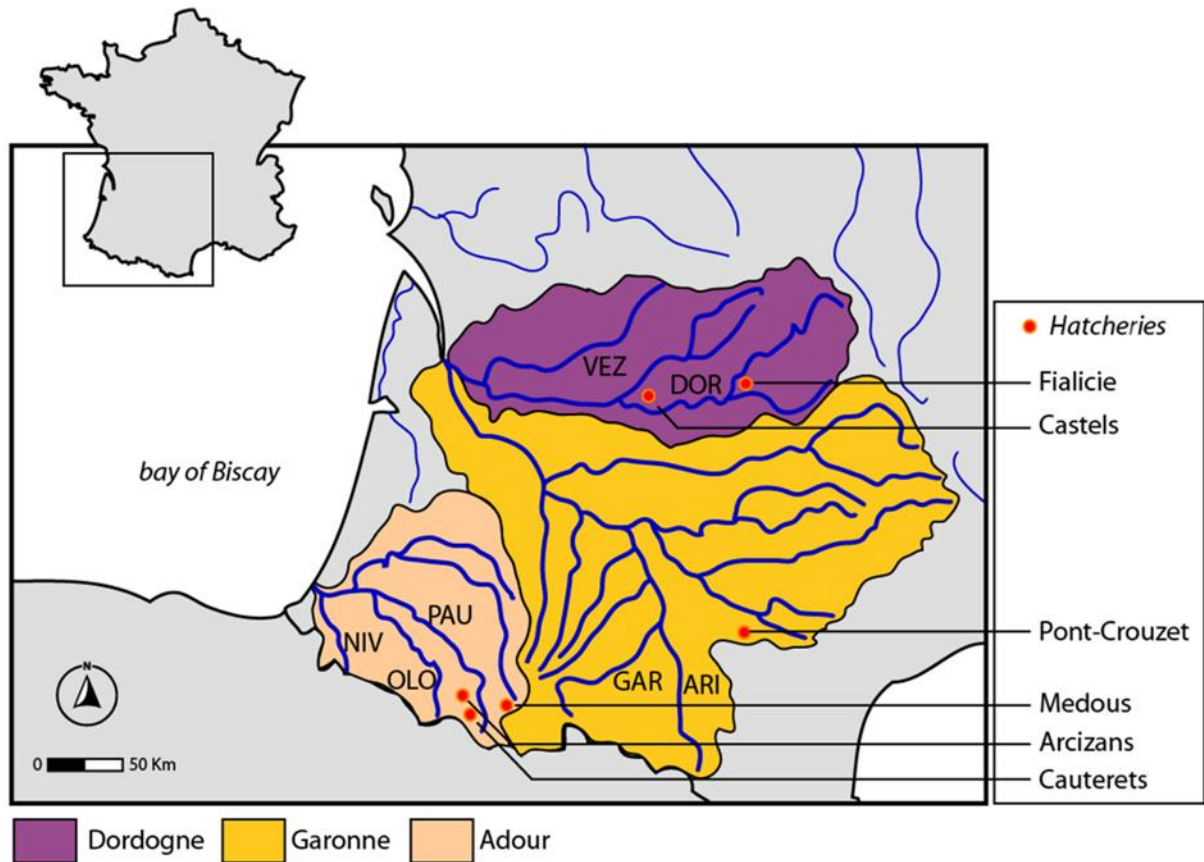


Figure 5-1: Map of the study sites showing every sub-basin of interest in this study. The hatcheries are represented by a red circle. Abbreviations: ARI, Ariège; DOR, Dordogne; GAR, Garonne; NIV, Nives; OLO, Oloron; VEZ, Vézère.

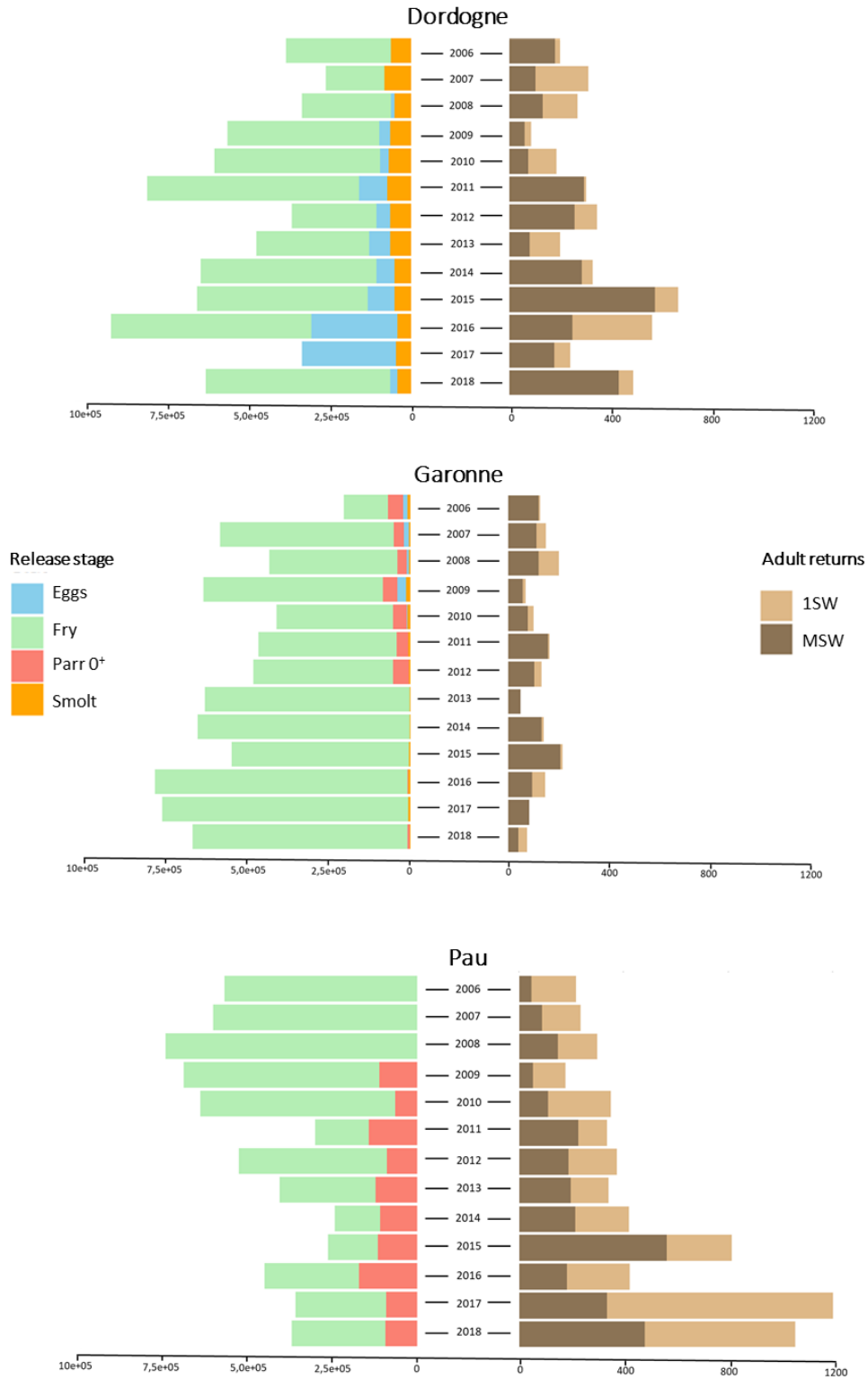


Figure 5-2: Rearing efforts, by stages-at-release, confronted to the number of returning adults in the Dordogne, Garonne and Pau sub-basins over the 2006-2018 period.

5.3.2 Sample collection

This research work follows an initial study where the authors investigated the inter-annual variability of dispersal rate for Atlantic salmon populations in the southern Bay of Biscay (Fontaine et al. 2024a, submitted in *Fisheries Research*). As the global objective of the present study is to assess the effect of rearing programs on adult returns in the Gironde and the Adour, we have only conserved individuals captured in the Gironde and Adour systems for which we were able to predict a geographical origin. Details of the complete otolith collection used in this study is shown in Table 5-1.

Assignment database

To estimate the natal origin (*i.e.* wild vs. hatchery) of every returning mature adult, an assignment dataset has been developed from juvenile (Adour) and adult fish (Gironde) for which the natal origin has been certified. In the Gironde, fish with certified origin were obtained from genetic parentage programs (Vandeputte et al., 2021) while in the Adour, wild or hatchery origin knowledge is based on a previous research work from which our samples originate (Martin et al., 2013b). In total, in the Gironde, the assignment dataset is composed of $n = 17$ and $n = 83$ of wild and hatchery fish respectively and we collected $n = 55$ and $n = 34$ of wild and hatchery salmon respectively in the Adour (Table 5-1). Samples were recovered from MIGADO and MIGRADO, two regional institutions responsible for monitoring migratory fish populations in the Gironde and Adour basins respectively.

Unknown adults' database

To examine the role of stocking programs in the proportion of hatchery-origin returning fish, 219 and 1133 otoliths from adult salmon, respectively collected in the Gironde and the Adour (Table 5-1) and for which we have previously determined an Adour, Garonne or Dordogne geographic origin (Fontaine et al. 2024a, submitted in *Fisheries Research*), were used. Immigrants of other

origins were discarded as no data on the geochemical signatures of hatchery-fish otoliths were available. Otoliths were collected from MIGADO, MIGRADO, in addition to recreational and professional fisherman in the Adour.

Table 5-1: Capture site, year of collection and number of otoliths used in this study to assign a natal origin to unknown returning adults from a certified database, in the Gironde and the Adour systems. Hatcheries are denoted in light blue background.

Sampling site		Assignment database			Unknown adults' database	
Geographic area	Natal origin	Number of known origin juveniles	Number of known origin adults	Years of collection	Number of adults with unknown natal origin	Years of collection
Adour	Wild	55			1133	2009-2018
	Médous-Arcizans	23		2009-2011		
	Sassis	11				
Gironde	Wild		17		219	2007-2016
	Castels		33	2010-2016		
	Fialicie		19			
	Pont-Crouzet		31			

5.3.3 Otolith preparation and analyses

Once the pair of sagittal otoliths were collected from salmon's heads, any calcified structure containing vaterite was excluded as it has been demonstrated that the presence of vaterite can result in significant differences in chemical composition compared to aragonite (Pracheil et al., 2019). After being cleaned, otoliths were mounted following the protocol described by Tabouret et al. (2010). Shortly, otoliths were embedded in epoxy resin (Araldite 2020, Escil) and grounded

in the sagittal plane to expose the nucleus. Prepared otoliths were then analyzed for barium (^{138}Ba), calcium (^{43}Ca), magnesium (^{24}Mg), manganese (^{55}Mn), strontium (^{86}Sr) and zinc (^{66}Zn), using an inductively coupled plasma mass spectrometer (ICP-MS DRC II, Perkin Elmer) paired with a high-repetition-rate infrared femtosecond laser ablation system (fs-LA Alfamet-Novalase, France). Additionally, we quantified the Sr isotopic ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) on the same otolith using a multicollector inductively coupled plasma mass spectrometer (Nu-Plasma MC-ICP-MS) coupled to the identical laser. All the analyses were conducted at the *Institut des Sciences Analytiques et de Physico-Chimie pour l'Environnement et les Matériaux* (IPREM), with analytical parameters set according to Martin et al. (2013a). For each analysis, the Ca signal was used as an internal standard, and we used the theoretical concentration of Ca in otoliths (Brown and Severin, 2009) to normalize the quantified elemental concentrations as Ba/Ca, Mg/Ca, Mn/Ca, Sr/Ca and Zn/Ca ratios. Three NIST standards (610, 612, and 614) were employed for calibration and accuracy was measured with two certified reference materials (CRM), NIES 22 and FEBS 1, both obtained from the otoliths of marine fish (*Lutjanus sebae* and *Lutjanus campechanus*, respectively). Detection limits were $0.02 \mu\text{g}\cdot\text{g}^{-1}$ for Ba, $0.28 \mu\text{g}\cdot\text{g}^{-1}$ for Mg, $0.13 \mu\text{g}\cdot\text{g}^{-1}$ for Mn, $0.06 \mu\text{g}\cdot\text{g}^{-1}$ for Sr and $0.66 \mu\text{g}\cdot\text{g}^{-1}$ for Zn. For the quantification of $^{87}\text{Sr}/^{86}\text{Sr}$, the laser spot width was adjusted according to the previously acquired Sr concentration (min: $50 \mu\text{m}$; max: $180 \mu\text{m}$) to ensure that the measured voltage exceeded the 2mV threshold, thereby guaranteeing reliable results.

5.3.4 Data analyses

Age estimation

As we needed to access to the cohort of every individual to efficiently study the effect of stocking programs on returning adults, we estimated the age of every captured fish by combining two methods. First, the river age of every salmon was predicted using the naïve functional clustering approach presented in Fontaine et al. (2024b), based on Zn profiles. Second, the sea age was

determined by scale reading (Baglinière et al., 1985), with the help of MIGRADOIR employees. However, as scales were not always available, we used the well-established relationships between the fork length (FL) and/or mass (depending on the information available) of individuals and their age when scalimetry was not accessible (Figure S 5-1). To ensure the comparability of the two methods, we compared sea age estimates across all individuals for whom we had data from all three approaches (scalimetry, mass-to-age estimation, and FL-to-age estimation) and observed a 94.9% agreement. Together, both the river and sea age were combined to determine the cohort according to the capture year.

Geographical origin assignments

As for age estimation, the geographical origin of every returning salmon was determined following a two-step approach. First, the regional (*i.e.* at a basin scale) origin has been predicted in Fontaine et al. (2024a, submitted in *Fisheries Research*). Briefly, a dataset exclusively composed of individuals with known origin, from all over the Bay of Biscay, was trained using a random forest (RF) approach (*randomForest* R package, version 4.7-1.1) to predict the geographical origin of every adults with unknown origin. This first step allowed to assign a regional origin for every captured fish, allowing to identify fish from the Dordogne, Garonne and Adour locations. Then, we applied a second “river-wide” RF model for every individual assigned to the Adour in order to characterize their sub-basin of origin (*i.e.* Pau, Oloron or Nives). The use of a “river-wide” model was preferred to a “sub-basin wide” model given the diversity of geochemical signatures within the Adour sub-basins. This second step was critical in this study as the management strategies are completely different in the Pau sub-basin (highly monitored) compared to the Oloron and Nives sub-basins (self-sufficient sub-populations, since 2011 for Oloron). The assignment dataset used for this discriminant analysis, in addition to the confusion matrix resulting from the RF are presented in Table S 5-1 and Table S 5-2 respectively.

Natal origin assignments

To predict the natal (*i.e.* wild vs. hatchery) origin of every returning salmon, we performed an univariate functional clustering approach (Bouveyron and Jacques, 2011) using the *funHDDC* package (version 2.3.1). The use of Ba/Ca, Sr/Ca, Sr/Ba and $^{87}\text{Sr}/^{86}\text{Sr}$ profiles (corresponding to freshwater residency, *i.e.* from individual birth to sea emigration), as well as every possible combination between all four variables was tested to predict natal origins. Here, using Sr elemental profiles alone (see Figure S 5-2) proved to be the most robust approach as it provides the best discrimination between every possible natal origin. Data treatment of Sr profiles followed the protocol presented in Fontaine et al. (2024b), but the parameters differed for both locations. In the Adour, a number of $k_1 = 10$ splines were set for the generalized additive model (GAM) while in the Gironde, we used $k_1 = 6$ splines in the GAM. Then, to perform the functional clustering analyses, a number of $k_2 = 7$ bases were established for the Adour whereas $k_2 = 10$ bases were fixed for the Gironde. These parameters have been tested and modified to provide the best estimations for each system. To examine the performance of the unsupervised approach, we conducted a stratified (ensuring the presence of every possible origin in both the training set and the test set) Out-of-Bag (OOB) sampling (training set: 75%, test set: 25%, number of iterations: 1000). Since the model naively provides a prediction at each iteration during the cross-validation, correspondences between the predicted and the real origin vary randomly. Therefore, we based our predictions on the average μ value of each individual. In the *funHDDC* package, μ is defined as “the mean of each cluster in the original space”. We then calculated the relative probability of belonging to each class as a function of the density of μ values (see Figure S 5-2). A summary of every analytical and methodological steps followed in this study is presented in Figure 5-3 to facilitate the understanding. Statistical analysis was performed using the R (version 4.2.1) software.

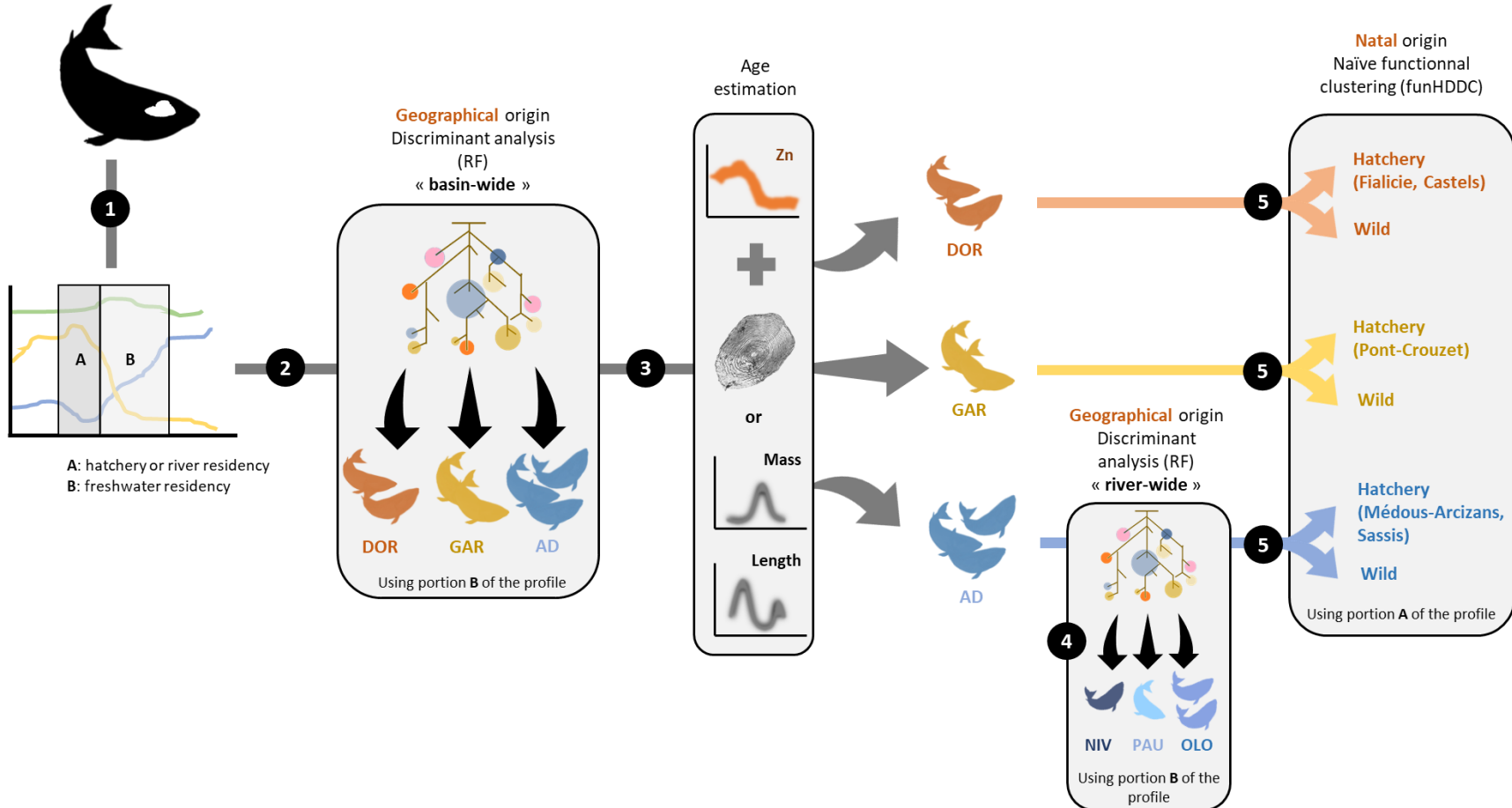


Figure 5-3: A schematic overview of every analytical and methodological steps followed in this paper. (1) Analyses of elemental (Ba, Ca, Mg, Mn, Sr and Zn) and isotopic ($^{87}\text{Sr}/^{86}\text{Sr}$) otoliths concentration. (2) The Ba/Ca, Sr/Ca, Sr/Ba and $^{87}\text{Sr}/^{86}\text{Sr}$ profiles were used in a random forest analysis (RF) to predict a “basin-wide” geographical origin. From this discriminant analysis, only the individuals captured in the Gironde (Garonne and Dordogne) and the Adour, and assigned to one of these three locations were retained. (3) For each individual, a functional clustering analysis was performed to estimate river age

using Zn/Ca profiles, while sea age was determined using scalimetry, or size-age or weight-age relationships when scales were not available. This step allowed us to access the cohort of every collected salmon. (4) For all individuals sampled in the Adour and assigned to the Adour by the “basin-wide” model, a second “river-wide” discriminant analysis was performed to determine the river of origin and therefore the sub-basin of origin (Pau, Oloron or Nives). Once we had for each individual (i) the cohort of origin and (ii) the sub-basin of origin (Dordogne, Garonne, Pau, Oloron or Nives), we predicted the natal origin (hatchery vs. wild) of every individual according to their geographical origin, again using a functional clustering approach.

Inter-annual investigations and the effects of stocking strategies

To study the temporal variation of the proportion of returning hatchery-origin fish, we provide results by year of capture, as it makes more sense for managers. However, to investigate the effect of stocking programs on returning spawners, we have worked by cohorts (otherwise we would have mixed several cohorts within the same return year, which would have made it difficult to assess the effects of management strategies on returning adults). To achieve this, robust linear models (rlm, MASS R package, version 7.3-60.0.1) were conducted for every management strategy of artificial supplementation (*i.e.* eggs, fry, parr 0⁺ and smolt) in relation to the relative proportion of hatchery adult salmon.

5.4 Results

5.4.1 Natal origin (hatchery vs. wild) of immigrants

As the vast majority of individuals collected in the Adour were sampled in the estuary, we could not assess the proportion of both natal origins in every sub-basin of interest (*i.e.* Pau, Oloron and Nives). Therefore, the proportion of immigrants from wild and hatchery-reared fish were estimated for the Dordogne, Garonne and Adour locations, and are presented in Figure 5-4. As a reminder, this estimate only considers part of the total immigration (from the Dordogne, Garonne or the Adour), since we did not have the geochemical “hatchery signatures” for the other donor populations. As expected, the majority of immigrants were stocked individuals both in the Dordogne (54%) and the Adour (63%) areas, which is in line with recent scientific literature. However, surprisingly, our results show that almost 75% of the individuals identified as immigrants in the Garonne sub-basin are assigned to a wild origin. Nevertheless, our observations should be considered in light of the relatively low number of immigrants identified in every location (Adour: $n = 18/954$, Garonne: $n = 16/73$, Dordogne: $n = 21/147$).

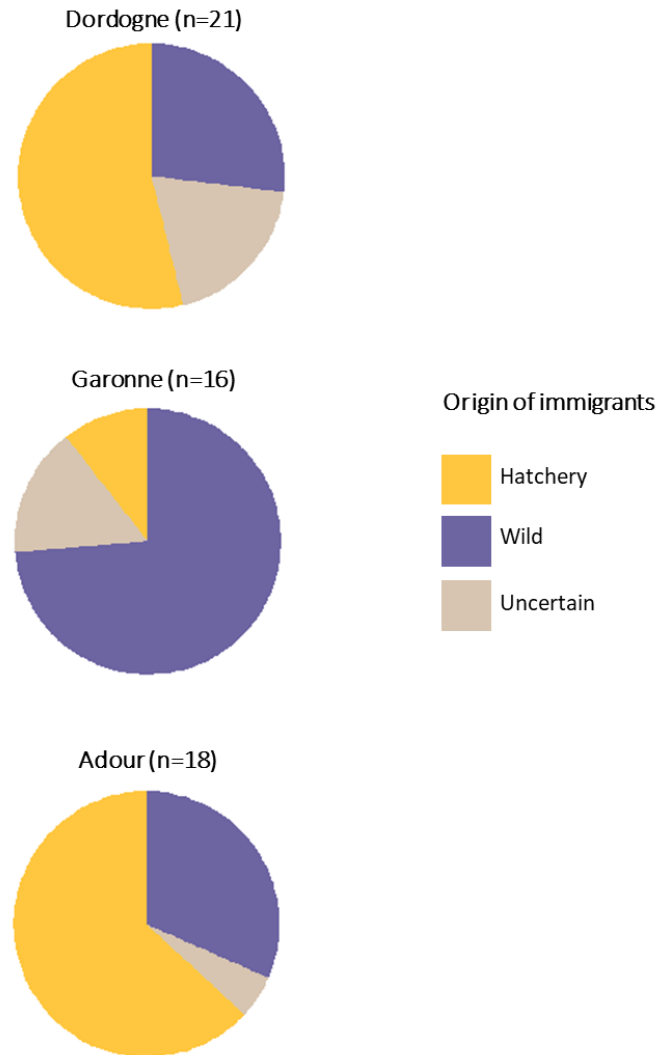


Figure 5-4: Proportion of wild and hatchery-fish identified as immigrants in the Dordogne, Garonne and Adour areas. Uncertainty was obtained using a correlation matrix from the stratified Out-of-Bag sampling performed in the naïve functional clustering analysis.

5.4.2 Inter-annual variability in the proportion of hatchery-origin salmon returning as mature adults

The inter-annual variation in the proportions of returning individuals identified as wild or hatchery-origin in the Garonne, Dordogne, Nives, Oloron and Pau sub-basins is shown in Figure 5-5. In the Garonne, every individual captured was determined as a hatchery-reared salmon, while

conversely in the Nives, every sampled fish was attributed to a wild origin. In the Oloron, with the exception of 4 individuals (two in 2012 and two in 2013) out of 818 from the 10-year period, every salmon was attributed to a wild origin. Therefore, in these three sub-basins (Garonne, Nives and Oloron), the sub-populations exhibited no mixture patterns between wild and hatchery fish, which was expected, as both the Nives and Oloron are considered as self-sufficient and no longer supplemented since 2011 while, in opposition, the Garonne sub-population heavily relies on stocking programs since its reintroduction. Our results are substantially different for the Dordogne and the Pau sub-basins. In the Dordogne, with the exception of 2009 (where we collected only three individuals), all sampling years are represented by a coexisting sub-population of wild and hatchery individuals. Even though an increase in the proportion of wild fish is observed in 2010 and 2011, the temporal variation of the proportions between the two origins is fairly stable over the last 5 years, which also corresponds to our most extensive sampling (in average, $63.7 \pm 7.5\%$ of returning adults is identified as hatchery-originated between 2012 and 2016, $n = 83$). In Pau, similarly to the Dordogne, the annual variation of the proportions of hatchery and wild fish is rather stable, albeit a slight decrease of wild returning salmon can be observed in years 2016 and 2017. Overall, an average of $31.2 \pm 14.4\%$ of hatchery salmon was estimated over the 10-year period ($n = 150$).

5.4.3 Effects of stocking practices in the proportion of hatchery-origin salmon returning as mature adults

The relationships between stocking practices and the proportion of hatchery-origin returning spawners are shown in Figure 5-6. However, because we only detected stocked individuals in the Garonne, we did not perform any rlm for this location as it would be incorrect to model a relationship with our binary data (proportion of 0: no available fish from a cohort; proportion of 1: every salmon was hatchery-originated). First of all, we observed distinct strategies from one

management unit to another. Indeed, the two Gironde sub-basins (Garonne and Dordogne) are the only ones to discharge eggs and smolts, while parr 0⁺ is produced in the Garonne and Pau sub-basins. Therefore, only the fry stage is common to all three sites. The intensity of egg releases in the Dordogne sub-basin has led to an overall decline in the proportion of hatchery fish returning salmon. Looking at the effect of fry release in the Dordogne and Pau sub-basins, we found a low decrease of mature adults from hatchery-origin in both locations with the increase of fry production, although the reduction is slightly more marked in the Dordogne than in Pau. The intensity of parr 0⁺ release did not have any effect on the proportion of hatchery adults captured in the Pau sub-basin. Finally, in the Dordogne area, we observed a marked positive relationship between the intensity of smolt releases and the proportion of hatchery fish identified, which strongly contrasts with all the other stages.

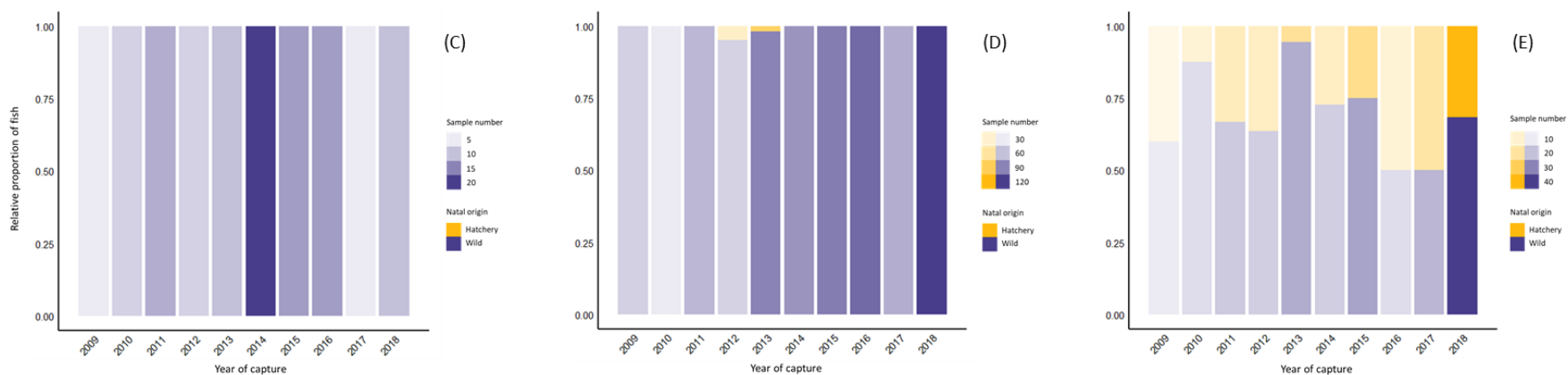
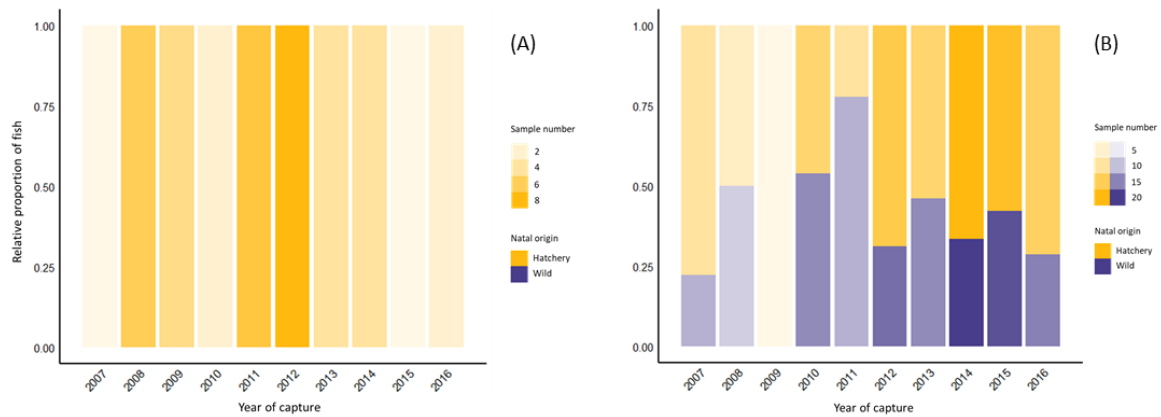


Figure 5-5: Inter-annual proportion of returning mature adults from hatchery and wild origins in the Garonne (A), the Dordogne (B), the Nives (C), the Oloron (D) and the Pau (E) sub-basins, from 2007 to 2016 in the Gironde sub-basins (A and B) and from 2009-2018 in the Adour sub-basins (C, D and E). The annual number of sampled individuals is shown by transparency in each stacked bar.

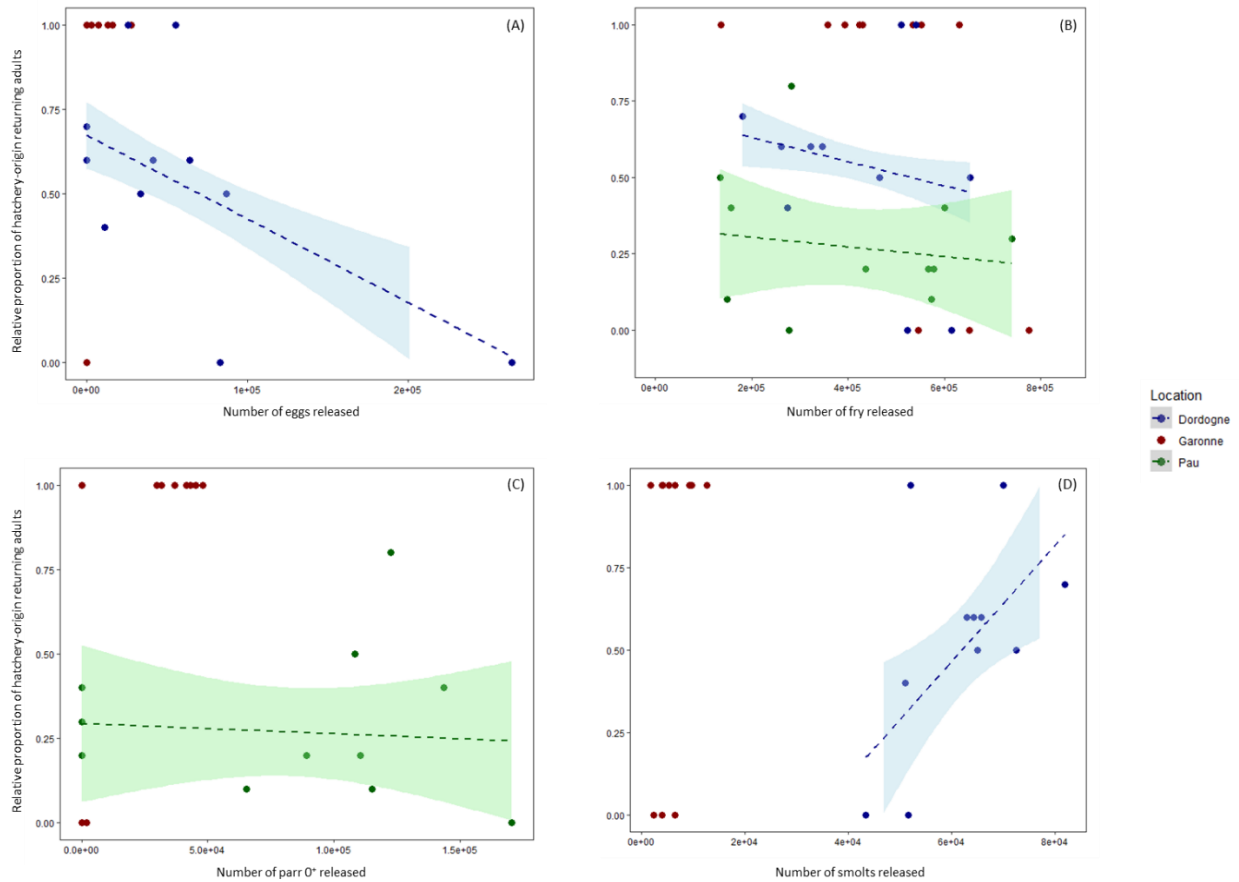


Figure 5-6: Robust linear models (rlm, in dotted lines) \pm standard error (α set to 0.05) investigating the relationships between (A) the number of eggs released, (B) the number of fry released, (C) the number of parr 0⁺ released and (D) the number of smolts released and the relative proportion of hatchery-origin returning as potential spawners. Each datapoint represents one cohort of return, associated with the stocking intensity. No model is provided for the Garonne sub-basin as our data were binary for this location (*i.e.* either a proportion of 0 or 1).

5.5 Discussion

Conservation and management of endangered or threatened species is particularly challenging in our rapidly changing world, where eco-evolutive characteristics of natural populations are confronted with drastic environmental disturbances (Lamarins, 2022). Migratory species such as diadromous fish are especially vulnerable to global change impacts as they face numerous dangers, in various environments and at distinct life stages to complete their life cycle (Bull et al., 2022; Crozier and Siegel, 2023). The Atlantic salmon (*Salmo salar*) is no exception as many of the wild, historical populations have seen their stocks sharply decline in the past 50 years (ICES, 2021). Resultingly, many stocking programs have been developed to cope with this massive collapse with the aim to maintain and ideally restore natural populations. However, undesirable effects of rearing programs have been demonstrated over the past three decades including, but not limited to, reduced biocomplexity of natural populations, genetic introgression, increased competition (Essington et al., 2000; Horreo et al., 2011; Huber et al., 2024). Yet, artificial restocking is still largely used to preserve a key species from economic, social and cultural perspectives. In the Bay of Biscay (western France and northern Spain), most Atlantic salmon populations are supplemented with stocked individuals, mainly produced from local strains since the 1990s (Perrier et al., 2013b; Almodóvar et al., 2023). Nevertheless, since the management of anadromous species is decided regionally, each population is governed independently, with varying strategies, both in terms of stage-at-release and intensity of production, which complicates the assessment of the temporal variability of stocking efficiency. Therefore, in this study and based on populations from the southern Bay of Biscay, we investigated the effects of rearing strategies on the proportion of hatchery-fish origin returning as spawners over the 2007-2018 period.

Natal origin of immigrants

In our study, hatchery individuals represented the main part of immigrants identified in the Dordogne and the Adour but not in the Garonne (although we only investigated exchanges between these three locations). An important number of studies has now demonstrated the higher dispersal rate of stocked individuals compared to their wild conspecifics (Jonsson et al., 2003; Brenner et al., 2012; Johnson et al., 2012). Our results in the Dordogne and the Adour corroborate previous research works and strengthen the potential harmful effects of hatchery fish on natural metapopulations. From a management perspective, we do not foresee direct demographic impacts on the receiving population considering the number of immigrants we identified, even though it may not be negligible, but rather indirect potential negative effects on the genetic make-up of untargeted populations. Such observations have already been highlighted for Atlantic (Horreo et al., 2011; Gudmundsson et al., 2013) and Pacific salmon (Jasper et al., 2013; Bett et al., 2017) or more recently in Baltic sea trout (Burimski et al., 2023) for example. However, in the Garonne, most of the immigrants were attributed to a wild origin, which sharply contrasts with the existing literature, but also within our system of study, the Garonne sub-basin being located in-between the Dordogne and the Adour. Interestingly, although the Garonne and the Dordogne share the same estuary, making each a fair candidate for proximate dispersal, 12 out of the 16 immigrants recorded in the Garonne and 19 out of 21 immigrants identified in the Dordogne were attributed to the Adour basin and more particularly to the Pau and Oloron sub-basins. In Fontaine et al. (2024a, submitted to *Fisheries Research*), the authors demonstrated that the Adour could be an important (although reasonable considering the size of the population) donor for receiving,

small populations. For instance, even a moderate source-sink dynamic from the Adour to the Dordogne and Garonne could explain the high percentage of wild fish found as immigrants.

Inter-annual variation in returning hatchery-reared fish

The investigation of potential temporal changes in the proportion of returning hatchery-reared adults is of critical importance from a management perspective. Indeed, while the main reason for rearing programs is to mitigate population collapse and sustain natural populations that still subsist, ideally, they also aim at “rebuild depleted populations of wild salmonids” (McMillan et al., 2023). However, the stability or even increase of a supplemented population, estimated solely via the count of potential spawners is not always a guarantee of good health for the natural population (Sweeting et al., 2003; Johnson et al., 2012; Sahashi et al., 2015). In their study, Johnson et al. (2012) demonstrated that increasing proportion of stocked-individuals were responsible for an illusory natural population growth. Therefore, a systematic monitoring of hatchery and wild fish observed on spawning grounds is highly recommended to assess the benefits (or not) of stocking programs (Ruggerone et al., 2010). Here, we observed three distinct sub-population dynamics over a 10-year period: (i) one was exclusively dependent on artificial releases (*i.e.* Garonne), (ii) on the opposite side, two were entirely based on wild salmon (*i.e.* Nives and Oloron) and (iii) two were co-mingled, with one mainly composed of hatchery fish (*i.e.* Dordogne) and the other mostly composed of wild individuals (*i.e.* Pau).

In the Nives and Oloron sub-basins, such results were expected as stocking programs are no longer used for the Nives and the Oloron since 2004 and 2011, respectively (Picoulet and Marty, 2020). Therefore, although still highly monitored, these two self-sufficient sub-populations demonstrated encouraging dynamics over the studied period. Conversely, in the Garonne, we did not identify any adult from a wild origin. The total absence of wild salmon during our study period is very surprising, as an estimated proportion of $86 \pm 3\%$ hatchery fish returning in the Garonne

sub-basin (from 2012 to 2016) using parentage analysis has been recently reported (Bosc et al., 2023). However, we acknowledge that our sample size is fairly low in this location ($n = 36$ between 2007 and 2016), therefore the misattribution of one or several individuals could considerably change our interpretation. Near the Garonne, the proportion of wild fish in the Dordogne varied in the first years before stabilizing in the second half of the study period ($36.3 \pm 7.5\%$, 2012-2016), which also corresponds to a larger sampling effort. Our observations mirror results from recent studies where the authors used parentage assignments to estimate the percentage of wild salmon (collected between 2008 and 2016, which is almost concurrent with our dataset) from the Gironde (31.3% , see Vandeputte et al., 2021) and their two sub-basins (Dordogne: $34 \pm 7\%$, Garonne: $14 \pm 3\%$, see Bosc et al., 2023). Taken together, these studies and the present research work do not indicate a temporal shift towards a greater proportion of hatchery or wild salmon returning as mature adults. The establishment of a captive broodstock from local fish have possibly enhanced hatchery individual fitness and survival, although it can rapidly decrease compare to wild reproduction (Araki et al., 2008; Milot et al., 2013). It also highlights the marked difference between the recoveries of the Dordogne and Garonne sub-populations, potentially because of dissimilar management strategies (discussed in the following section). Finally, as in the Dordogne, we identified a similar mixed sub-population in the Pau sub-basin but with inverse proportions (roughly one-third of the individuals originated from hatcheries and two-thirds from natural reproduction). We also showed a relatively stable inter-annual pattern, which is interesting according to the net augmentation in the annual number of spawners since 2015 (see Figure 5-2). It would therefore indicate a similar increase of both wild and hatchery-origin salmon returns, and potentially reflect the benefits of ongoing restoration and ecological continuity efforts that have been underway for several years along the Gave de Pau axis. In addition to rearing measures, local stakeholders have implemented significant actions to facilitate the free movement of

migratory species, particularly to access previously inaccessible areas that exhibit favorable ecological functionality (Picoulet and Marty, 2022).

Effects of rearing strategies on hatchery-origin salmon returns

In our changing world, a variety of management strategies (e.g. number, stage, timing, location of release) is highly desirable to avoid potential negative effects such as reduced biocomplexity and portfolio effects (Huber et al., 2024), but consequently quite challenging to evaluate as rearing programs can evolve rapidly in space and time (James et al., 2023). Here, we investigated the effects of stage (*i.e.* eggs, fry, parr 0⁺ or smolts) and biomass of release on the proportion of returning hatchery fish. Our results strengthen two positions that are mostly established in the literature, (i) releasing a larger biomass is not leading to a larger proportion of hatchery-origin spawners and (ii) the bigger, presumably the better (James et al., 2023; McMillan et al., 2023). First, our study demonstrates a probable density-dependent effect regarding the intensity of stocking. Rearing programs are often targeting production objectives, but the release of an important number of stocked individuals (too important for a specific environment with limited habitat and food resources) is often deleterious for wild fish in coexisting populations. Previous studies have shown the reduction of both the abundance and productivity of wild salmon when density-dependent mechanisms occur because hatchery releases (McMillan et al., 2023 and references therein). Therefore, rather than a target number, supplementation should consider habitat capacity, functionality and productivity to avoid competition behaviors. Second, although some studies have demonstrated a lower reproductive success for smolt-stocked Atlantic salmon compared to fry-stocked individuals (Milot et al., 2013), it is globally acknowledged that late stage-at-release (e.g. smolt) express a higher survival than young stage-at-release (e.g. fry). This is usually explained by the higher tolerance to environmental stressors such as extreme temperatures or hydrological conditions, predation avoidance and smolts are generally greater competitors for food and habitat (James et al., 2023 and references therein). As smolt release

has been more widely employed in the Dordogne sub-basin than in the Garonne, it might be one factor explaining the slight positive dynamic of annual returns in the Dordogne. However, smolts are more difficult to produce in quantity for obvious reasons, and according to Bosc et al. (2023), smolt stocking only accounted for 6% of fry equivalent discharge. Such a small smolt contribution may partly explain the limited effect on returns.

Nevertheless, we argue that multiple management strategies of release should be conserved to favor life history diversity (Thorson et al., 2014; Huber and Carlson, 2015; Nelson et al., 2019; Sturrock et al., 2019; Des Roches et al., 2021). An important point raised in McMillan et al. (2023) is the lack of knowledge transfer between studies (and therefore scientists, managers and policymakers), generally because they concern different species and locations. Yet, a substantial number of studies have now demonstrated that diminishing life history traits (stage and/or location and/or timing-at-release) in stocked fish can lead to an overall decrease in population biocomplexity, which is critical to promote for enhancing population resilience to global change (Hilborn et al., 2003). As the primary objective of rearing programs is to maintain and rebuild depleted natural populations, management decisions should consider the population stability, aiming to maximize portfolio effects. This apparent antagonism highlights one of the most difficult tasks in biodiversity conservation, “balancing short-term (e.g., abundance) against long-term (e.g., stability) goals” (Sturrock et al., 2019). Therefore, while the “smolt strategy” might be part of the positive return dynamic in the Dordogne, we encourage other related practices, such as habitat restoration and ecological continuity plans, which will most presumably contribute to population sustainability. For instance, in the Garonne, individuals have to be transported over long distances due to numerous impassable obstacles to access favorable spawning grounds (Cornu and Lascaux, 2019), but trucking is known to considerably affect individual fitness (Sturrock et al., 2019). Even if such obstacles are also present on the Dordogne axis, human intervention is more limited for natural reproduction.

5.6 Conclusion

The conservation and appropriate management of Atlantic salmon populations represent a major challenge for the coming years. It's a shifting spatio-temporal balance, which needs to conjugate contrasting yet completely dependent objectives (Sturrock et al., 2019; McMillan et al., 2023). Although it is difficult to isolate the effects of biomass and stage-at-release from the many other parameters that will also influence individual survival (*i.e.* carry-over effects), our study tends to show that (i) we should consider the potential density-dependence effect when releasing an important number of hatchery individuals, particularly in supplemented coexisting populations and (ii) stage-at-release has contrasting effects on reared salmon returns. From our perspective, management strategies need to be designed and implemented in coherence with the ecological and functional characteristics specific to each environment, while including the notion of metapopulation which, by definition, encompasses distinct populations, genetic and phenotypic adaptations to specific environments. This translates into varied management, with the aim of maintaining sufficient biocomplexity to enable populations to cope with increasingly rapid and intense environmental change (Crozier and Siegel, 2023). Here also, it represents a considerable challenge, as managers and policymakers have to deal with short-term considerations, aiming at preserving a sufficient number of returns to meet all the demands (*i.e.* cultural, economic, recreational) that this key species generates (Thorstad et al., 2021). Finally, in parallel with stocking plans, a strong emphasis should be placed on ecological continuity programs to enable the free movement of migratory populations to reach functional habitats according to their ontogenic stage (*e.g.* breeding sites for spawning, nursery areas for young stages, favorable habitats for downstream migration).

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5.8 Supplemented figures

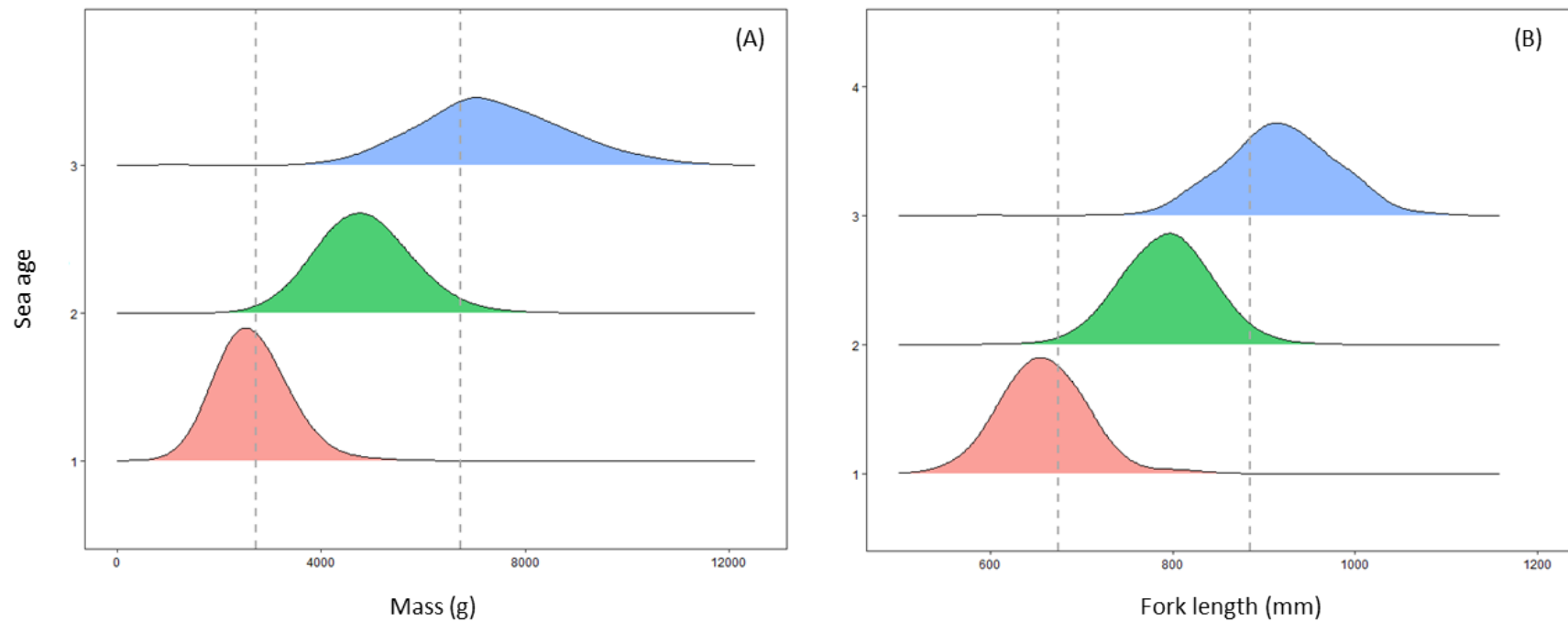


Figure S 5-1: Data distribution of the relationships between individual mass (A), fork length (B) and sea age of Atlantic salmon (*Salmo salar*), from 1987 to 2020. Individual data for mass (n=8478) and length (n=8524) were recovered from an open-access database of the *Centre national d'interprétation des captures de salmonidés migrants* (CNICS, <https://professionnels.ofb.fr/>). Dotted grey lines represent the decision thresholds calculated from the same dataset.

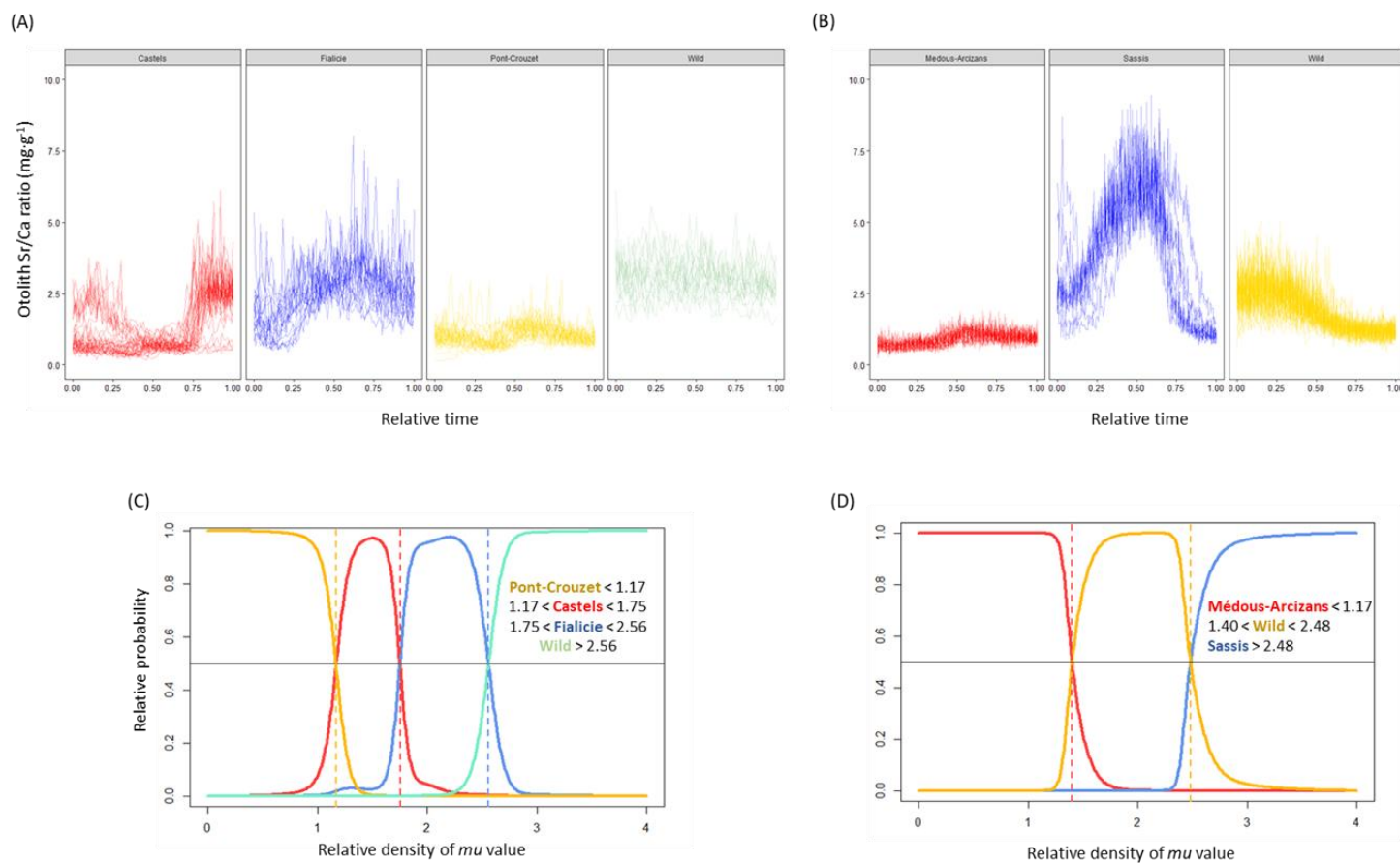


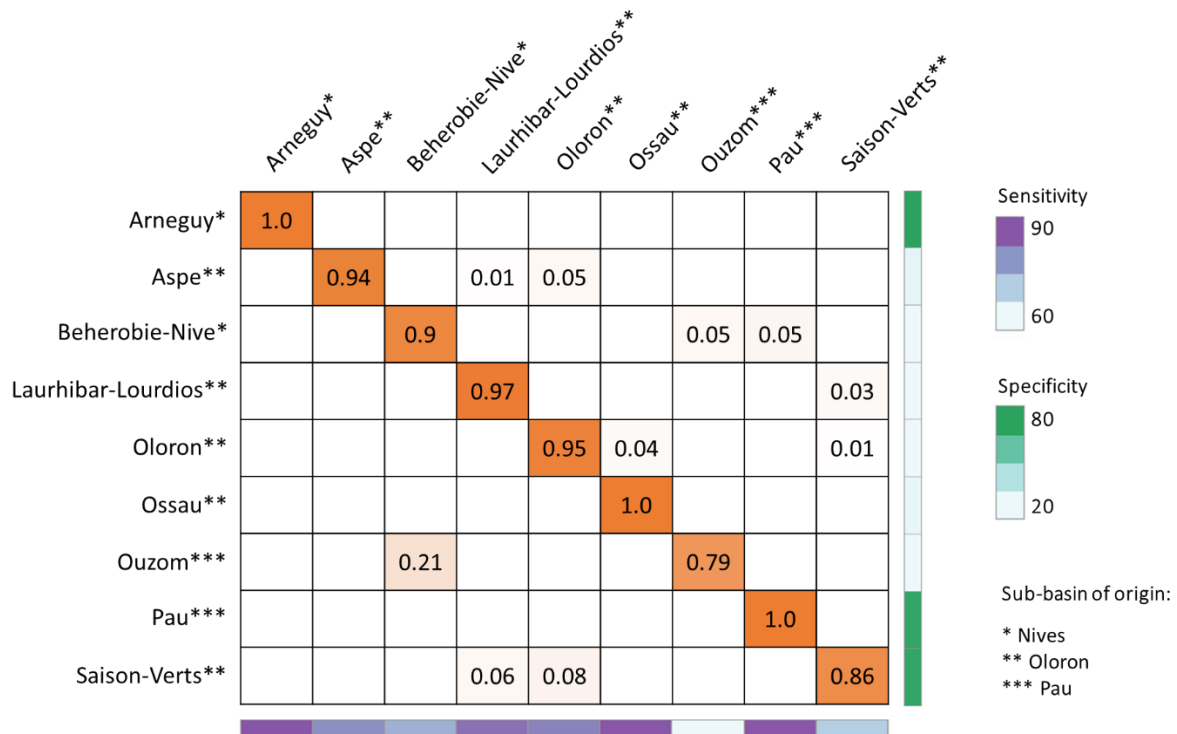
Figure S 5-2: Raw data distribution of Sr/Ca profiles from Atlantic salmon sagittal otolith captured in the Gironde (A) and the Adour (B). For each location, data distribution is presented for wild and hatchery-origin individuals. The relative time [0; 1] was obtained using the otolith length between the *primordium* and the outmigration (sea departure). Panels (C) and (D) show the method used to discriminate natal origin in the Gironde and the Adour, respectively, based on the relative density of μ value. The density thresholds are represented as dotted lines and were obtained from an Out-of-Bag sampling with $n = 1000$ iterations. A relative probability of 0.5, represented as a solid line, has been chosen as the natal origin attribution threshold.

5.9 Supplementary tables

Table S 5-1: Number, origin (capture site), and sampling year(s) of Atlantic salmon (*Salmo salar*) used in the assignment database for the “river-scale” model.

Sampling site		Assignment database	
Sub-basin	River	Number of known origin juveniles	Years of collection
Nives	Arnéguy	20	2011, 2014, 2017
	Béhérobie	21	2011, 2014, 2017
	Laurhibar	9	2011, 2014, 2017
	Nive	6	2011
Oloron	Aspe	14	2009, 2010, 2014, 2017
	Lourdios	12	2009, 2010
	Oloron	22	2009, 2010, 2014, 2017
	Ossau	31	2009, 2010, 2014, 2017
	Saison	15	2009, 2010, 2014, 2017
	Verts	10	2009, 2010
Pau	Ouzom	16	2006, 2009, 2010, 2014, 2017
	Pau	30	2006, 2009, 2010, 2014, 2017

Table S 5-2: Confusion matrix showing the probabilities of reattribution for each river or cluster. The certified origin is provided in line while the origin predicted by the discriminant analysis (random forest) is presented in columns. The specificity and the sensitivity of the model are provided in heatbars. Empty boxes represent values inferior to 0.01.



Note: One cluster gathers two rivers from two distinct sub-basins, *i.e.* Laurhibar (Nives) – Lourdios (Oloron). For the purpose of the study, every individual assigned to a Laurhibar-Lourdios origin was considered as from the Oloron sub-basin considering the very low number of mature adults that are observed in the Laurhibar (<https://www.migradour.com/>).

5.10 References Chapter 5

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TAKE-HOME MESSAGES

- Emigrants from co-mingling populations were mainly from hatchery-origins
- A larger biomass-of-release did not (except for smolts) enhance the proportion of reared-origin adults, possibly demonstrating density-dependence effects
- Size-at-release has provided different results, with a “bigger is better” hypothesis
- Stocking programs should consider the portfolio approach to maximize biocomplexity

Future need:

Investigate the role of habitat mosaic (diversity, connectivity) from a management perspective

Future need:

Include the timing-at-release in addition to environmental data such as water flow and temperature



IN THE NEXT CHAPTER

- Since we have shown that (i) dispersal is rather stable between the interconnected populations from the southern Bay of Biscay, and (ii) distinct stocking strategies are not leading to a greater proportion of returning reared-individuals, what can be the factors explaining the positive dynamics observed in the Adour and the Dordogne?
- In Chapter 6, we investigate the diversity of life strategies over a natural gradient of coexisting populations (from highly dependent to fully independent) as a potential answer

6 A TEMPORAL INVESTIGATION OF ATLANTIC SALMON LIFE STRATEGIES IN COEXISTING POPULATIONS

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6.1 Abstract

Spatial synchrony, the phenomenon where populations from distinct geographic areas fluctuate in a coordinated manner, has recently been observed in multiple species and ecosystems, including diadromous fish such as salmon. In the context of climate change, such findings are particularly concerning for salmon as the diversity of intra-specific life histories is critical to face the numerous stressors encountered along the freshwater-estuarine-sea continuum, allowing to maintain viable populations. Therefore, a better understanding, mitigating the drivers of spatial synchrony, especially in the face of global change, is essential for the conservation of salmon species. In this study, we take advantage of a natural gradient of coexisting Atlantic salmon (*Salmo salar*) populations in the southern Bay of Biscay, from highly dependent on stocking programs to completely self-sufficient. More specifically, we investigate the temporal variability of phenological traits in multi-sea winter (MSW) salmon (*i.e.* parr and smolt sizes, river and marine ages) in four sub-populations using nine successive cohorts (2007-2015). Our results demonstrate (i) an ecological bottleneck in smolt size diversity, (ii) a stable or slight but general increase in size-at-outmigration for every location, and (iii) a spatial synchrony in the temporal variability of the relative proportions of return age classes. Particularly, the relative proportion of one river-winter (1RW) individuals in adult returns has increased over the years in every sub-basin, plausibly demonstrating environmental pressure acting synergistically in time and space. Our study reinforces previous research works reporting a large-scale spatial synchrony, and points out a similar ecological response in hatchery and wild fish. From a conservation perspective, this stresses the need to rapidly adapt our management strategies in order to preserve this threatened species.

Keywords: Synchrony, *Salmo salar*, life-history diversity, phenological traits

6.2 Introduction

In scientific literature, intraspecific variation is recognized to be a fundamental characteristic in natural populations to promote resilience in a rapidly changing world (Des Roches et al., 2017). From a long-term perspective, “life-history diversity can both increase production and buffer population fluctuations” (Greene et al., 2010) by spreading risks across multiple individuals and populational tactics (*i.e.* portfolio effect), strengthening the overall stability (Anderson et al., 2015). Among others, Salmonid species are perfect illustrations of the importance of such biocomplexity as wide ranges of life strategies are known to occur in response to environmental variations (or historically at least) for *Salmo salar* (Otero et al., 2014; Armstrong et al., 2018; Erkinaro et al., 2019), *Oncorhynchus tshawytscha* (Sturrock et al., 2020; Sorel et al., 2023; Murdoch et al., 2024), *Oncorhynchus nerka* (Freshwater et al., 2023), *Oncorhynchus kisutch* (Chittenden et al., 2010; James et al., 2023), *Oncorhynchus mykiss* (Westley et al., 2013; Huber et al., 2024), *Salmo trutta* (Mikheev et al., 2021; Adams et al., 2022; Källo et al., 2023) or *Salvelinus alpinus* (Klemetsen et al., 2003). However, in recent years, the same alarming situation has been reported for several diadromous species across the northern hemisphere: the portfolio effect is weakening (Satterthwaite and Carlson, 2015; Sturrock et al., 2019; Huber et al., 2024) and natural populations are expressing greater synchrony (Olmos et al., 2020; Harvey et al., 2022; Freshwater et al., 2023). In their study, Harvey et al. (2020) even showed that Atlantic salmon and Brown trout from the same river respond similarly to environmental cues and initiate their downstream migration in synchrony. Resultingly, various studies have been carried out to disentangle the possible reasons for this threatening, almost uniform report. From the plausible hypotheses advanced, three main factors are highlighted and possibly interconnected: (i) the impacts of climate change and human-induced ecosystem alterations, (ii) the effects of hatchery practices and (iii) what are defined as the carry-over effects. While the adverse consequences of drastic changes in riverine, estuarine, or marine conditions (*e.g.* increased temperature, strong

variations of water flows, habitat fragmentation) on natural population biocomplexity is evident (Otero et al., 2014; Olmos et al., 2020; Sturrock et al., 2020; Legrand et al., 2021; Freshwater et al., 2023), although complex, investigations on the two last hypotheses are scarcer and challenging. Yet, most of the diadromous fish species such as salmon exhibit a metapopulation structure (Schtickzelle and Quinn, 2007) via migratory flows between spatially distinct populations, which are sometimes co-mingled. Therefore, a better understanding of local drivers that may contribute to synchronous response is essential in this very complex mosaic to preserve natural populations.

Rearing programs have been increasingly used, broadly over the past 50 years, to conserve and ideally rebuild weakened populations over the globe. However, numerous undesirable effects associated with stocking practices have been pointed out in the literature (McMillan et al., 2023). Indeed, because hatchery individuals exhibit a lower fitness than their wild counterparts (Araki et al., 2008), the intense release of reared fish (mainly defined to cope with short-term objectives) is presumably jeopardizing the long-term viability of natural populations via a suite of ecological threats, e.g. genetic introgression leading to homogenization, density-dependence mechanisms, competition for habitat and food resources (Horreo et al., 2011; Laffaille, 2011; Milot et al., 2013). For example, an increased synchrony in wild populations (Satterthwaite and Carlson, 2015) and a decreased biocomplexity because of the “replacement” of wild individuals (Johnson et al., 2012; Zaporozhets and Zaporozhets, 2012) have been described in the literature.

In addition to stocking practices, carry-over effects have been suggested as a potential factor that can influence life history diversity. Studies on Atlantic salmon populations from western Europe have notably demonstrated an earlier downstream migration of smolts (Kennedy and Crozier, 2010; Russell et al., 2012; Teichert et al., 2020), as a response to increased water temperatures (Otero et al., 2014). Yet, an anticipated seaward migration can have strong

subsequent consequences such as a mismatch in estuarine and ocean-entry conditions (Satterthwaite et al., 2014) or greater predation risks and a generally lower fitness (Gregory et al., 2019) because of a reduced size-at-migration. In Norway, Alioravainen et al. (2023) showed that freshwater growth of Atlantic salmon has globally decreased in three distinct populations, and the more time the young salmon spent in the river, the less energy they could allocate to growth. Regarding the marine stage, Power et al. (2023) highlighted probable carry-over effects from the first summer of feeding on the second one for multi-sea winter (MSW) individuals, based on stable isotope methods. Additionally, considering the condition of returning mature adults, several studies show a decrease in body size and a delay in upstream migration for potential spawners (Bal et al., 2017; Adams et al., 2022), plausibly demonstrating synchronous responses to large-scale climate-induced change (Olmos et al., 2020). Overall, a large corpus of studies suggests an increased synchrony in natural populations, possibly related to carry-over effects and human-induced disturbances such as stocking practices.

In southern France, Atlantic salmon populations exhibit a metapopulation structure (Fontaine et al. 2024a, submitted to *Fisheries Research*), but every component of this metapopulation displays very distinct dynamics in terms of population size and sustainability (Perrier et al., 2013; André et al., 2021). More particularly, the Gironde watershed hosts two sub-populations, *i.e.* the Dordogne and the Garonne, while approximately 230km south of the Gironde, the Adour watershed carries three sub-populations, *i.e.* Pau, Oloron, and Nives. From a management perspective, every system is fairly different as the Garonne population relies almost exclusively on stocked individuals (~ 90%), the Dordogne and Pau are co-mingled sub-populations in opposite proportions (in the Dordogne, roughly 60% of the population is represented by reared individuals while in the Pau, hatchery fish represent approximately 30% of the sub-population) and the Oloron and Nives are self-sufficient (Fontaine et al. 2024b, to be submitted in *Environmental Management*). Interestingly, in the last decade, while the Dordogne

and Pau sub-populations showed a positive trend in the number of returning adults, the other locations did not exhibit any pattern, with annual returns being rather stable (<http://www.migado.fr/>; <https://www.migradour.com/>). To address the reasons for these positive observations in the Dordogne and Pau, several hypotheses have been tested in previous research including (i) an increase of immigration from adjacent locations and (ii) independent stocking strategies resulting in higher return rates, but none of these initial thoughts were fair candidates to explain such differences. Therefore, in a third hypothesis, higher survival rates associated with distinct life strategies were put forward as a potential factor contributing to increased returns.

Here, the southern Bay of Biscay offers a natural geographical gradient of co-mingled populations (from highly dependent on stocking programs to completely independent) to test the relative importance of life history diversity on returning adults. Specifically, in this research work and based on otolith chemistry, we investigated the temporal variations of phenological traits (*i.e.* size-at-outmigration, river and sea ages) in four locations (*i.e.* Dordogne, Garonne, Pau, and Oloron) to explore the potential carry-over effects as a plausible factor contributing to adult returns.

6.3 Materials and methods

6.3.1 Study system

The Gironde and Adour watersheds are located in the southern Bay of Biscay (Figure 6-1), which includes the west coast of France and the north coast of Spain (Borja et al., 2019). In the Gironde, each of the Garonne and the Dordogne sub-populations heavily rely on rearing programs after the entire collapse of both populations at the end of the 19th century (Vandeputte et al., 2021). Although positive results are observed in the Dordogne compared to the Garonne, both systems need to be highly monitored and sub-populations remain very low ($n = 374 \pm 170$ and $n = 125 \pm 52$ returning adults in the Dordogne and Garonne basins respectively, over the 2010-2018 period, from <http://www.migado.fr/>). Near the Spanish border, the Adour basin gathers very distinct sub-populations in three sub-basins, *i.e.* the Nives, Oloron and Pau (Figure 6-1). Regarding the sustainability, while the Nives and Oloron sub-basins are considered self-sufficient (the releases of stocked individuals have completely stopped since 2004 and 2011, respectively), the Pau sub-basin still benefits from hatchery releases (Picoulet and Marty, 2020). Aside from management strategies, the relative importance of each sub-basin is also entirely different with nearly 70% of the adult salmon entering the Adour estuary migrating to the Oloron sub-basin ($n = 2212 \pm 626$, from 2010 to 2018), 20% to Pau ($n = 590 \pm 340$, from 2010 to 2018), and only 10% to the Nives (no tracking information available) (<https://www.migradour.com/>). Unfortunately, because of a low sample number, the Nives sub-basin could not be integrated in this study. Therefore, taken together, sub-populations from the Gironde (*i.e.* Garonne and the Dordogne) and the Adour (*i.e.* Oloron and Pau) offer a natural gradient in terms of structure (proportion of wild and hatchery fish) and size (number of returning adults) (Figure 6-1).

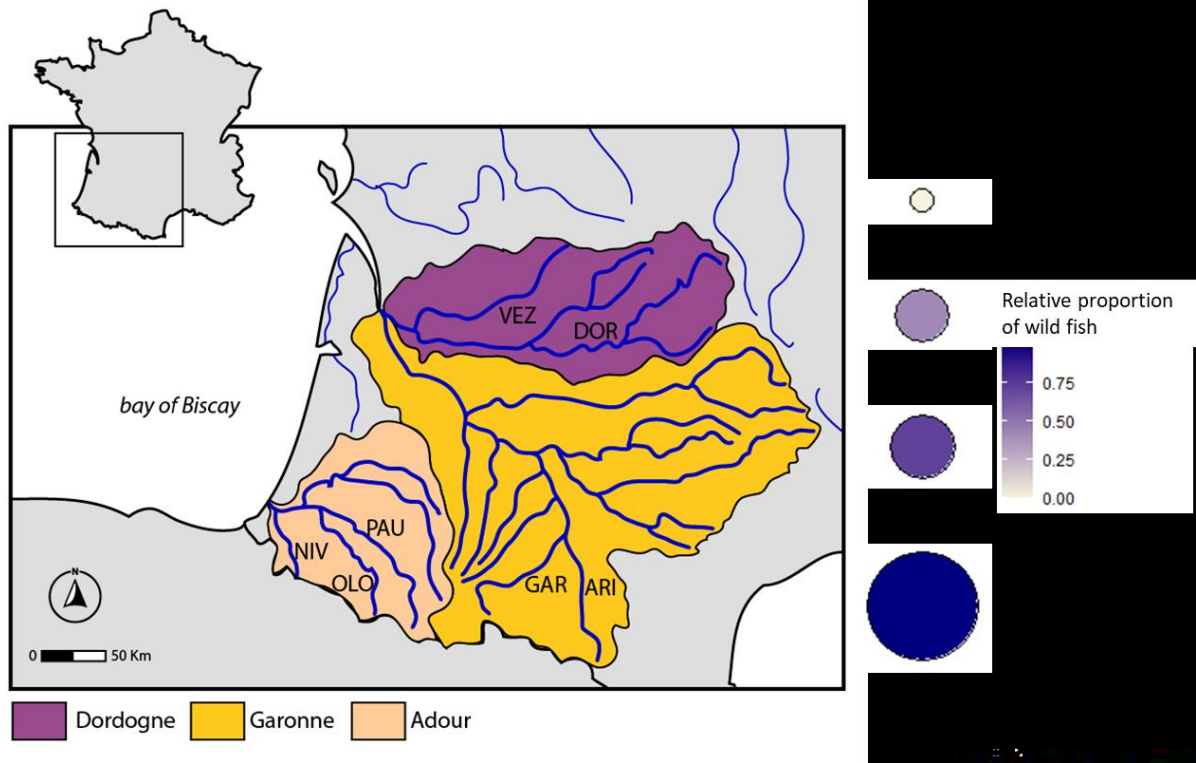


Figure 6-1: Map of the studied system in this research work. On the right, the size of the circles represents the average population size of each sub-basin of interest, as well as the relative proportion of wild fish for every location, between 2010 and 2018. Abbreviations: ARI, Ariège; DOR, Dordogne; GAR, Garonne; NIV, Nives; OLO, Oloron; VEZ, Vézère.

6.3.2 Sampling effort

As previously mentioned, the present study follows two initial research works where the authors examined (i) the inter-annual variability of dispersal in the southern Bay of Biscay (Fontaine et al. 2024a, submitted in *Fisheries research*) and (ii) the potential effects of stocking strategies on adult return rates (Fontaine et al. 2024b, to be submitted in *Environmental Management*). As a result, the current study takes advantage of both investigations in which numerous ecological knowledge have been estimated for every sampled fish including the geographical origin (at different spatial scales, *i.e.* from the watershed to the river), the natal origin (wild vs. hatchery), and the river and sea ages which enabled us to access the cohort. Therefore, here, we have only conserved

a regional origin corresponding to the capture site (the “homers”), we applied a second RF analysis, to estimate the river of origin according to their basin. This second “river-scale” model is identical to the “basin-scale” model, the only difference being the sources (individuals with certified origin at a river scale) and the subsequent predictions.

Natal origins were obtained from Fontaine et al. (2024b, to be submitted in *Environmental Management*). In brief, we performed a naïve univariate functional clustering analysis (*funHDDC* R package, version 2.3.1), using Sr profiles. The methodology is based on an “expectation-maximization” (EM) algorithm (Bouveyron and Jacques, 2011) and allows the clustering of functional data according to their similarities, e.g. minimum or maximum values along the profile or curve amplitudes. Every possible combination of multivariate was also tested, in addition to other univariate possibilities, but the use of Sr profiles provided the best discriminatory performances.

River and marine ages

To estimate the river age of returning adults, we used the method presented in Fontaine et al. (2024c). Shortly, as for the natal assignment, the method is based on an unsupervised univariate functional clustering analysis and we used Zn profiles corresponding to freshwater residency (*i.e.* from the nucleus to the outmigration) to predict the river age. Besides, two distinct methods were used to investigate the marine age. First, when available (50.1% of the total sampling), scale-reading was performed by MIGRADOURE employees to provide a sea age (Baglinière et al., 1985). When scalimetry was not possible, we used the mass-to-age or fork length-to-age relationships as a secondary approach. To ensure that the two methods provided reliable results, we compared the estimated sea age for all individuals who had every set of information, and found a correspondence of 94.9%.

Estimations of parr and smolt sizes

The parr (or the juvenile size at the first river winter) and smolt (or the size-at-outmigration) sizes were estimated using the relationship between the size of juveniles (fork length) and the size of the otolith radius (OR). The OR of juveniles was measured on the ventral-dorsal axis using a Zeiss Primo Star microscope and Moticam 3.0. For the back-calculation of the parr size, we determined the otolith distance between the nucleus and the first sharp decrease in Zn/Ca ratio, as a marker of the first winter season (Fontaine et al., 2024c). Regarding the size-at-outmigration, we determined the otolith distance between the nucleus and the inflection point where a concurrent sharp increase of Sr/Ca and strong decrease of Ba/Ca ratios occurs, corresponding to ocean-entry (Walther and Limburg, 2012). To back-calculate the parr and smolt sizes, the following equation was used:

$$y = 0.2453x - 6.113$$

Relationships between the size of juvenile individual (fork length) and the ventral-dorsal OR is shown in Figure S 6-1.

6.3.5 Statistical investigations

As previously mentioned, our dataset is mostly composed of MSW individuals. Therefore, we have focused our investigations on the following age classes as they represent, besides one-sea winter (1SW) fish, the main age classes found in Atlantic salmon populations from the Bay of Biscay (André et al., 2021; <https://professionnels.ofb.fr/>): one- and two-river winter (1RW and 2RW) for the freshwater stage, two- and three-sea winter (2SW and 3SW) for the marine stage, and 3- and 4-years (3Y and 4Y) individuals for the total age. First, to visualize the relative importance of both river ages in the variation of size-at-emigration, we performed linear models (lm) for every sub-basin (*stats* R package, version 4.2.1). Then, we conducted Wilcoxon-Mann-

Whitney rank tests (*stats* R package, version 4.2.1) to assess the difference of size-at-outmigration between 1RW and 2RW individuals. Because the number of 1RW and 2RW individuals was different in every sub-population, we used dynamic time warping (DTW) algorithms (*dtw* R package, version 1.23-1) to capture the degree of covariation and correlation between the proportion of 1RW and 2RW fish. Briefly, DTW involves computing a warping path that minimizes the cumulative distance between the aligned points of the two series (here 1RW and 2RW), thus allowing for a meaningful comparison despite their differing lengths (*i.e.* number of observations). Finally, we calculated synchrony indices (expressed between 0, for asynchrony, and 1, for synchrony) to estimate the degree of population synchrony, using the following formula:

$$\varphi_x = \frac{\sigma_x^2}{(\sum_i \sigma_{x_i})^2}$$

where φ_x is the synchrony index, σ_x^2 the detrended network variance and σ_{x_i} the population detrended standard deviation (Lamarins et al., 2022). Every statistical analysis was performed using the R software (version 4.2.1).

6.4 Results

6.4.1 Variability in size-at-outmigration

The spatio-temporal distribution of the estimated size-at-outmigration for returning mature adults in the Dordogne, Garonne, Oloron, and Pau sub-basins is shown in Figure 6-2. Concerning the diversity (*i.e.* range) of smolt sizes from cohort 2007 to cohort 2015, our results tend to highlight a non-negligible ecological bottleneck over the years. During the first cohorts of interest in this study (2007-2009), we observed a diversity of sea departure sizes up to around 225mm, with a substantial number of individuals larger than 180mm. Although the majority of individuals emigrate at a size of 150mm approximately, the proportion of individuals entering the sea at a larger size decreases over time, the right tail of the distribution becoming less pronounced from 2010 to 2015. Similarly, in the three last cohorts (2013-2015), the left tail of the distribution narrows towards the center of the distribution, indicating a low representation of smaller (<125mm) smolts among returning adults from these cohorts.

The relative importance of both river ages (1RW and 2RW) in the variation of size-at-emigration is presented in Figure 6-3 (see Figure S 6-2 for the variation of parr size). First of all, in every location except the Garonne, individuals that have spent two successive years in freshwater before starting their outmigration are significantly larger than 1RW individuals (Oloron, $p < 0.001$; Pau, $p < 0.001$; and Dordogne, $p < 0.05$). Globally, although a slight increase in smolt size can be observed over the cohorts, results from the lm are non significant in every sub-basin. Finally, there are no apparent differences in the variation of size-at-outmigration between 1RW and 2RW salmon, since every alignments performed with DTW algorithms provided estimates of correlation ranging from 0.62 to 0.78 (see Figure S 6-3). As previously hypothesized in Figure 6-2, our results suggest that the average smolt size is comparable in every location.

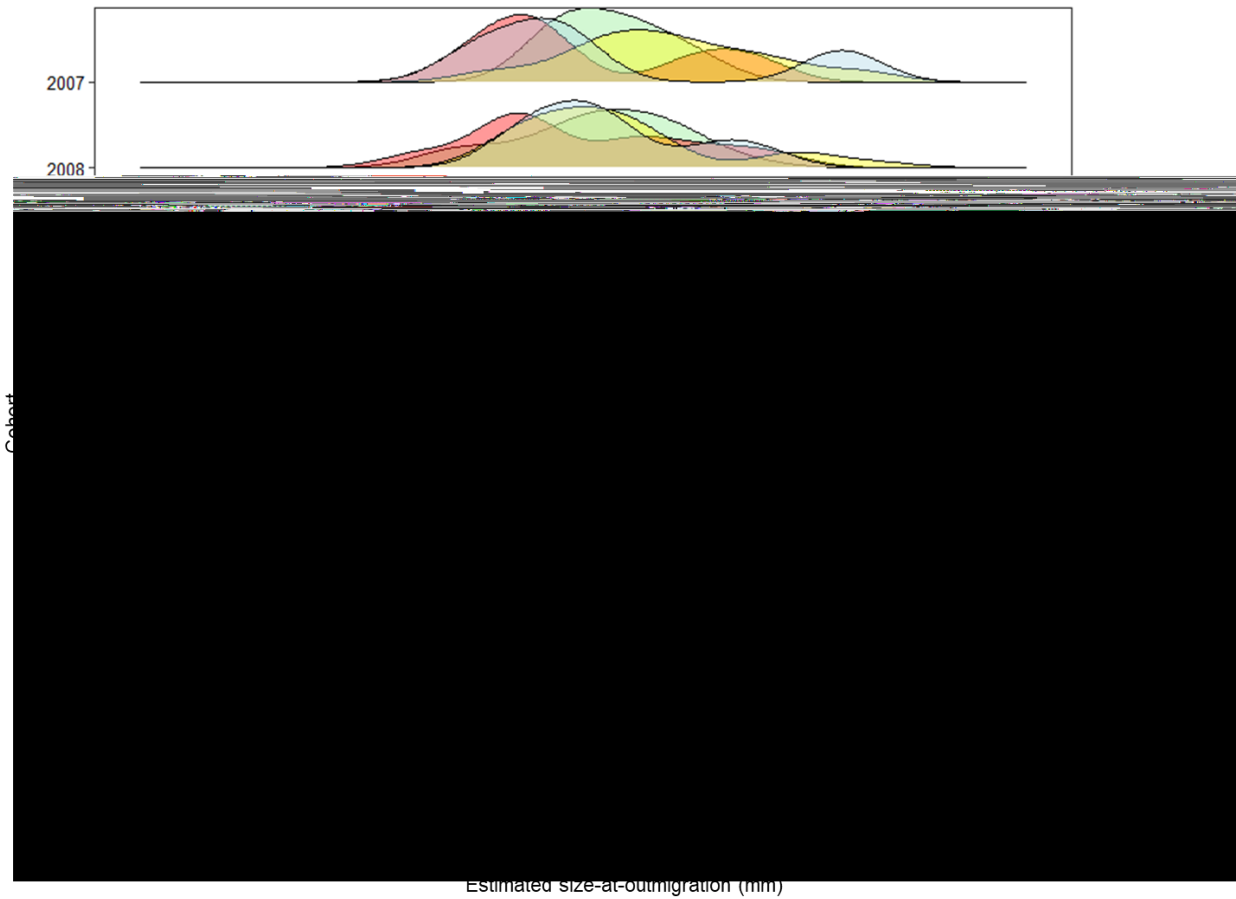


Figure 6-2: Density distribution of the estimated sizes-at-outmigration in the Dordogne, Garonne, Oloron and Pau sub-basins, from the cohort 2007 to the cohort 2015. Results could not be provided for the Garonne in 2012, 2014 and 2015 and the Dordogne in 2014 and 2015 because of the absence of data or a low sample size to estimate densities.

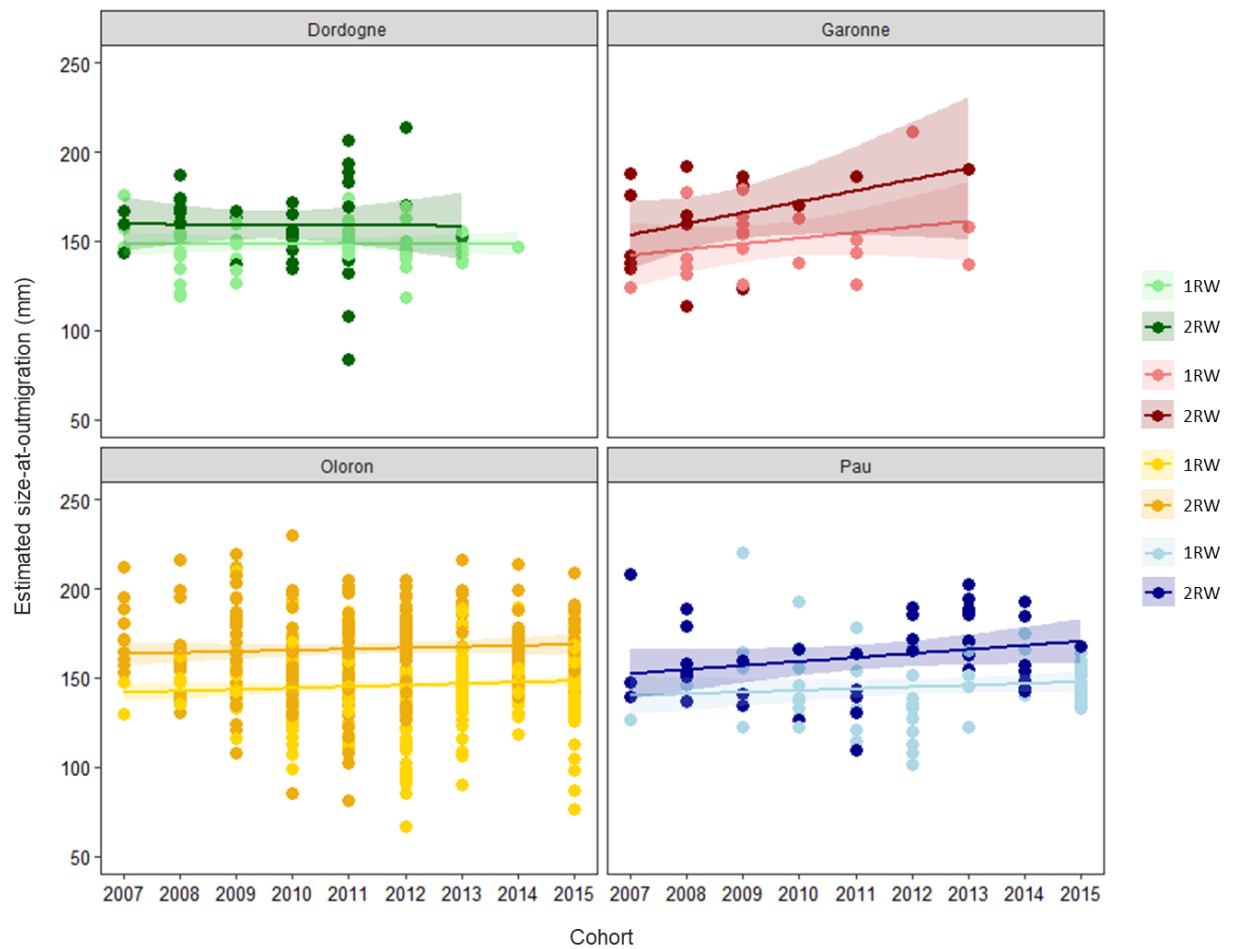


Figure 6-3: Linear regressions representing the distribution of the estimated size-at-outmigration for each sub-basin (Dordogne, Garonne, Oloron and Pau) according to their river age (1RW or 2RW), from the cohort 2007 to the cohort 2015. The confidence interval (95%) is denoted by a shaded area for every lm performed. No results could be provided for the Garonne in 2014 and 2015 and in the Dordogne in 2015.

6.4.2 Variability in return age classes

The temporal variation of the relative proportions of 1RW, 2SW and 3Y in returning adults from the Garonne, Dordogne, Oloron, and Pau sub-basins can be found in Figure 6-4. Our results exhibit a moderate spatial synchrony ($\phi = 0.21$, $\phi = 0.21$ and $\phi = 0.23$ for 1RW, 2SW and 3Y age classes respectively) for every location from the cohort 2007 to the cohort 2015. Regarding the

freshwater stage, a global increase of the proportion of 1RW (at the cost of 2RW proportions) individuals can be observed in returning salmon. Although some variations are discernible (e.g. cohort 2010 in the Dordogne, cohorts 2013 and 2014 in Pau), the proportions of 1RW fish were always between 25 and 50% in the first studied cohorts, reaching proportions of 80 to 90% for every location (except in 2013 for the Garonne) in the latest cohorts studied. From the marine stage, the likelihood of a spatial synchrony for an increase of 2SW returns is visually less obvious, as the proportions of this age class are naturally very high (> 0.75) in each of the sub-basins for MSW fish. Nevertheless, an increase in this proportion (at the cost of 3SW and 4SW individuals) in the Dordogne and Oloron sub-basins can be observed, while the temporal pattern is fairly stable in the Pau sub-basin, and even slightly decreasing in the Garonne sub-basin. Combined together, the obvious increase in the proportion of 3Y mature salmon can be detected in every sub-basin (at the cost of 4Y and 5Y fish), demonstrating a plausible spatial synchrony in the timing of return. This augmentation is likely resulting from the global increase in the proportion of 1RW, as both curves are very similar.

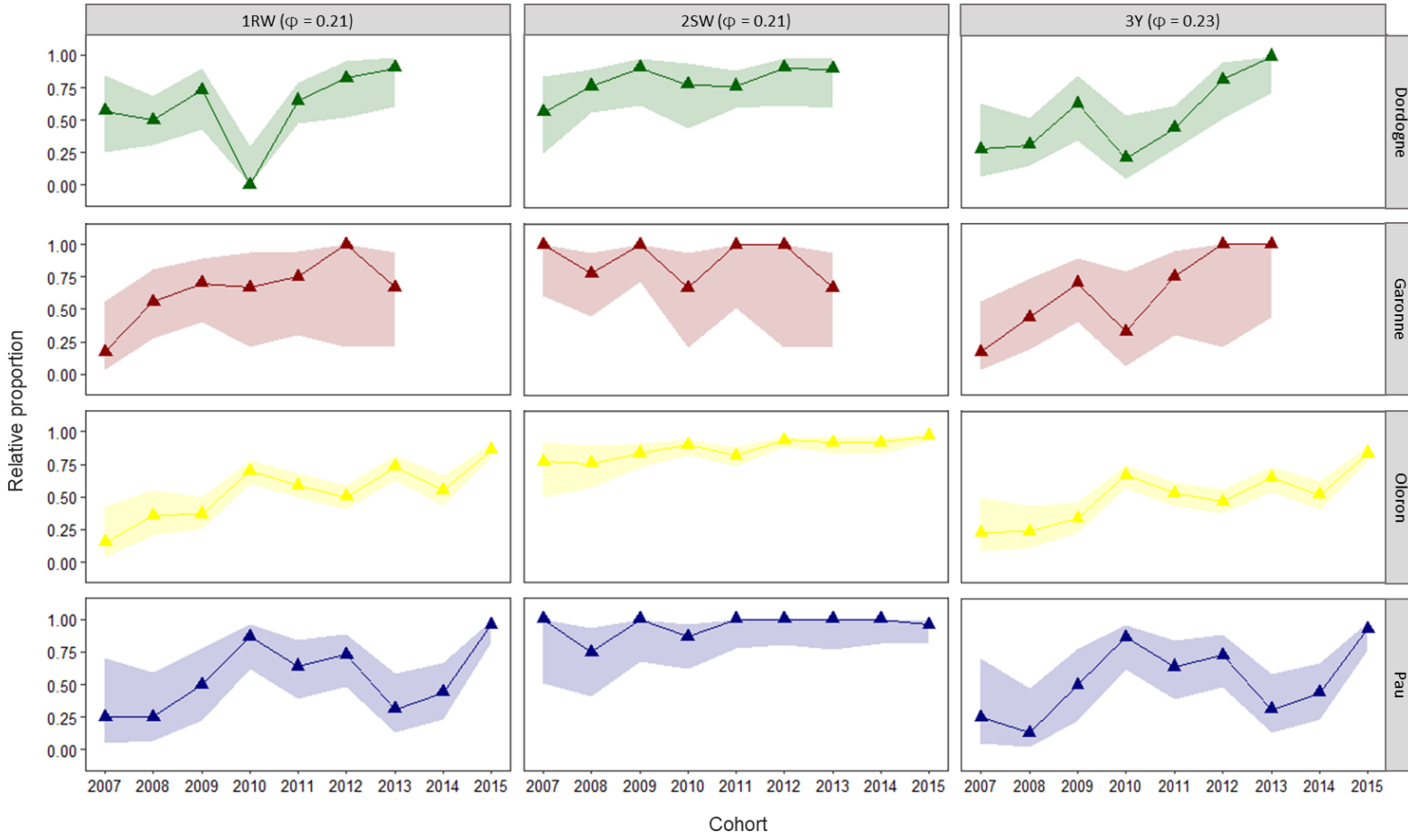


Figure 6-4: Panel representing the relative proportions of one river-winter (1RW), two sea-winter (2SW) and three years old (3Y) individuals in every sub-basin of interest, from the cohort 2007 to the cohort 2015. To accurately represent our data, a 95% confidence interval using the Wilson score interval method is employed to visualize the error associated with the calculations of every relative proportion. In cohorts 2014 and 2015, no results could be provided for the Garonne and Dordogne sub-basins. The synchrony index (ϕ) is provided under brackets.

6.5 Discussion

In a global change context, where the frequency and intensity of extreme climatic events (*e.g.* elevated temperatures, flash floods, and droughts) are constantly increasing, the biocomplexity of natural populations is critical to maintain an overall spatio-temporal stability (Anderson et al., 2015). Regarding diadromous salmonid species, numerous studies have recently demonstrated a sharp decline in the diversity of life histories, in addition to an increase in spatial synchrony, greatly weakening the portfolio effect for these populations (Satterthwaite and Carlson, 2015; Olmos et al., 2020; Huber et al., 2024). The reasons for the reduction in biocomplexity are diverse and most often interconnected. For example, carry-over effects from the juvenile stage may result from climate-induced changes (*e.g.* long periods of warm freshwater temperature) and/or human-induced alterations (*e.g.* direct and indirect effects of stocking programs). Although disentangling the various components that may contribute to the decline in life history diversity and the increased spatial synchrony is highly complex, a better understanding of the factors involved is critical to preserve a viable population, capable of facing the numerous stressors throughout their life cycle (Thorstad et al., 2021). In the present study, we investigated the possible temporal variation of Atlantic salmon individuals' tactics, *i.e.* phenological traits, in four locations from the southern Bay of Biscay representing distinct dynamics in terms of size and sustainability.

6.5.1 Variability in size-at-outmigration

Our results exhibited a substantial ecological bottleneck over the years (cohorts) regarding the size-at-outmigration of mature adults that have successfully returned to their basin of origin in the four sites, whatever the extent of stocking practices. More particularly, a marked reduction in the proportion of larger individuals entering the open ocean is perceptible. Unfortunately, such observations were expected as a large corpus of studies has pointed out the earlier timing of

Atlantic salmon smolt emigration for many populations across the northern hemisphere (Kennedy and Crozier, 2010; Russell et al., 2012; Otero et al., 2014; Teichert et al., 2020). As smolts emigrate earlier, this is likely to generally reduce their size-at-outmigration because of a shorter period of growth in freshwater, which is undesirable considering the extent of literature demonstrating that “the bigger is better” regarding smolt-to-adult survival (Armstrong et al., 2018; Gregory et al., 2019; Rodger et al., 2024). Yet, in our study, although the portfolio of smolt sizes appeared to decrease over the cohorts, which likely reflects an earlier emigration timing, the estimated size-at-outmigration has remained stable in every sub-basin of interest. Potentially, this may result from climate change, and more particularly warming riverine temperatures as it has been shown that elevated (but tolerable) temperatures will increase juvenile growth, especially in spring (Russell et al., 2012; Thorstad et al., 2021). Therefore, the fact that we observed a global decrease in smolt size diversity concurrently with a stable mean size of outmigration in returning adults may indicate two possibilities. First, our results could suggest a selective mortality against larger smolts, which would highly contrast with the current scientific literature considering that smolt body length (and other indicators of good condition) is a fair predictor of adult Atlantic salmon survival (Gregory et al., 2019; Simmons et al., 2022). However, “strong and consistent selection along the migratory corridor, acting against small, early dispersing fry and large, late migrating smolts” have been demonstrated for Chinook salmon in a study by Sturrock et al. (2020). The authors hypothesized that time-selective mortality could influence different phenotypes' survival, with late emigrants being more affected by warm summer temperatures (in addition to other possible stressors such as parasite load or a longer exposition to contaminants). A similar scenario could be presumed in our study system as the contribution of both small and large individuals decreased over the years. Second, our observations may reflect a spatial synchrony in the size-at-outmigration, therefore plausibly in the timing at sea entrance, resulting from large-scale climate-induced changes. Indeed, several studies have shown patterns of spatial

synchrony on medium and large spatial scales, reflecting a common “phenological shift” to large-scale climatic phenomena (Otero et al., 2014; Bal et al., 2017; Olmos et al., 2020). Finally, the fact that the variation in smolt size was similar in four contrasted sub-populations in terms of hatchery supplementation probably discredits a third hypothesis, namely that earlier timing of outmigration could result from undesirable density-dependence effect due to stocking programs (Satterthwaite and Carlson, 2015; Sorel et al., 2023).

In the Adour watershed, thanks to monitoring programs organized by the MIGRADOIR association, a database including parr 0⁺ measurements (usually from September campaigns) on all rivers frequented by Atlantic salmon was available. Therefore, in addition to our estimations of parr sizes (which likely correspond to the winter rather than the fall period), we had the opportunity to compare the spatial (*i.e.* inter-river) variability in juvenile size diversity between young-of-the-year individuals (based on monitoring programs) and the diversity of estimated parr size in returning adults (see Figure 6-5). Interestingly, while we observed marked spatial differences in sizes between young-of-the-year individuals, the signal is completely homogeneous for the parr stage in returning adults. This suggests that, although distinct rivers produce diverse individual tactics in response to specific ecosystem characteristics (*e.g.* water temperature and flow, habitat diversity), a size-based selection appears common to all systems. As previously mentioned, it is highly difficult to disentangle every possible factor acting on juvenile-to-adult survival (Thorstad et al., 2021; Bull et al., 2022; Crozier and Siegel, 2023). Yet, as we demonstrate a similar ecological response in adjacent but distinct environments, this strongly suggests that common environmental pressures, acting synchronously, are exerting themselves on Atlantic salmon populations.

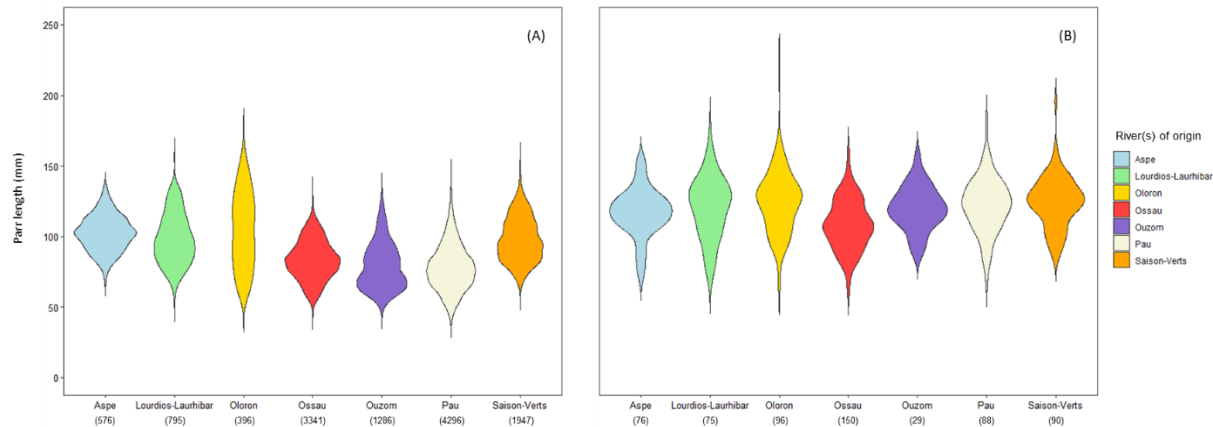


Figure 6-5: Distribution of parr sizes (A) measured during monitoring programs and (B) estimated from Zn/Ca otolith profiles in returning adults, from cohorts 2007 to 2015. A direct comparison between the two sizes is not the aim of this figure, since annual monitoring generally occurs in September, whereas our estimations using the variations of Zn/Ca ratio in otolith likely reflect the winter period, resulting in a time lag of a few months between the two measurements. The sample number available from each river of study is indicated in brackets.

6.5.2 Variability in return age classes

Our study demonstrates a substantial temporal variation in the proportion of return age classes. Specifically, a global increase of 1RW individuals can be observed in every sub-basin of interest, which corroborates previous studies highlighting an overall decrease of Atlantic salmon smolt age on both sides of the Atlantic (Russell et al., 2012 and references therein). As this general increase is observed in all four locations, it again suggests a large-scale response to a common environmental pressure, likely from climate-induced change (Otero et al., 2014). These results also strengthen the ecological bottleneck identified in the previous section, as a strong diminution in 2RW salmon will necessarily be reflected in a relative diminution of larger smolts in returning mature adults. Nevertheless, our study strengthens the importance of life history diversity under varying environmental conditions (Greene et al., 2010; Schindler et al., 2010; Anderson et al., 2015), as we found a moderate synchrony despite the similar, overall pattern. This is likely due to

local response, in the face of spatially restricted environmental stressors (such as flash floods), which again, demonstrate the value of diverse portfolios (Sturrock et al., 2015).

Similarly, our study also indicates a slight increase in the relative proportion of 2SW fish, except for the Garonne sub-basin. Here again, our results mirror previous studies where the authors indicated a large-scale synchrony resulting from a common change in marine conditions (Bal et al., 2017; Olmos et al., 2020; Tréhin et al., 2023). In scientific literature, the general increase in sea mortality is supposed to be one of the main factors explaining the overall worldwide stock decline of Atlantic salmon (Chaput, 2012). However, what causes this increased mortality is complex, as we all face the survivor bias. Considering the global increase in the relative proportion of 1RW individuals across all sub-basins, and the well-established importance of smolt and post-smolt stages in marine survival (Kennedy and Crozier, 2010; Friedland et al., 2017; Chaput et al., 2019), carry-over effects from the freshwater stage are likely to play a key role in subsequent marine survival. From the possible hypotheses, a large-scale effect of climate-induced change is very plausible, as pointed out by numerous studies (Russell et al., 2012; Otero et al., 2014). In their research work, Olmos et al. (2020) suggested that “antagonistic effects of direct and indirect mechanisms may also act in synergy”. For example, if global warming is leading to a faster growth rate and subsequent earlier emigration, mismatch conditions can occur at sea entrance (Wilson et al., 2023). Synergistically, as warmer conditions may imply higher metabolic rate but also higher energy demands, a decline in growth, which has been documented in up-migrating spawners (Bal et al., 2017; Armstrong et al., 2018), can result from an unbalanced energy demand/energy supply ratio. Such inferences are impossible to explore in this study, but our results provide further evidence of spatial synchrony in distinct Atlantic salmon populations, disregarding their reliance on stocking programs.

6.5.3 Limits and perspectives

A recent corpus of studies demonstrates that, just as the “ecological portfolio effect” (*i.e.* the intra-specific diversity in phenological traits) is critical for salmon species, it has its counterpart in habitat diversity and connectivity (Coleman et al., 2022; Cordoleani et al., 2024; Goertler et al., 2024; Rodger et al., 2024). An increased mosaic of habitats is likely to provide complex and various ecosystems, resulting in a greater variability of individual tactics. In our study system, substantial restoration programs are ongoing to enhance habitat connectivity and diversity, however, it was impossible to consider this factor at the time of the study. Therefore, future research could assess the direct and/or indirect effects associated with ecological continuity work and accessible ecosystems, as it may enhance intra-specific diversity. Another limitation of this study lies in the study design itself, as only a couple of 1SW individuals have been sampled and only a few samples were available for some sites and cohorts (Table 6-1). Since fishing is mainly warranted in the period of 1SW salmon upstream migration, we mostly collected MSW individuals, making it impossible to depict a spatio-temporal variation in 1SW return rates. Finally, we could not investigate the variability in the downstream and upstream migration timing. Yet, it would have provided valuable information into the spatial diversity (or not) of phenological traits as individual's length and age are not necessarily correlated to migration timing, depending on environmental conditions. Further efforts could address this knowledge gap by combining otolith chemistry with additional methods such as tagging or telemetry to provide accurate data on migration timing.

6.6 Acknowledgements

The authors are very grateful to the founders of this study: the regional water agency (*Agence de l'Eau Adour-Garonne*), the regional administration (*Région Nouvelle-Aquitaine*), the *Office français de la biodiversité* (OFB), the North Atlantic Salmon Conservation Organization (NASCO) and the *Centre National de la Recherche Scientifique* (CNRS). We would like to thank all the collaborators that have helped in otolith collection: MIGRADOUR, *Fédérations de pêche* 64 and 65, Barthouil and Jean-Marc Casteigt companies, Patrick Balesta, MIGADO, and recreational anglers. Finally, we thank Jordan Lacoste, Christophe Pécheyran, Fanny Claverie and Gaëlle Barbotin for their valuable support in the preparation and/or the analyses of otoliths.

6.7 Supplementary figures

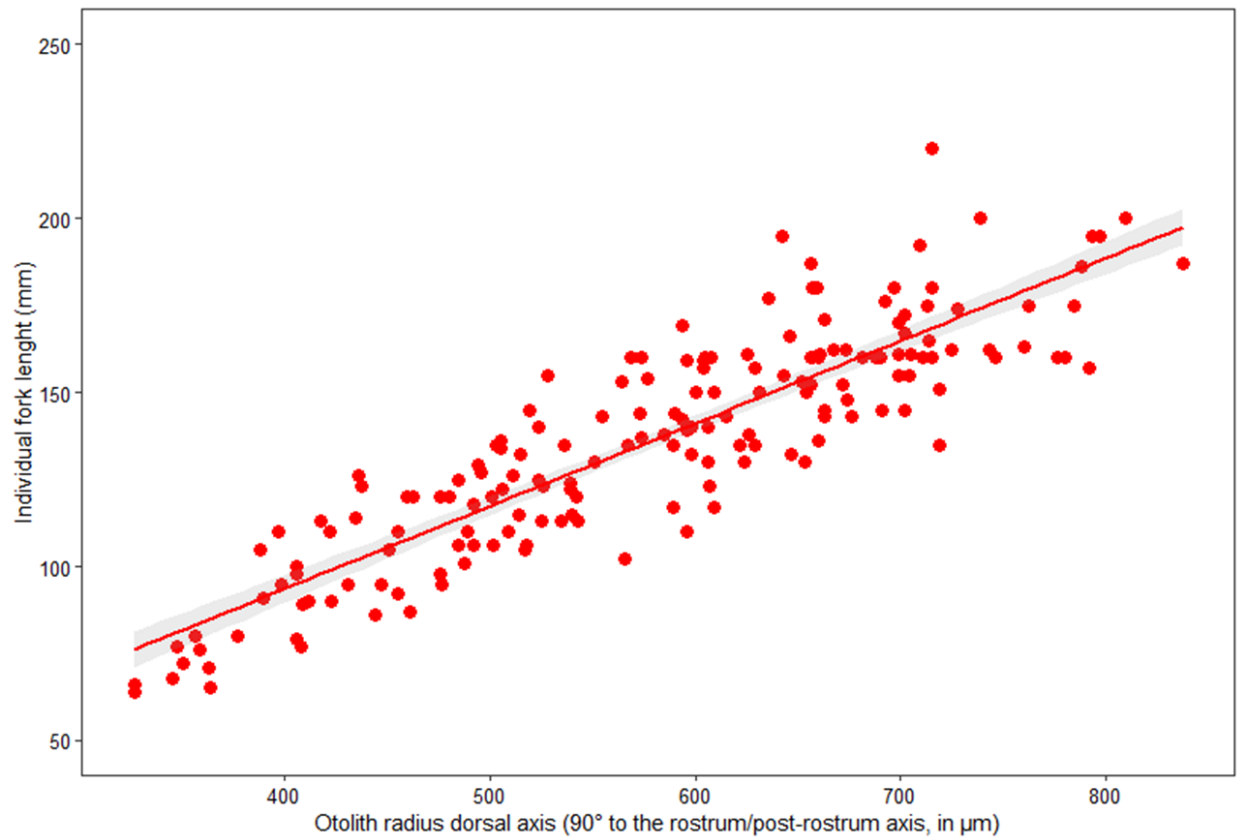


Figure S 6-1: Relationship between the individual length (fork length) and the otolith radius in the ventral-dorsal axis. The confidence interval (95%) is displayed in shaded area

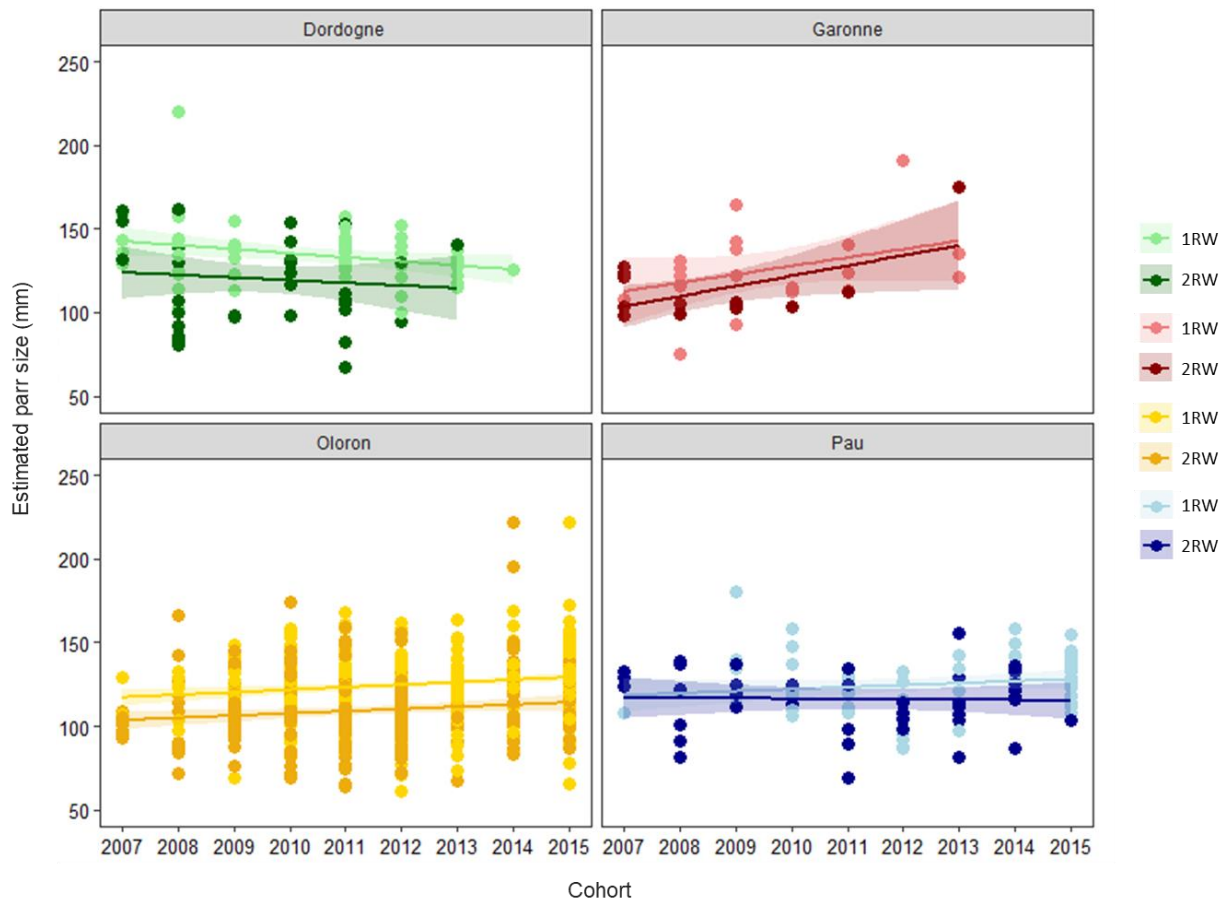


Figure S 6-2: Linear regressions representing the distribution of the estimated parr sizes (young-of-the-year) for each sub-basin (Dordogne, Garonne, Oloron and Pau) according to their river age (1RW or 2RW), from the cohort 2007 to the cohort 2015. The confidence interval (95%) is denoted by a shaded area for every lm performed. No results could be provided for the Garonne in 2014 and 2015 and in the Dordogne in 2015.

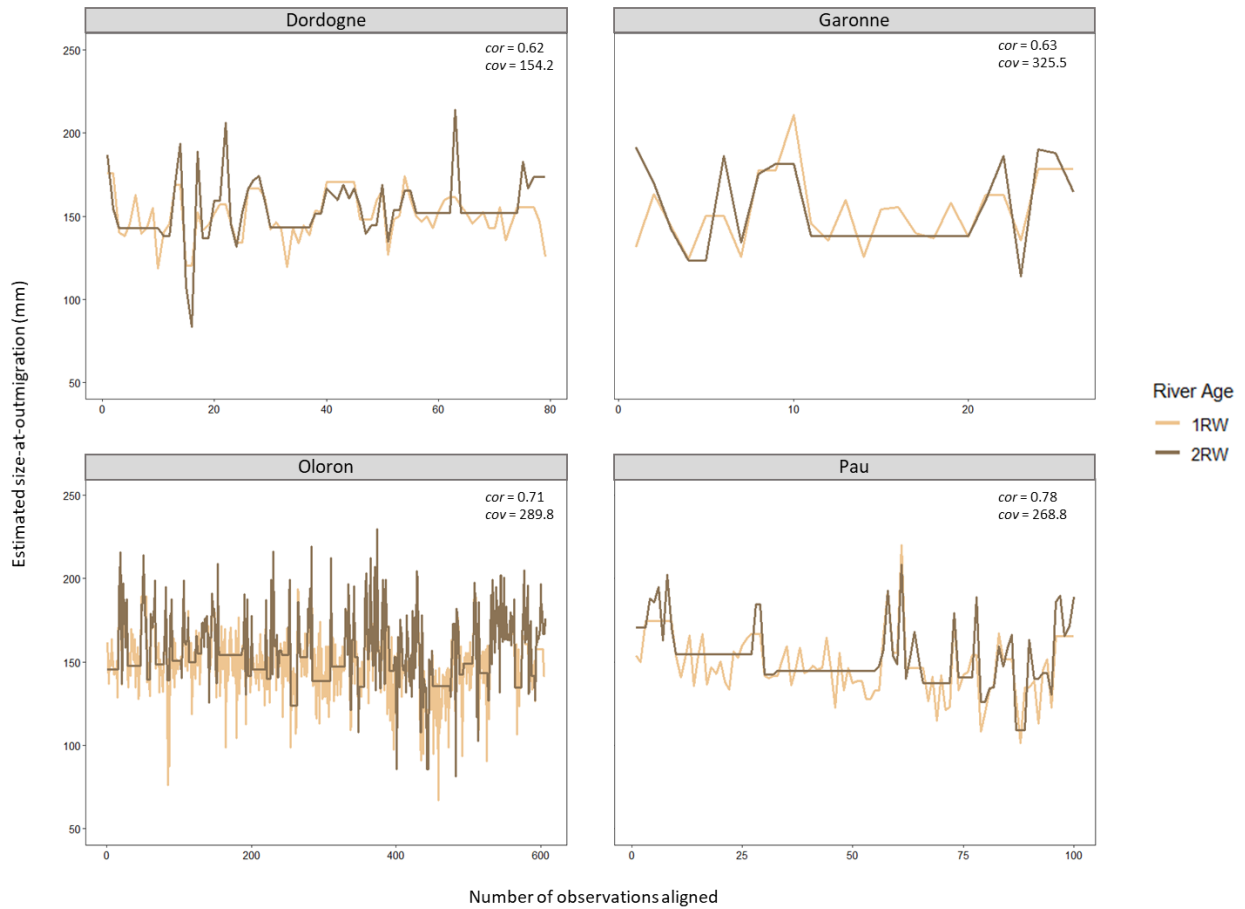


Figure S 6-3: Illustrations of the application of Dynamic Time Warping (DTW) algorithms to align 1RW and 2RW observations in the four sub-basins of interest. The estimated correlation (*cor*) and covariation (*cov*) between both time-series are also provided.

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7 GENERAL DISCUSSION AND CONCLUSION

The main objective of this thesis was to better understand the presupposed metapopulation structure of Atlantic salmon from southern France, and to provide insights into the variability, both in space and time, in dispersal, the effects of stocking programs, and life strategies. More specifically, the thesis aimed at (i) quantifying the inter-annual variation of dispersal and the level of connectivity between southern populations from the Bay of Biscay (see Chapter 3), (ii) investigating the effects of stocking strategies on the metapopulation structure and the adult return rates (see Chapter 5), and (iii) examining the role of spatio-temporal variability in life strategies as potential key drivers of adult returns (see Chapter 6). To address these knowledge gaps, we used the various properties of otolith chemistry, which implies an asset of diverse methodological, analytical, and statistical tools (see Chapters 2 and 4). In the following, I will first discuss the main findings of my research work and their implications in light of the current knowledge and overall status of the Atlantic salmon. Then, I will consider the benefits and the limits of otolith chemistry to investigate the aforementioned thesis objectives, before introducing the perspectives and probable future research needs resulting from this work as a conclusion.

7.1 Thesis results and their implications

A schematic representation of the main results from my thesis is presented in Figure 7-1. First of all, in Chapter 3, I clearly highlight a metapopulation structure in the southern Bay of Biscay, with stable (10-years period) dispersal patterns between spatially distinct populations (responding to knowledge gap 2). More particularly, the Adour population may play a determinant role in the maintenance of the system as a whole, since we demonstrated an asymmetric dispersal (which must be considered relative to the population size) between the Garonne, the Dordogne, the Adour, and the Nivelle. This observation is fundamental regarding the regional management that

has been ongoing for many years now (André et al., 2021). As explained in Lamarins (2022), ignoring the movements of individuals between interconnected populations (*i.e.* connectivity) might hamper the “stability, persistence, and adaptive response of local populations of Atlantic salmon to perturbations and exploitation”. Yet, the observed biocomplexity is rarely, if ever, considered from a management perspective (Chapter 5) although migratory flows could buffer against environmental stochastic events, potentially leading to demographic and/or genetic rescue effects (Lamarins and Buoro, 2024). In our study system, Chapter 3 suggests a key role of the Adour population, acting both as a source and a sink, for proximate, small, and heavily supplemented populations (see Chapter 5). Therefore, any actions (such as professional fisheries of *Salmo salar* in the Adour) on the donor population could indirectly, negatively affect adjacent populations.

Combining results from Chapters 3 and 5, stocking actions may have significant impacts on the metapopulation structure, as the dispersal rate was found to be substantially higher in stocked, coexisting populations. Although managers and policymakers need to cope with short-term objectives/imperatives (often accompanied by a target number of individuals produced and released), results from Chapter 5 exhibited an asymptotic relationship between the biomass of stocked-fish released and the proportion of hatchery-origin returning mature adults (responding to knowledge gap 3). Therefore, and in line with McMillan et al. (2023), I argue that management strategies should consider (or put forward) the ecological characteristics (*e.g.* carrying capacity of the supplemented population, habitat functionality, and productivity) and promote diversity of the managed population from a long-term, conservation perspective. In such a position, the portfolio approach (encouraging the importance of habitat mosaic and connectivity) should be favored according to the outputs from this thesis and the massive corpus of scientific literature guiding in this direction (Greene et al., 2010; Anderson et al., 2015; Satterthwaite and Carlson, 2015; Schindler et al., 2015; Des Roches et al., 2017; Sturrock et al., 2019).

In the last chapter (Chapter 6), we demonstrated a net spatial autocorrelation between the Garonne, the Dordogne, Pau, and Oloron sub-populations. More particularly, a clear spatial synchrony (*i.e.* a “correlated temporal fluctuations among populations” (Walter et al., 2017)) occurred in the proportion of 1RW individuals returning as mature adults, in addition to an apparent, but less obvious, spatial synchrony in the proportion of 2SW adults (responding to knowledge gap 4). Spatial synchrony may result from one or more factors that can act independently, successively, or synergistically along the migration routes including (i) spatially correlated environmental fluctuation (Desharnais et al., 2018) also known as the Moran effect (Moran, 1953), (ii) migratory flows among locations (Desharnais et al., 2018; Bouchard et al., 2022), and (iii) synchronized density-dependent mechanisms (Walter et al., 2017; Bouchard et al., 2022). In the literature and regarding salmon species, most of the authors agree that in freshwater (or the juvenile stage), spatial synchrony probably arises from shared environmental variation across distinct habitats, *i.e.* Moran effect (Russell et al., 2012; Otero et al., 2014; Bouchard et al., 2022). In marine waters, while similar conclusions were generally advanced (Bal et al., 2017; Olmos et al., 2019, 2020), recent studies show more contrasted results (Tirronen et al., 2022; Imlay et al., 2024). However, caution must be exercised when interpreting the results as the studies may discuss distinct issues from the same environment, *e.g.* return rates, mortality by age group, body conditions, and timing of return.

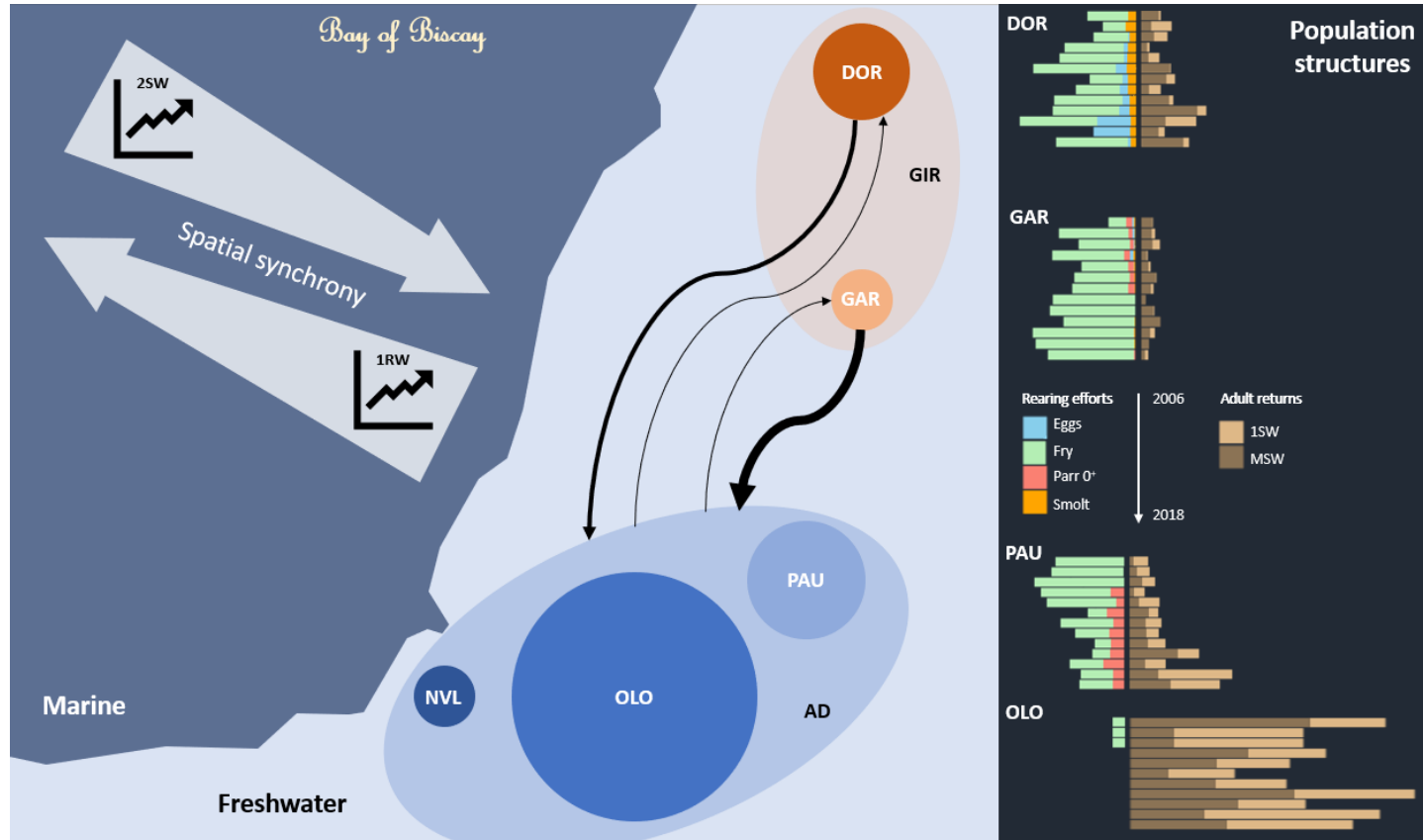


Figure 7-1: A schematic representation of the main results provided in this thesis. The black arrows represent migratory flows between the populations under study, and the intensity of exchanges (relative to the size of each population) is indicated by the thickness of the line. In the marine part (on the left), a common pattern, represented by two thick grey arrows, is illustrated for the synchrony observed in the phenological characteristics of returning individuals in the Garonne, the Dordogne, Pau, and Oloron. The right-hand side of the graph shows the effort of stocking programs and the number of returning adults for each sub-basin between 2006 and 2018 (or 2008-2018 for Oloron). No further results could be provided for the Nivelle because of a low sample size. Abbreviations: AD, Adour; DOR, Dordogne; GAR, Garonne; GIR, Gironde; NVL, Nivelle; OLO, Oloron.

Combined together, results from Chapters 3 to 6 lead to several questions, which are discussed in the following. Firstly, the spatio-temporal stability observed in migratory flows may be, as aforementioned, an essential vector for maintaining a healthy metapopulation structure (Anderson et al., 2015; Schindler et al., 2015). Nevertheless, in a metapopulation composed of homogeneous local populations (expressing similar phenological traits), the dispersal effects of local stabilization and spatial autocorrelation may cancel each other out (Wang et al., 2015). Here, we described the global estimate of immigration and emigration (to an extent) rates (Chapter 3), without knowing the proportion of effective dispersal. Therefore, disentangling the relative importance of population connectivity and/or a possible Moran effect to explain the observed spatial synchrony (Chapter 6) is deeply complex. For instance, coupling our observations with genetics would be highly valuable to investigate the extent to which, local populations from the metapopulation benefit (in term of reproduction, leading to self-sufficient population) or not from stable exchanges of individuals. For example, approaches combining demographic and genetic characteristics of Atlantic salmon, *i.e.* demogenetic models, have been developed to examine how environmental stressors may influence the evolutionary demography (Piou and Prévost, 2012). Additionally, environmental data (*e.g.* variations in water temperature and flow, habitat functionality) would be strongly desirable to test the effects of synchronized environmental fluctuations on the metapopulation dynamic, as performed in recent studies (Bjerck et al., 2021; Bouchard et al., 2022). What is the role of stocking programs in all this? In my thesis, we highlighted that most of the salmon emigrating from coexisting populations were hatchery-origin individuals. Therefore, rearing programs may strengthen the effect of dispersal, whether it is beneficial (*i.e.* stabilizing) or controversial (*i.e.* synchronizing), although the beneficial aspect is debatable as genetic hybridization between wild and hatchery fish induces local domestication and lower fitness for the next generations (Araki et al., 2008), the positive aspect of hatchery dispersal mostly being associated with the colonization of new or restored habitats (Willmes et

al., 2021). Considering results from Chapter 6, stocking programs do not appear to strongly affect populational phenological traits under study (*i.e.* age and size-at-outmigration, marine age), as every sub-population (from highly dependent on hatchery-fish to completely self-sufficient) displayed synchronous responses, which corroborates previous research (Teichert et al., 2020). However, synchronized density-dependent mechanisms associated with the biomass of hatchery releases could be further studied as one potential factor (probably among others) leading to greater synchrony.

Therefore, my thesis provided valuable information into the dynamic of the Atlantic salmon metapopulation from the Bay of Biscay. As in most thesis work, it opens new research prospects to better understand the relative importance of ecological (*e.g.* dispersal, life history diversity), environmental (*e.g.* habitat characteristics), and human-induced (*e.g.* management strategies) components in the metapopulation stability and persistence, especially with regard to recent, worldwide synchronous responses that can erode spatial portfolios (Sullaway et al., 2021).

7.2 Benefits and shortcomings of otolith chemistry

Otolith chemistry has become a robust and reliable tool to reconstruct fish life history (Wang et al., 2019), and especially for diadromous species (Walther and Limburg, 2012). In my thesis, the diversity and depth of information extracted from otolith chemistry make it a natural marker of first choice for studying the geographical origin at large- (Chapter 3) and fine-spatial scale (Chapters 5 and 6), the natal origin (Chapter 5), and age structures (Chapter 4) of Atlantic salmon. With the appropriate analytical and statistical investigations, which have both consistently improved for 25 years now, otoliths offer a very wide range of key information to better understand and manage endangered fish species, with complex life cycles such as *Salmo salar*. Nevertheless, as for any method, otolith chemistry could highly benefit from complementary approaches to counteract and reinforce its application limits.

Recently, several studies have demonstrated the robustness of joining otolith chemistry with genetics to further understand the intra-specific diversity (Willmes et al., 2024) or the patterns of population connectivity (Källo et al., 2023) in diadromous fish species. In my thesis, genetics would provide valuable insight into the proportion of effective dispersal and the role of stocking programs in metapopulation stability. Similarly, combining otolith chemistry with tagging/telemetry has proven very useful to accurately address the timing of individual movement (Bradbury et al., 2008; Crook et al., 2017; Roloson et al., 2020). Here, such knowledge would be strongly desirable, especially in Chapter 6, to strengthen our understanding of movement patterns and the key factors driving spatial autocorrelation. Thirdly, the use of otolith is not dedicated to chemistry as otolith morphometry has also been successfully used to investigate knowledge gaps in fisheries science (Mahé et al., 2016; Koeberle et al., 2020; Smoliński et al., 2020). During my thesis, the combined use of otolith chemistry and morphometry to predict the geographical origin of Atlantic salmon has been the topic of two masters' internships but with inconclusive results (*i.e.* the combination of both approaches did not outperform the use of otolith chemistry solely). Finally, I highly suggest, when possible, the implementation of habitat characteristics concurrently with the study of life histories as numerous recent researches have shown the importance of habitat mosaic in the stability and persistence of natural populations (Phillis et al., 2018; Brennan et al., 2019; Coleman et al., 2022; Cordoleani et al., 2024). In our study system, ecological continuity programs have been ongoing for several years, and improving habitat connectivity and functionality may be an essential factor in the positive dynamic of adult returns in sub-basins (potentially responding to gap 1?). Such inferences are speculative but very plausible as young-of-the-year individuals were observed on restored habitats, in the year following restoration and connectivity work (MIGRADOIR, pers. com.).

7.3 Perspectives and future needs

In our very volatile world, I truly believe that collaborative work will promote our ability to rapidly adapt, correctly inform managers and policymakers with regards to a common objective. The persistence and stability of threatened species such as Atlantic salmon is, in essence, a long-term ambition requiring diverse expertise and constant adjustments. As I like to say in light of this thesis, the conservation of Atlantic salmon is about maintaining a “shifting spatio-temporal balance”, and that for many aspects. Indeed, stakeholders may cope with local (*i.e.* population or sub-population) and large-scale (*i.e.* metapopulation) areas, deal with short-term (*i.e.* population abundance) and long-term (*i.e.* population stability) objectives, or adapt to current observations but still promote a portfolio approach. Undoubtedly, such trade-offs are highly complex to implement, especially considering the large audience that Atlantic salmon bring together (*e.g.* international, national, and regional management institutions, scientists, water agencies, commercial and recreational fisheries). For instance, solely based on my thesis and scientific research, I have sometimes found it difficult to link the (perhaps overwhelming) information available on the topic as similar questions can be investigated with distinct methodologies (*e.g.* genetics, modeling, telemetry). Yet, building a “social-ecological connectivity is particularly important in dynamic boundary systems (*e.g.*, estuaries) and for protecting species characterized by trans-boundary movements (*e.g.*, between rivers and seas, or across jurisdictional borders) if we are to maximize the benefits for nature and humans alike” (O’Gorman et al., 2024). Since this thesis has opened up new research opportunities, I strongly suggest a holistic approach, gathering diverse expertise fields, to further investigate the role of life history and habitat diversity in metapopulation stability.

7.4 References Chapter 7

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8 SUMMARY DOCUMENT OF THE THESIS DISSERTATION IN FRENCH

Cette thèse porte sur la variabilité dans la dispersion, les pratiques de repeuplement et les stratégies de vie de populations mixtes de saumon Atlantique (*Salmo salar*) à l'aide de la chimie des otolithes. Dans cette section, une traduction du contexte de l'étude, des résumés de chaque chapitre ainsi que de la discussion générale est fournie.

8.1 Contexte

Pendant des siècles, l'économie mondiale a reposé sur un système agricole traditionnel à travers le monde. Les populations humaines vivaient alors de cultures locales et d'échanges de proximité. La révolution industrielle (Ashton, 1997) que notre planète a connue pendant environ soixante-dix ans (1760-1830) a marqué un tournant incontestable pour l'économie (Xu et al., 2018), mais pas seulement. Le développement du commerce international, la multiplication des sites d'exploitation et les innovations visant à accélérer la production à grande échelle et à la rendre plus efficace ont considérablement modifié notre environnement. Alors que les méthodes traditionnelles étaient limitées par la calorie humaine, la révolution industrielle a ouvert de nouvelles perspectives pour l'expansion et l'intensification de la production, tant sur les continents que dans les océans, avec des conséquences environnementales sans précédent. Entre 1985 et 1990, Jean Jouzel et Claude Lorius ont publié une série d'articles démontrant pour la première fois la relation significative entre les émissions de dioxyde de carbone (CO₂) et le changement climatique (Lorius et al., 1985 ; Jouzel et al., 1987 ; Lorius et al., 1990). Depuis lors, les climatologues et les paléoclimatologues ont identifié des effets considérables des activités humaines sur les émissions de gaz à effet de serre et l'impact environnemental qui en découle (Annexes 1, 2). Parmi eux, on observe une élévation anormalement rapide de la température de

la surface terrestre, la fonte prématurée des plus grandes zones glaciaires, et l'intensification des événements climatiques extrêmes, prévus depuis plus de 30 ans dans le premier rapport du Groupe d'experts intergouvernemental sur l'évolution du climat (GIEC) (IPCC et WMO, 1992). Cependant, le changement global n'affecte pas uniquement le climat, mais également la grande majorité des biotopes et biocénoses connus sur Terre (IPCC, 2023a). D'après les travaux de Soulé (1991), le Conseil national de la recherche des États-Unis a proposé cinq composantes du changement global : (1) la dégradation et la fragmentation des milieux naturels ; (2) la surexploitation des espèces sauvages via la surpêche, la déforestation et le braconnage ; (3) la modification des cycles biogéochimiques et hydrologiques ainsi que la pollution de l'eau, du sol et de l'air ; (4) l'introduction d'espèces exotiques envahissantes et ; (5) le changement climatique (United States National Research Council, 2000). L'un des enjeux majeurs du changement global est sans conteste la vitesse exceptionnelle à laquelle il se déroule dans notre monde contemporain (IPCC, 2023b), et la manière dont elle contraste fortement avec les processus éco-évolutifs qui se sont déroulés au fil des millénaires. En conséquence, de nombreuses stratégies évolutives suivant les variations saisonnières sont aujourd'hui fortement perturbées ou menacées par le changement global.

Des fourmis jusqu'aux baleines, les phénomènes de migration sont largement répandus dans le règne animal (Milner-Gulland et al., 2011) et représentent l'une des stratégies de vie les plus fascinantes et complexes (Maggini et al., 2022) en réponse aux *stimuli* biotiques et abiotiques. Comme le décrit Shaw (2012), il existe trois raisons pour lesquelles un animal bénéficie de la migration : chercher un refuge, se reproduire, ou suivre les ressources environnementales. Cependant, étant donné que la migration est principalement dictée par les conditions environnementales (e.g. la température, la photopériode, la disponibilité des ressources alimentaires ou la prédation), il est crucial de comprendre dans quelle mesure le changement climatique affecte les « pressions sélectives sur le comportement de déplacement »

(Shaw, 2016). Dans les écosystèmes aquatiques, les poissons diadromes peuvent être catégorisés selon trois stratégies de vie : (i) les poissons anadromes, où les adultes migrent de l'océan, où ils ont complété leur croissance somatique, vers les eaux douces pour frayer, (ii) les poissons catadromes qui suivent le cycle inverse et (iii) les poissons amphidromes, qui exercent des migrations entre eau douce et eau de mer sans un but ultime de reproduction (Myers, 1949 ; McDowall, 1988). Bien que la diadromie soit relativement rare parmi les espèces de poissons, avec environ 250 espèces documentées (McDowall, 2008), ce qui représente seulement 0,8% des espèces de poissons à nageoires rayonnées (Corush, 2019), beaucoup de ces espèces sont bien connues en raison de leur grande valeur économique et patrimoniale à travers le monde (Lassalle et al., 2009). De plus, des études récentes ont démontré le fort potentiel des services écosystémiques (Annexe 3) que peuvent offrir les espèces diadromes (voir le projet DiadES : <https://diades.eu/>), renforçant ainsi leur importance écologique. Pourtant, au cours des cinq dernières décennies, les poissons diadromes ont subi un déclin massif (Limburg et Waldman, 2009 ; Tamario et al., 2019 ; Almeida et al., 2023) (Figure 1.1), principalement en raison des pressions anthropiques (e.g. les altérations de l'habitat telles que les barrages et les obstacles anthropiques, la surexploitation, le changement climatique, la pollution). Compte tenu de la complexité particulière des cycles de vie diadromes et des effets néfastes du changement global sur les écosystèmes naturels, il est essentiel d'améliorer notre compréhension des stratégies de vie des poissons et de mettre en œuvre des actions de gestion adaptées (McDowall, 1999) pour préserver ces espèces, bien que cela demeure extrêmement complexe (Gallagher et al., 2022).

Le saumon Atlantique (*Salmo salar*, Linnaeus 1758) est probablement le poisson diadrome le plus emblématique de l'Atlantique Nord, en raison de son importance culturelle, économique, récréative et de subsistance très élevée (Thorstad et al., 2021). Comme de nombreuses autres espèces diadromes, les populations de saumon Atlantique ont fortement diminué au cours des 50 dernières années, avec une chute d'environ 80% des captures

nominales mondiales entre 1975 et 2000 (ICES, 2021). Bien que cette importante baisse soit principalement attribuée à une réduction de la survie en milieu marin (Chaput, 2012 ; ICES, 2021), il reste encore difficile de comprendre comment les facteurs de stress environnementaux affectent les populations de saumon Atlantique. En réalité, chaque stade de vie peut être impacté de manière distincte (Figure 1.2) par des facteurs de stress interactifs, ce qui peut entraîner des altérations à la fois individuelles et au niveau des populations (Forseth et al., 2017 ; Crozier et Siegel, 2023 ; Vehanen et al., 2023). Il demeure donc très complexe de cerner les conséquences des pressions naturelles et anthropiques combinées, qui varient selon les stades de vie, tant sur le plan spatial que temporel, particulièrement dans un monde en constante mutation (Crozier et Siegel, 2023).

Chez le saumon Atlantique, la migration vers les zones de reproduction se caractérise par un fort comportement de fidélité (*homing*) au site natal, généralement compris entre 90 et 95% dans les populations sauvages (Jonsson et al., 2003 ; Keefer et Caudill, 2014 ; Lamarins et Buoro, 2023). En conséquence, ce *homing* élevé favorise l'adaptation locale des populations et justifie de préférence une gestion à l'échelle régionale ou des bassins versants (Thorstad et al., 2021), afin de maintenir les bénéfices adaptatifs pour les générations futures. Cela est particulièrement vrai pour les vastes programmes de repeuplement qui ont été adoptés dans de nombreuses rivières de l'Atlantique Nord où les saumons frayent ou frayaient autrefois (ICES, 2021), en réponse à l'effondrement des populations (Chaput, 2012 ; ICES, 2019). Parallèlement, la dispersion joue également un rôle fondamental pour *Salmo salar*, en s'adaptant aux signaux environnementaux à la fois immédiats (e.g. la qualité de l'habitat) et ultimes (e.g. évitement de la compétition) (revue dans Lamarins, 2022). Ainsi, les populations de saumon présentent souvent une structure de métapopulation, grâce aux échanges d'individus (Schtickzelle et Quinn, 2007), ce qui peut varier spatialement et/ou temporellement, tant en termes de direction que d'intensité. La durabilité de cette complexe mosaïque naturelle (i.e. la biocomplexité) dans les cycles de vie

est essentielle pour éviter la synchronisation des populations et la déstabilisation de l'effet *portfolio* (Greene et al., 2010 ; Schindler et al., 2010 ; Satterthwaite et Carlson, 2015 ; Sturrock et al., 2015), en particulier dans un contexte de changement global (Anderson et al., 2015 ; Herbold et al., 2018 ; Crozier et Siegel, 2023). Bien que de nombreux travaux aient été réalisés sur la dispersion et la connectivité des saumons du Pacifique (Candy et Beacham, 2000 ; Brenner et al., 2012 ; Willmes et al., 2021) ainsi que dans les régions nordiques de distribution du saumon Atlantique (Jonsson et al., 2003 ; Pedersen et al., 2007), nous manquons encore d'informations sur sa zone de répartition sud-ouest, en particulier concernant les variations spatiales et temporelles, ainsi que les effets potentiellement néfastes du soutien aux effectifs (Jonsson et al., 2003 ; Horreo et al., 2012 ; Ford et al., 2015 ; Jonsson et Jonsson, 2017).

Dans ce contexte, et en se basant sur la chimie des otolithes, cette thèse vise à (i) étudier et quantifier la variabilité interannuelle des comportements de dispersion des populations de saumon Atlantique dans le sud du golfe de Gascogne, (ii) examiner le rôle des programmes de repeuplement dans le retour des adultes et (iii) mieux comprendre les stratégies de vie, ainsi que potentiellement les facteurs déterminants des saumons de retour dans les populations mixtes.

8.2 Matériels et méthodes

Afin de répondre aux objectifs fixés, nous avons utilisé les multiples potentialités de la chimie des otolithes pour en extraire des informations essentielles. Dans le deuxième chapitre de ma thèse, un horizon des choix méthodologiques, analytiques et statistiques est présenté pour accéder aux informations suivantes : origine géographique à grande (régionale ou bassin-versant) et petite (rivière) échelle, origine natale (sauvage ou piscicole), estimation de l'âge pour accéder aux cohortes et enfin, estimation de la taille des tacons de l'année et à leur départ en mer (smolt).

8.3 Stabilité interannuelle de la dispersion au sein de la métapopulation de saumon Atlantique du golfe de Gascogne

La biocomplexité naturelle, caractérisée par la diversité génétique et phénotypique, renforce la résilience des métapopulations en amortissant les fluctuations environnementales et les événements stochastiques. Cette diversité agit comme une protection naturelle, où différentes populations peuvent prospérer dans des conditions variées, garantissant ainsi la stabilité et la survie globales de l'espèce. Concernant les espèces migratrices de Salmonidés, l'effet *portfolio* est particulièrement important en raison de leurs cycles de vie complexes et de leur dépendance à des habitats diversifiés et interconnectés au cours de leur migration ontogénique. À ce jour, peu d'information est disponible quant à la variabilité temporelle des mouvements de dispersion, tant en termes d'intensité que de direction. Cependant, il est attendu que le comportement de dispersion varie au cours des prochaines décennies, en réponse aux nombreux facteurs de stress (biotiques et abiotiques, d'origine naturelle et anthropique) auxquels les Salmonidés sont confrontés. Dans cette étude, nous avons étudié les schémas de dispersion du saumon Atlantique à une échelle régionale en Europe de l'Ouest, c'est-à-dire dans le golfe de Gascogne, en utilisant la chimie des otolithes. Nos résultats montrent une connectivité significative entre les sous-populations de saumons, notamment celle de l'Adour, qui semble jouer un double rôle de source et de puits pour les populations adjacentes. Bien que des changements dans la dispersion du saumon Atlantique soient attendus avec l'accélération et l'intensification des effets du changement global, notre étude révèle des taux de philopatrie et de dispersion très stables au cours de la dernière décennie. Combinées aux études génétiques, nos observations suggèrent que la structure de la métapopulation pourrait contribuer à la stabilité du système, probablement via un effet de secours démographique, voire peut-être génétique.

8.4 Estimation non supervisée de l'âge au départ en mer du saumon Atlantique à l'aide de la chimie des otolithes

L'estimation de l'âge de départ en mer des saumons Atlantique de retour est essentielle pour mieux comprendre le rôle du timing d'émigration dans la survie. Parmi les méthodes disponibles, l'utilisation de la chimie des otolithes peut être difficile chez les poissons anadromes, car les éléments souvent utilisés (*i.e.* le magnésium, le manganèse et le zinc) peuvent refléter conjointement le métabolisme individuel et les conditions environnementales. Dans ce contexte, nous présentons une nouvelle méthode non supervisée et robuste pour estimer avec succès l'âge de l'émigration des saumons atlantique dans le golfe de Gascogne, basée sur les concentrations en zinc dans les otolithes.

8.5 Gestion d'une espèce migratrice quasi menacée dans un monde volatil : étude de cas du saumon Atlantique dans le sud du golfe de Gascogne

La conservation des espèces en danger est particulièrement difficile dans un environnement en rapide mutation, car déterminer les actions appropriées et réalisables pour gérer et préserver efficacement les espèces menacées dans leurs habitats naturels est très complexe. Les espèces de poissons diadromes, y compris le saumon Atlantique (*Salmo salar*), ont connu des déclinés dramatiques, principalement en raison du réchauffement climatique et des pressions anthropiques telles que l'altération des habitats. En conséquence, des programmes de repeuplement ont été largement mis en œuvre pour contrer les effondrements de populations, mais ces efforts soulèvent des préoccupations, notamment l'augmentation des taux de dispersion chez les poissons issus de pisciculture, ce qui peut entraîner une introgression génétique et une dynamique de population altérée. Dans le golfe de Gascogne (ouest de la France et sud de l'Espagne), la gestion régionale des populations de saumon avec des stratégies de déversement

variées complique l'évaluation de leur efficacité, ce qui a incité cette étude à examiner l'impact des différentes pratiques d'élevage sur les taux de retour des saumons d'origine piscicole. Dans cette étude, nous avons démontré que (i) les poissons issus de pisciculture se dispersent davantage que leurs homologues sauvages, (ii) le déversement d'une biomasse plus importante ne conduit pas à une plus grande proportion de retours, car nous avons trouvé une relation assez stable entre la proportion de saumons sauvages et piscicole revenant en tant que reproducteurs potentiels, et (iii) le stade de déversement influence probablement la survie individuelle selon l'hypothèse « *bigger is better* ». Ensemble, nos résultats soulignent la nécessité de promouvoir la structure de métapopulation d'un point de vue gestionnaire, en particulier dans notre système d'étude qui englobe un ensemble de populations locales, souvent mixtes. Il est essentiel de considérer les caractéristiques locales telles que la fonctionnalité de l'habitat et la capacité d'accueil avec une gestion variée, visant à maintenir la biocomplexité naturelle pour aider les populations à naviguer dans des changements environnementaux de plus en plus rapides et extrêmes.

8.6 Évaluation temporelle des stratégies de vie du saumon Atlantique dans des populations mixtes

La synchronie spatiale, phénomène selon lequel les populations issues de zones géographiques distinctes fluctuent de manière coordonnée, a récemment été observée chez plusieurs espèces et dans divers écosystèmes, y compris chez les poissons diadromes tels que le saumon. Dans le contexte du changement climatique, de telles constatations sont particulièrement préoccupantes pour le saumon, car la diversité des histoires de vie intra-spécifiques est cruciale pour faire face aux nombreux stress rencontrés tout au long du continuum eau douce-estuaire-mer, permettant ainsi le maintien de populations viables. Par conséquent, une meilleure compréhension et une atténuation des facteurs de synchronie spatiale, notamment face aux changements globaux, sont

essentielles pour la conservation des espèces de saumon. Dans cette étude, nous tirons parti d'un gradient naturel de populations mixtes de saumon Atlantique (*Salmo salar*) dans le sud du golfe de Gascogne, allant de celles fortement dépendantes des programmes d'alevinage à celles complètement autonomes. Plus spécifiquement, nous examinons la variabilité temporelle des traits phénologiques chez les saumons de plusieurs hivers de mer (PHM), tels que la taille à l'émigration, l'âge en rivière et l'âge en mer, dans quatre sous-populations à l'aide de neuf cohortes successives (2007-2015). Nos résultats démontrent : (i) un goulot d'étranglement écologique dans la diversité des tailles de smolts, (ii) une légère mais générale augmentation de la taille à l'émigration pour chaque localisation, et (iii) une synchronie spatiale dans la variabilité temporelle des proportions relatives des classes d'âge de retour. En particulier, la proportion relative d'individus d'un hiver de rivière (1HR) a augmenté au fil des ans dans chaque sous-bassin, démontrant probablement une pression environnementale issue de la vie en eau douce agissant de manière synergique dans le temps et l'espace. Notre étude renforce les travaux de recherche antérieurs rapportant une synchronie spatiale à grande échelle et met en évidence une réponse écologique similaire chez les poissons piscicoles et sauvages. D'un point de vue de conservation, cela souligne la nécessité d'adapter rapidement nos stratégies de gestion afin de préserver cette espèce menacée.

8.7 Discussion générale

L'objectif principal de cette thèse était de mieux comprendre la structure présumée en métapopulation du saumon Atlantique dans le sud de la France, et de fournir des éclairages sur la variabilité, tant dans l'espace que dans le temps, de la dispersion, des effets des programmes de repeuplement et des stratégies de vie. Plus précisément, la thèse visait à (i) quantifier la variation interannuelle de la dispersion et le niveau de connectivité entre les populations du sud du golfe de Gascogne (voir Chapitre 3), (ii) étudier les effets des stratégies de repeuplement sur

la structure de la métapopulation et les taux de retour des adultes (voir Chapitre 5), et (iii) examiner le rôle de la variabilité spatio-temporelle des stratégies de vie comme potentiels facteurs clés des retours des adultes (voir Chapitre 6). Pour aborder ces objectifs, nous avons utilisé les diverses propriétés de la chimie des otolithes, ce qui implique un ensemble d'outils méthodologiques, analytiques et statistiques variés (voir Chapitres 2 et 4). Dans ce qui suit, je discuterai d'abord des principales conclusions de mes travaux de recherche et de leurs implications à la lumière des connaissances actuelles et de l'état général du saumon Atlantique. Ensuite, j'examinerai les avantages et les limites de la chimie des otolithes pour étudier les objectifs de thèse mentionnés, avant d'introduire les perspectives et les besoins de recherche futurs découlant de ce travail en conclusion.

8.7.1 Résultats de la thèse et leurs implications

Une représentation schématique des principaux résultats de ma thèse est présentée dans la Figure 7 1. Tout d'abord, dans le Chapitre 3, j'ai clairement mis en évidence une structure en métapopulation dans le sud du golfe de Gascogne, avec des schémas de dispersion stables (sur une période de 10 ans) entre des populations spatialement distinctes (répondant à la lacune de connaissance 2). Plus particulièrement, la population de l'Adour pourrait jouer un rôle déterminant dans le maintien du système dans son ensemble, car nous avons démontré une dispersion asymétrique (qui doit être considérée par rapport à la taille de la population) entre la Garonne, la Dordogne, l'Adour et la Nivelle. Cette observation est fondamentale concernant la gestion régionale qui est en cours depuis de nombreuses années (André et al., 2021). Comme expliqué dans Lamarins (2022), ignorer les mouvements des individus entre les populations interconnectées (*i.e.* la connectivité) pourrait nuire à la stabilité, à la persistance et à la réponse adaptative des populations locales de saumon Atlantique face aux perturbations et à l'exploitation. Cependant, la biocomplexité observée est rarement, voire jamais, considérée d'un

point de vue de gestion (Chapitre 5), bien que les flux migratoires pourraient amortir les événements stochastiques environnementaux, menant potentiellement à des effets de secours démographique et/ou génétique (Lamarins et Buoro, 2024). Dans notre système d'étude, le Chapitre 3 suggère un rôle clé de la population de l'Adour, agissant à la fois comme source et comme puits pour des populations proches, petites et fortement supplémentées (voir Chapitre 5). Par conséquent, toute action (telle que la pêche professionnelle de *Salmo salar* dans l'Adour) sur la population donneuse pourrait affecter indirectement et négativement les populations adjacentes.

En combinant les résultats des Chapitres 3 et 5, il apparaît que les actions de repeuplement peuvent avoir des impacts significatifs sur la structure de la métapopulation, car le taux de dispersion était sensiblement plus élevé dans les populations mixtes. Bien que les gestionnaires doivent faire face à des objectifs/impératifs à court terme (souvent accompagnés d'un nombre cible d'individus produits et déversés), les résultats du Chapitre 5 ont montré une relation asymptotique entre la biomasse de poissons de repeuplement déversés et la proportion d'adultes matures d'origine piscicole revenant (répondant à la lacune de connaissance 3). Par conséquent, et conformément à McMillan et al. (2023), je soutiens que les stratégies de gestion devraient prendre en compte (ou mettre en avant) les caractéristiques écologiques (e.g. la capacité d'accueil de la population supplémentée, la fonctionnalité de l'habitat et la productivité) et promouvoir la diversité de la population gérée d'un point de vue de conservation à long terme. Dans une telle position, l'approche *portfolio* (encourageant l'importance d'une mosaïque d'habitats et de la connectivité) devrait être privilégiée selon les résultats de cette thèse et le corpus massif de la littérature scientifique guidant dans cette direction (Greene et al., 2010 ; Anderson et al., 2015 ; Satterthwaite et Carlson, 2015 ; Schindler et al., 2015 ; Des Roches et al., 2017 ; Sturrock et al., 2019).

Dans le dernier chapitre (Chapitre 6), nous avons démontré une autocorrélation spatiale nette entre les sous-populations de la Garonne, de la Dordogne, de Pau et d'Oloron. Plus particulièrement, une synchronie spatiale claire (*i.e.* des fluctuations temporelles corrélées entre les populations (Walter et al., 2017)) s'est produite dans la proportion d'individus 1HR revenant en tant qu'adultes matures, en plus d'une synchronie spatiale apparente, mais moins évidente, dans la proportion d'adultes 2HM (répondant à la lacune de connaissance 4). La synchronie spatiale peut résulter d'un ou plusieurs facteurs pouvant agir indépendamment, successivement ou de manière synergique le long des routes migratoires, notamment (i) des fluctuations environnementales spatialement corrélées (Desharnais et al., 2018), également connues sous le nom d'effet Moran (Moran, 1953), (ii) des flux migratoires entre les sites (Desharnais et al., 2018 ; Bouchard et al., 2022), et (iii) des mécanismes de densité-dépendance synchronisés (Walter et al., 2017 ; Bouchard et al., 2022). Dans la littérature concernant les espèces de saumon, la plupart des auteurs s'accordent à dire qu'en eau douce (ou au stade juvénile), la synchronie spatiale provient probablement d'une variation environnementale partagée à travers des habitats distincts, c'est-à-dire l'effet Moran (Russell et al., 2012 ; Otero et al., 2014 ; Bouchard et al., 2022). En mer, bien que des conclusions similaires aient généralement été avancées (Bal et al., 2017 ; Olmos et al., 2019, 2020), des études récentes montrent des résultats plus contrastés (Tirronen et al., 2022 ; Imlay et al., 2024). Cependant, il convient de faire preuve de prudence lors de l'interprétation des résultats, car les études peuvent aborder des problématiques distinctes dans le même environnement, par exemple, les taux de retour, la mortalité par groupe d'âge, la condition et le timing du retour.

Les résultats combinés des Chapitres 3 à 6 soulèvent plusieurs questions, qui sont discutées ci-dessous. Tout d'abord, la stabilité spatio-temporelle observée dans les flux migratoires peut être, comme mentionné précédemment, un vecteur essentiel pour maintenir une structure de métapopulation saine (Anderson et al., 2015 ; Schindler et al., 2015). Néanmoins,

dans une métapopulation composée de populations locales homogènes (exprimant des traits phénologiques similaires), les effets de dispersion de la stabilisation locale et l'autocorrélation spatiale peuvent s'annuler mutuellement (Wang et al., 2015). Ici, nous avons décrit l'estimation globale des taux d'immigration et d'émigration (dans une certaine mesure) (Chapitre 3), sans connaître la proportion de dispersion effective. Par conséquent, démêler l'importance relative de la connectivité des populations et/ou d'un éventuel effet Moran pour expliquer la synchronie spatiale observée (Chapitre 6) est profondément complexe. Par exemple, coupler nos observations avec des données génétiques serait très précieux pour examiner dans quelle mesure les populations locales de la métapopulation bénéficient (en termes de reproduction, menant à une population autosuffisante) ou non d'échanges d'individus stables. Des approches combinant les caractéristiques démographiques et génétiques du saumon Atlantique, c'est-à-dire des modèles démo-génétiques, ont été développées pour examiner comment les stress environnementaux peuvent influencer la démographie évolutive (Piou et Prévost, 2012). De plus, des données environnementales (e.g. variations de la température et du débit de l'eau, fonctionnalité de l'habitat) seraient fortement souhaitables pour tester les effets des fluctuations environnementales synchronisées sur la dynamique de la métapopulation, comme cela a été effectué dans des études récentes (Bjerck et al., 2021 ; Bouchard et al., 2022). Quel est le rôle des programmes de repeuplement dans tout cela ? Dans ma thèse, nous avons mis en évidence que la plupart des saumons émigrant de populations mixtes était des individus d'origine piscicole. Par conséquent, les programmes de repeuplement peuvent renforcer l'effet de dispersion, qu'il soit bénéfique (*i.e.* stabilisateur) ou controversé (*i.e.* synchronisateur), bien que l'aspect bénéfique soit discutable car l'hybridation génétique entre les poissons sauvages et piscicoles induit une domestication locale et une réduction de la *fitness* pour les générations suivantes (Araki et al., 2008). L'aspect positif de la dispersion de poissons piscicoles étant principalement associé à la colonisation de nouveaux habitats ou d'habitats restaurés (Willmes et al., 2021). En tenant

compte des résultats du Chapitre 6, les programmes de repeuplement ne semblent pas affecter fortement les traits phénologiques des populations étudiées (*i.e.* l'âge et la taille au départ, l'âge mer), chaque sous-population (allant de très dépendante aux programmes de soutien aux effectifs à complètement autosuffisante) affichant des réponses synchronisées, ce qui corrobore des recherches précédentes (Teichert et al., 2020). Cependant, les mécanismes de densité-dépendance synchronisés associés à la biomasse de déversement pourraient être étudiés plus en détail comme l'un des facteurs potentiels (probablement parmi d'autres) menant à une plus grande synchronie.

Ainsi, ma thèse a fourni des informations précieuses sur la dynamique de la métapopulation de saumon Atlantique du golfe de Gascogne. Comme dans la plupart des travaux de thèse, elle ouvre de nouvelles perspectives de recherche pour mieux comprendre l'importance relative des composantes écologiques (*e.g.* la dispersion, la diversité des histoires de vie), environnementales (*e.g.* caractéristiques de l'habitat) et anthropiques (*e.g.* stratégies de gestion) dans la stabilité et la persistance de la métapopulation, notamment par rapport au constat mondial de la synchronie observée, qui peut éroder les effets *portfolios* (Sullaway et al., 2021).

8.7.1 Avantages et limites de la chimie des otolithes

La chimie des otolithes est devenue un outil robuste et fiable pour reconstruire l'histoire de vie des poissons (Wang et al., 2019), en particulier pour les espèces diadromes (Walther et Limburg, 2012). Dans ma thèse, la diversité et la profondeur des informations extraites de la chimie des otolithes en font un marqueur naturel de premier choix pour étudier l'origine géographique à grande (Chapitre 3) et à fine échelle spatiale (Chapitres 5 et 6), l'origine natale (Chapitre 5) et les structures d'âge (Chapitre 4) du saumon Atlantique. Grâce aux outils analytiques et statistiques appropriés, qui se sont constamment améliorés depuis 25 ans, les otolithes offrent une large gamme d'informations clés pour mieux comprendre et gérer les espèces de poissons menacées,

avec des cycles de vie complexes comme *Salmo salar*. Néanmoins, comme pour toute méthode, la chimie des otolithes pourrait grandement bénéficier d'approches complémentaires pour contrer et renforcer ses limites d'application.

Récemment, plusieurs études ont démontré la robustesse de l'association entre la chimie des otolithes et la génétique pour mieux comprendre la diversité intra-spécifique (Willmes et al., 2024) ou les modèles de connectivité des populations (Källo et al., 2023) chez les espèces de poissons diadromes. Dans ma thèse, la génétique fournirait des informations précieuses sur la proportion de dispersion effective et le rôle des programmes de repeuplement dans la stabilité des métapopulations. De même, la combinaison de la chimie des otolithes avec la télémétrie (ou le marquage individuel – *tag*) s'est révélée très utile pour traiter avec précision les mouvements individuels (Bradbury et al., 2008 ; Crook et al., 2017 ; Roloson et al., 2020). Ici, une telle connaissance serait fortement souhaitable, notamment dans le Chapitre 6, pour renforcer notre compréhension quant aux facteurs clés qui influencent la synchronie spatiale. Troisièmement, l'utilisation des otolithes ne se limite pas à la chimie, car la morphométrie des otolithes a également été utilisée avec succès en sciences halieutiques (Mahé et al., 2016 ; Koeberle et al., 2020 ; Smoliński et al., 2020). Au cours de ma thèse, l'utilisation combinée de la chimie des otolithes et de la morphométrie pour prédire l'origine géographique du saumon Atlantique a été l'objet de deux stages de maîtrise, mais les résultats n'ont pas été concluants (la combinaison des deux approches n'ayant pas surpassé l'utilisation exclusive de la chimie des otolithes). Enfin, je suggère vivement, lorsque cela est possible, la mise en œuvre des caractéristiques de l'habitat en parallèle avec l'étude des histoires de vie, car de nombreuses recherches récentes ont montré l'importance de la diversité des habitats dans la stabilité et la persistance des populations naturelles (Phillis et al., 2018 ; Brennan et al., 2019 ; Coleman et al., 2022 ; Cordoleani et al., 2024). Dans notre système d'étude, des programmes de continuité écologique sont en cours depuis plusieurs années, et l'amélioration de la connectivité et de la fonctionnalité de l'habitat

peut être un facteur essentiel dans la dynamique positive des retours des adultes dans les sous-bassins (répondant potentiellement à la lacune de connaissance 1 ?). De telles inférences sont spéculatives mais très plausibles, car des juvéniles de l'année ont été observés dans des habitats restaurés, l'année suivant les travaux de restauration et de connectivité (MIGRADOIR, comm. pers.).

8.7.1 Perspectives et besoins futurs

Dans notre monde extrêmement changeant, je suis convaincu que le travail collaboratif favorisera notre capacité à nous adapter rapidement et à informer correctement les gestionnaires concernant un objectif commun. La persistance des espèces menacées comme le saumon Atlantique est, par essence, une ambition à long terme nécessitant une expertise diversifiée et des ajustements constants. Comme j'aime le dire à la lumière de cette thèse, la conservation du saumon atlantique consiste à maintenir un « équilibre spatio-temporel mouvant », et cela sous de nombreux aspects. En effet, les parties prenantes doivent s'attacher à des zones à petite (populations ou sous-populations) et grande échelle (métapopulations), gérer des objectifs à court (abondance de la population) et à long terme (stabilité de la population), ou s'adapter aux observations actuelles tout en promouvant une approche de *portfolio*. Sans aucun doute, de tels compromis sont très complexes à mettre en œuvre, en particulier compte tenu du large public que le saumon Atlantique rassemble (les institutions de gestion internationales, nationales et régionales, les scientifiques, les agences de l'eau, les pêcheurs commerciaux et récréatifs). Par exemple, uniquement sur la base de ma thèse et de mes recherches scientifiques, j'ai parfois trouvé difficile de relier les informations (peut-être écrasantes) disponibles sur le sujet, car des questions similaires peuvent être abordées avec des méthodologies distinctes (e.g. la génétique, la modélisation, la télémétrie). Pourtant, établir une connectivité socio-écologique est particulièrement important dans les systèmes aux limites dynamiques (e.g. les estuaires) et pour

protéger les espèces caractérisées par des mouvements transfrontaliers (*e.g.* entre les rivières et les mers, ou à travers des frontières juridictionnelles) si nous voulons maximiser les avantages pour la nature et les humains (O’Gorman et al., 2024). Étant donné que cette thèse a ouvert de nouvelles opportunités de recherche, je recommande vivement une approche holistique, rassemblant divers domaines d'expertise, pour mieux examiner le rôle de la diversité des histoires de vie et des habitats dans la stabilité des métapopulations.

REMERCIEMENTS

Je souhaiterais en tout premier lieu remercier mon directeur de thèse, Gilles, pour m'avoir offert la chance de mener à bien ce projet de doctorat. Malgré toutes les péripéties qui ont jalonné ces 3 années, j'ai eu la chance de côtoyer quelqu'un de profondément humain, animé par une passion dévorante pour ce projet, et toujours bienveillant, quelles que soient les circonstances. Merci Gilles. Je souhaite bien évidemment aussi remercier mes deux co-encadrant(e)s, Matthias et Hélène. J'ai été très chanceux de profiter de vos expertises respectives tout au long de ma thèse, d'en apprendre toujours un peu plus, et surtout d'avoir la certitude de trouver un vrai accompagnement, qu'importe le sujet de ma question. Plus qu'un simple encadrement, grâce à vous trois j'ai vécu une aventure en équipe, où j'ai toujours trouvé du soutien et de la compréhension, je vous en remercie énormément.

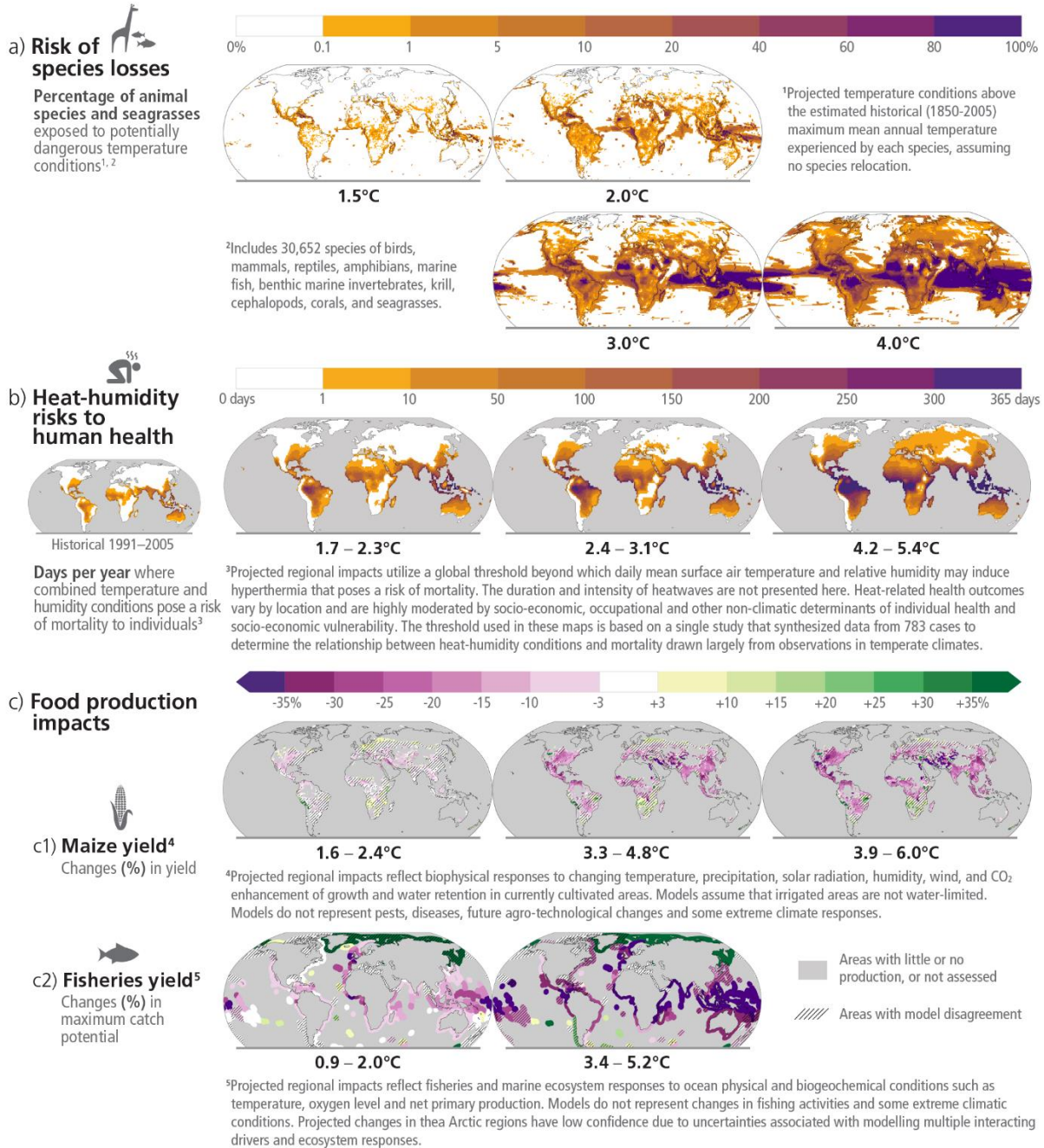
J'ai une pensée particulière pour Patrice et Mackenzie, qui ont largement participé à mes premiers pas dans le monde scientifique au Canada. Quelques années se sont écoulées depuis ces débuts et sans vous l'histoire aurait sans doute été bien différente, merci à vous.

Un projet de thèse qui se termine c'est un aboutissement professionnel mais qui, sans aucun doute, nécessite un entourage personnel sans faille. Alors merci à Quentin et Maëva, j'ai eu le bonheur de vous avoir à mes côtés tout au long de cette thèse, merci les copains ! Je remercie aussi tous les amis de l'IPREM et les copains de Pau pour tous les bons moments passés ensemble.

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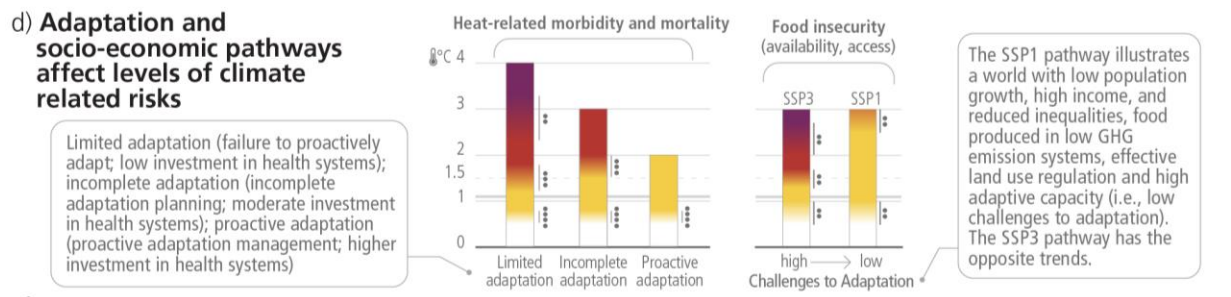
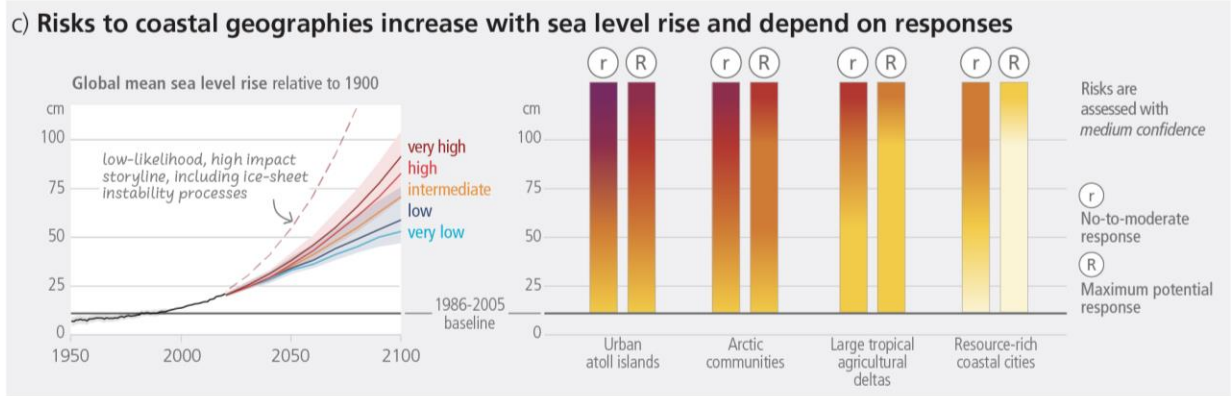
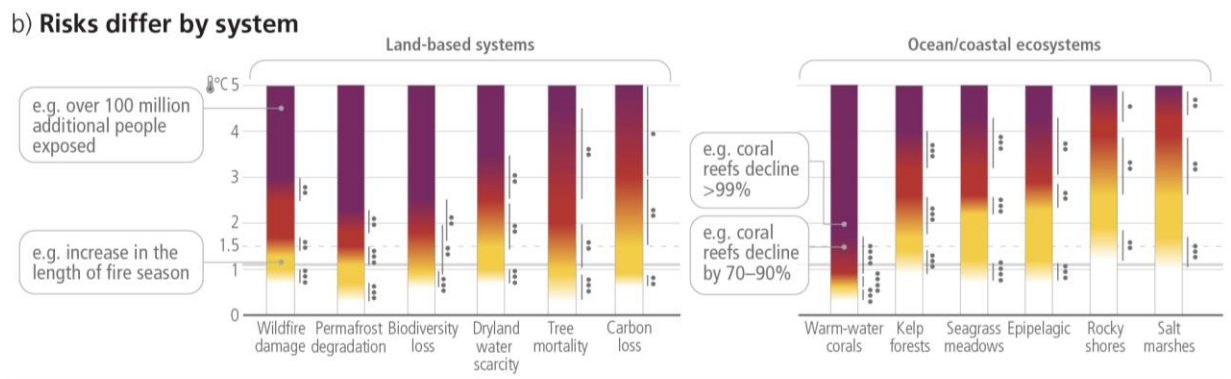
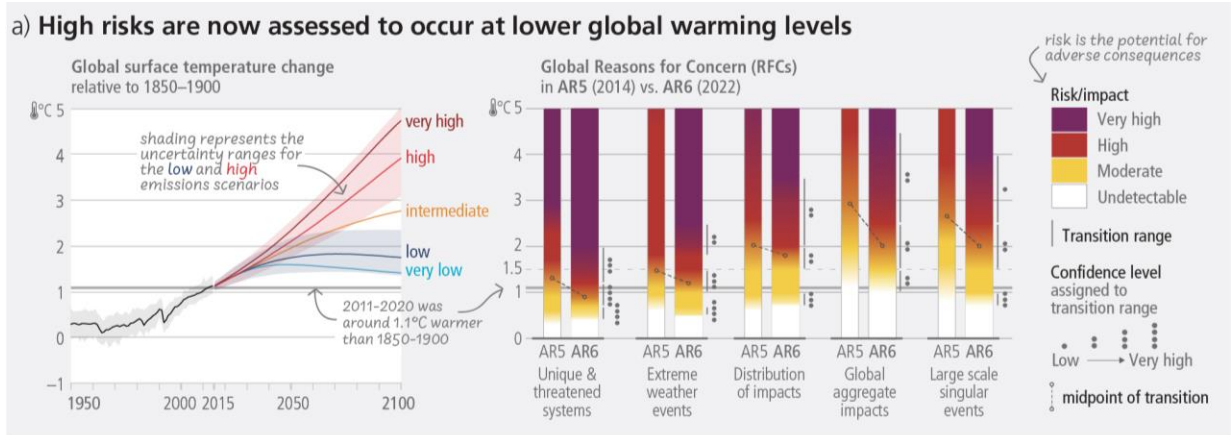
APPENDICES

Appendix 1: Projected risks and impacts of climate change on natural and human systems at different global warming levels (GWLs) relative to 1850–1900 levels, from IPCC 6th Assessment Report synthesis report (IPCC, 2023c).

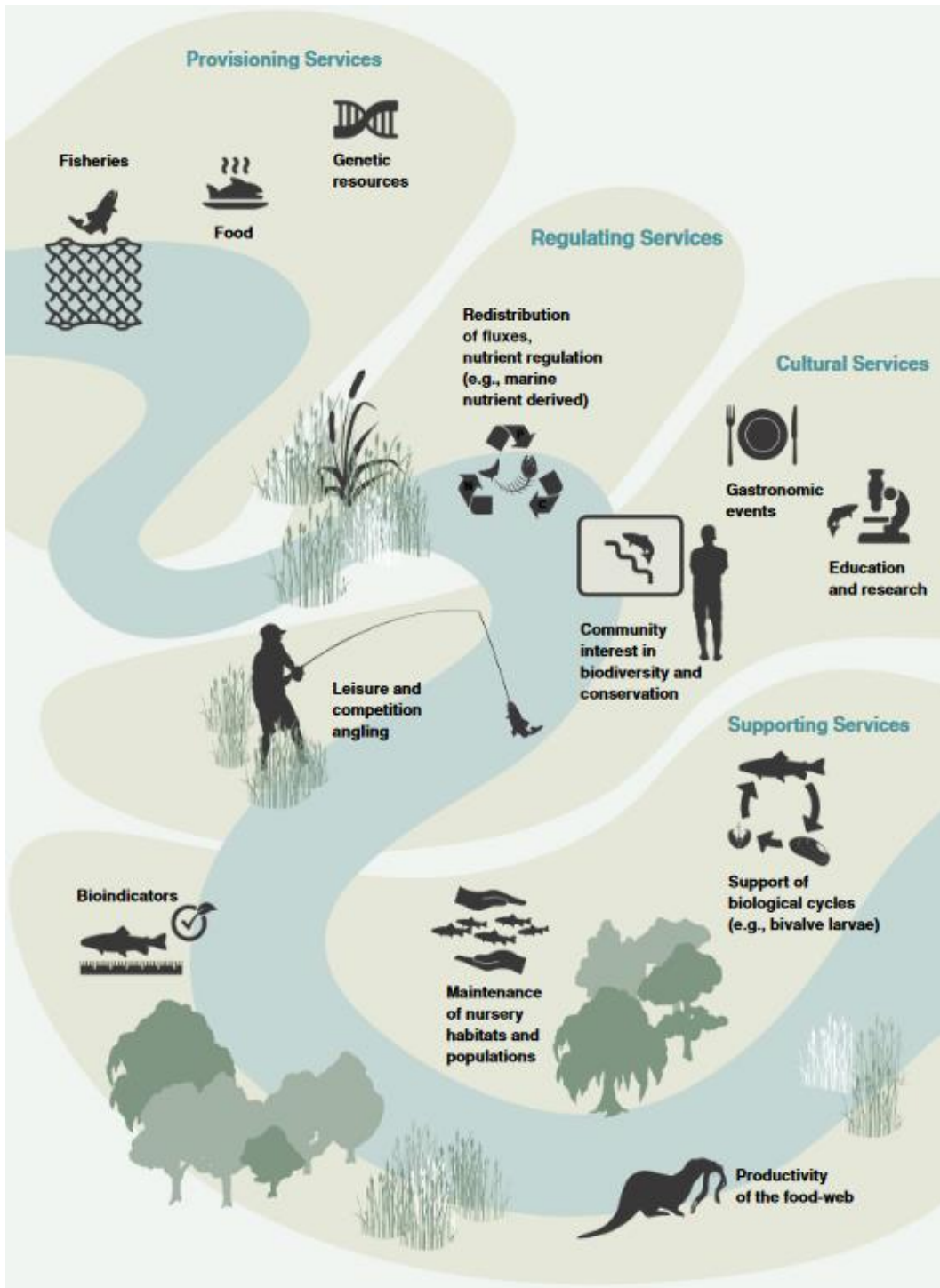


Appendix 2: Subset of assessed climate outcomes and associated global and regional climate risks, from IPCC

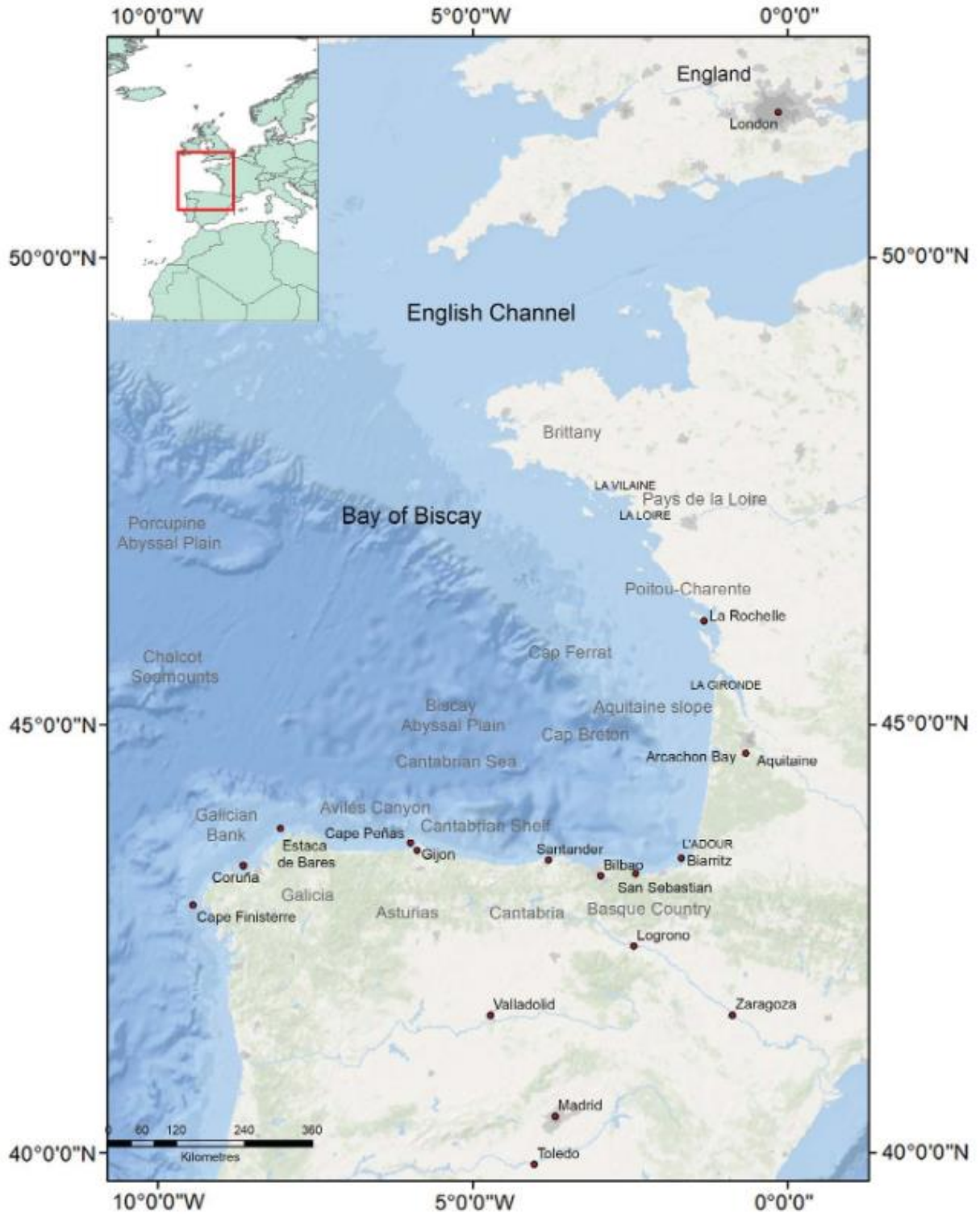
6th Assessment Report synthesis report (IPCC, 2023c).



Appendix 3: Examples of ecosystem services generated by anadromous fishes in the Iberian Peninsula, from Almeida et al. (2023).



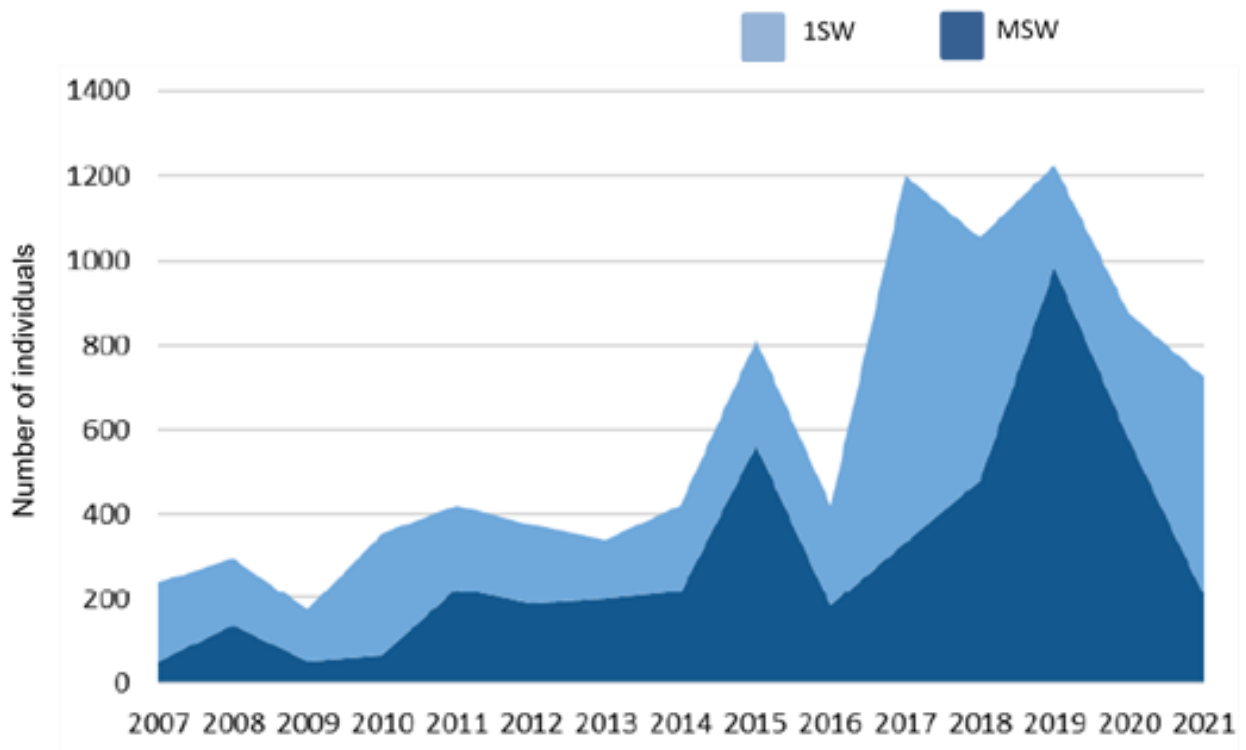
Appendix 4: Map of the Bay of Biscay, from Borja et al. (2019).



Appendix 5: Map of French management committees for migratory fish (COGEPOMIs), from the *Office Français de la Biodiversité* (OFB); <https://www.ofb.gouv.fr/en/international-year-salmon-2019>.



Appendix 6: Assessment of the proportion of one sea-winter (1SW) and multi sea-winters (MSW) individuals from 2007 to 2021 in the Gave de Pau. Source: MIGRADOUR (<https://www.migradour.com/>).



Appendix 7: (A) The position of the teleost inner ear relative to the brain. (B) Detail of inner ear components in the cichlid *Steatocranus tinanti*. Three-dimensional (3D) reconstructions based on micro-computed tomography (micro CT) imaging are shown in lateral (A) and medial (B) views illustrating the following inner ear components: (1) Semicircular canals: anterior (asc), horizontal (hsc), and posterior (psc) canals; ampulla of the anterior (aa), horizontal (ha), and posterior (pa) canals; cc, common canal (= crus commune); (2) otolith end organs: utricle, saccule, lagena; (3) sensory epithelia: cristae of the anterior (ca), horizontal (ch), posterior (cp) canals; maculae of the utricle (mu), saccule (ms), and lagena (ml); (4) otoliths: uot, utricular otolith (= lapillus), sot, saccular otolith (= sagitta), and lot, lagenar otolith (= asteriscus). a, anterior; d, dorsal. From Schulz-Mirbach et al. (2019).

